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Mental Blocks: The behavioural effects and neural encoding of obstacles when reaching and grasping

Craig S. Chapman, *University of Western Ontario*

Supervisor: Dr. Melvyn A Goodale, *The University of Western Ontario*

A thesis submitted in partial fulfillment of the requirements for the Doctor of Philosophy degree in Psychology

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MENTAL BLOCKS: THE BEHAVIOURAL EFFECTS AND NEURAL ENCODING OF OBSTACLES WHEN REACHING AND GRASPING

(Spine title: Behavioural Effects and Neural Encoding of Obstacles)

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by

Craig S. Chapman

Graduate Program in Psychology

A thesis submitted in partial fulfilment
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The University of Western Ontario
London, Ontario, Canada

THE UNIVERSITY OF WESTERN ONTARIO
School of Graduate and Postdoctoral Studies

CERTIFICATE OF EXAMINATION

Supervisor	Examiners
Dr. Melvyn Goodale	Dr. Daniel Ansari
Supervisory Committee	Dr. Paul Gribble
Dr. Jody Culham	Dr. Chris Viger
	Dr. Paul Cisek

The thesis by

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Abstract

The ability to adeptly interact with a cluttered and dynamic world requires that the brain simultaneously encode multiple objects. Theoretical frameworks of selective visuomotor attention provide evidence for parallel encoding (Baldauf & Deubel, 2010; Cisek & Kalaska, 2010; Duncan, 2006) where concurrent object processing results in neural competition. Since the end goal of object representation is usually action, these frameworks argue that the competitive activity is best characterized as the development of visuomotor biases. While some behavioural and neural evidence has been accumulated in favour of this explanation, one of the most striking, yet deceptively common, demonstrations of this capacity is often overlooked; the movement of the arm away from an obstacle while reaching for a target object is definitive proof that both objects are encoded and affect behaviour. In the current thesis, I discuss three experiments exploring obstacle avoidance.

While some previous studies have shown how visuomotor biases develop prior to movement onset, the dynamics of the bias during movement remains largely unexplored. In the first experiment I use the availability and predictability of vision during movement as a means of exploring whether obstacle representations might change during a reach (Chapter 2, Chapman & Goodale, 2010b). While the visuomotor system seems optimized to use vision, I found no difference between reaching with and without vision, providing no evidence that obstacle representations were altered. To more directly test this question, in the second experiment participants made reaches to a target that sometimes changed position during the reach (Chapter 3, Chapman & Goodale, 2010a). The automatic online corrections to the new target location were sometimes interfered with by an obstacle. Using this more direct approach we found definitive evidence that obstacle representations were accessed or updated during movement.

In the third experiment, I directly tested the neural encoding of obstacles using functional magnetic resonance imaging (Chapter 4, Chapman, Gallivan, Culham, & Goodale, 2010). When participants planned a grasp movement that was interfered with by an obstacle versus when the grasp was not interfered with, one area in the left posterior intraparietal sulcus was activated. This activity was concurrent with a suppression of early visual areas that were responsive to the position of the obstacle. This study confirmed that the PPC was involved with the encoding of obstacles, and demonstrated that one effect of interference was the suppression of the visual cortical signal associated with the obstacle.

These findings extend our understanding of competitive visuomotor biases. Critically, in a world filled with potential action targets, the selection of one target necessarily means all other objects in the workspace are potential obstacles. My results indicate that the visuomotor biasing signal to inhibit obstacle activity is putatively provided by the PPC, which in turn causes the visual cortical representation of the obstacle to be suppressed. The behavioural result of biasing the visual input is the propogation of this suppression to the motor output - ultimately resulting in a reach which intelligently deviates away from potential obstacles.

Keywords: obstacle avoidance, reaching, grasping, selective visuomotor attention, inhibition, competitive bias, visual feedback, online correction, fMRI, posterior parietal cortex

Co-Authorship

All of the research contained within this doctoral thesis dissertation was conducted in collaboration with my advisor, Dr. Melvyn A. Goodale. Dr. Goodale supervised and contributed to all aspects of the projects contained within this thesis dissertation (e.g. experimental design, data analysis, interpretation, writing of manuscripts). I also collaborated with Dr. Jody Culham and Jason Gallivan on the project described in Chapter 4. Both assisted with experimental design, data collection, data analysis, interpretation, and gave useful feedback on all drafts of the project. Dustin Kishen assisted with data collection for the experiment described in Chapter 2 and Ravi Doobay assisted with data collection for the experiment described in Chapter 3. At the time of examination, Chapter 2 and Chapter 3 are published with Chapter 4 submitted. The written material in this thesis is my own work, but, as my advisor, Dr. Goodale provided assistance in editing and revising all of the material contained within this thesis.

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I would like to thank all the members of the GAP / CAPnet labs – the undergraduate students, the RAs and support staff, the grad students, the post-docs, and the PIs. Being surrounded by intelligent and friendly people is what makes doing grad school such a great experience.

I would like to extend a particular thanks to Dr. Haitao Yang, Adam McLean, Lynne Mitchell, Paula Perdue and Lucy van Eimeren the technical and administrative wizards in our group. Without them, our science, and this thesis would not be possible.

There are a few specific colleagues I’d like to single out as being critical to my success. First to Dr. Jon Cant and Ken Valyear – thanks for the stimulating discussions and collaborations. Second to my Full Scale team members (and office mates), Daniel Wood and Jen Milne – our work together has been the most exciting of my career and I look forward to future projects. Finally, to the other half of the Chapmallivan empire, and the other founding father of team Full Scale, Jason Gallivan – working with you has been an absolute pleasure. Every meeting, project and manuscript is exctiting and rewarding and I know our work together is just beginning.

Of course, I would like to acknowledge and thank my advisor, Dr. Melvyn Goodale. Mel’s skills as a scientist are matched as a mentor. He has taught me to be a critical and creative researcher and under his tutelage I have flourished.

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Oh yes – and to my dog Hugo for making me leave my desk at least once a day during the long days of thesis writing.

Finally, I end with a quote of personal inspiration, from John F. Kennedy's speech made on September 12, 1962 at Rice University. He speaks of why we pursue lofty scientific goals, in this case the exploration of space, and taking man to the moon. I believe the sentiments extend to all of our scientific endevours:

> "There is no strife, no prejudice, no national conflict in outer space as yet. Its hazards are hostile to us all. Its conquest deserves the best of all mankind, and its opportunity for peaceful cooperation many never come again. But why, some say, the moon? Why choose this as our goal? And they may well ask why climb the highest mountain? Why, 35 years ago, fly the Atlantic? Why does Rice play Texas?
>
> We choose to go to the moon. We choose to go to the moon in this decade and do the other things, not because they are easy, but because they are hard, because that goal will serve to organize and measure the best of our energies and skills, because that challenge is one that we are willing to accept, one we are unwilling to postpone, and one which we intend to win, and the others, too."

Table of Contents

List of Tables

List of Figures

List of Appendices

List of Abbreviations

1-L-In: one object in the left-in position

1-L-Out: one object in the left-out position

1-R-In: one object in the right-in position

1-R-Out: one object in the right-out position

2-B-In: two objects, both left and right objects in the in position

2D: two dimensional

2-L-In: two objects, one in the left-in position, one in the right-out position

2-R-In: two objects, one in the right-in position, one in the left-out position

3D: three dimensional

ANOVA: Analysis of variance

BOLD: blood oxygenation level dependent

cm: centimeters

EPI: echo planar imaging

ERP: event related potential

FEF: frontal eye fields

fMRI: functional magnetic resonance imaging

H&T: Houghton & Tipper model of inhibition

H&T-Reach: Houghton & Tipper model of inhibition for reaching

Hz: hertz

IPS: intraparietal sulcus

IRED: infrared marker

IT: inferior temporal cortex

LCD: liquid crystal display

LED: light emitting diode

LGN: lateral geniculate nucleus

LIP: lateral intraparietal area

m: meter

MANOVA: multivariate analysis of variance

MFG: medial frontal gyrus

mm: millimeters

ms: milliseconds

NV: no vision, or reaches where vision was not available during the reach

OA: optic ataxia

pIPS: posterior intraparietal sulcus

PPC: posterior parietal cortex

RAM: response activation model

RFX: random effects

RM: repeated measures

s: seconds

SOA: stimulus onset ansynchrony

TE: echo time

TMS: transcranial magnetic stimulation

TR: repetition time

V: vision, or reaches where vision is available during the reach

V1: primary visual cortex or striate cortex

V4: 4th area of visual cortex

VFA: visual form agnosia

Chapter 1

1. General Introduction

1.1. Preamble

1.1.1. Why Study Action?

In order to gain experimental traction, the careful scientist asks very specific questions. Specific questions can be the most meaningful precisely because they are the most answerable. But, by necessarily asking specific questions, we sometimes lose sight of the big picture – the overarching principles that simply must be true. If our very specific answers are to questions that have become too far removed from the real world, then we may have gained traction, but it is on a road that goes nowhere. Two general truths that mainstream psychology sometimes strays from are revealed in the two following quotes, each by authors whose thinking has shaped my own. The first, in a recent review by Dr. Paul Cisek and his collaborator Dr. John Kalaska reads, "One of the most important facts we know about the brain is that it evolved" (2010, p. 275). The second by Dr. Alan Allport states, "Indeed, I find it difficult to get any clear conception of what 'perception' might be, as a subject of scientific study, isolated from its role in the control of action" (1987, p. 395). Taken together, these quotes remind us that the human brain didn't evolve to solve math problems, write novels, ruminate on the beauty of the world or conduct science, but rather it evolved to control our actions. The first simple organism that could not just sense where there was a higher concentration of a nutrient, but could propel itself toward it had a huge evolutionary advantage. Scaling the analogy up several orders of magnitude, complex animals that make economical action choices expend less energy accomplishing more rewarding goals. This filter of efficient action choices must necessarily, I believe, inform how we think about people's performance in almost every experimental psychology task. Certainly, as Dr. Allport argued, the idea of action choices must be applied when studying how we visually perceive the world. Visual perception is, after all, merely a part of the processing that necessarily concludes with (at least) the intention to act. Our conscious experience of the world may be breathtaking, but it is also almost entirely without meaning if it does not result in action. Given the complexity of the human brain, these actions can, of course, be abstract and complicated, but a percept without an action is like that organism that senses the nutrient but cannot move.

Studying action, therefore, is a window into one of the most primitive, and by extension most important, aspects of the human condition – the ‘Why we are here?’ (to shape our environments to our greatest benefit) and ‘How do we do it?’ (by performing maximally efficient actions) questions. Of course these are big questions, and by virtue of what I said earlier, not suitable for good science. An intelligent scientist, however, will remain cognizant of these fundamental principles as he or she approaches the more narrowly defined questions that are the tools of the trade.

1.1.2. Why Study Obstacles?

The current thesis explores the more specific questions of how obstacles to action affect our behaviour and where obstacles are coded in the brain. I say more specific, because even these questions are not completely amenable to careful scientific inquiry. Consider even the notion of what an obstacle to an action is (even restricting the definition of action to reaching movements, which is the topic of the current thesis). It is one of those deceptively simple yet complicated concepts. Is an object an obstacle to a reach only if the intended movement would result in a collision with the obstacle? This seems unlikely, given that motor variability demands a margin of error be incorporated into almost every movement. The regress of questions from this simple answer is obvious: how much of a margin is necessary, does this margin change with context, and a myriad of other questions. Given these problems, I provide a tentative answer to the question of what an obstacle is that avoids some of the problems of definition, but inevitably creates many more problems that must be solved. For the purposes of this thesis, an obstacle is *any* object in our immediate environment that is not the current target of action. That means that we encounter obstacles everywhere, all the time. It suggests that, given that most of our actions will have only a single target among many other objects, objects that are obstacles are more ubiquitous than objects that are targets. It also suggests that studying actions performed toward single objects presented in isolation does not provide an accurate depiction of the demands that shaped the evolution of our visuomotor system.

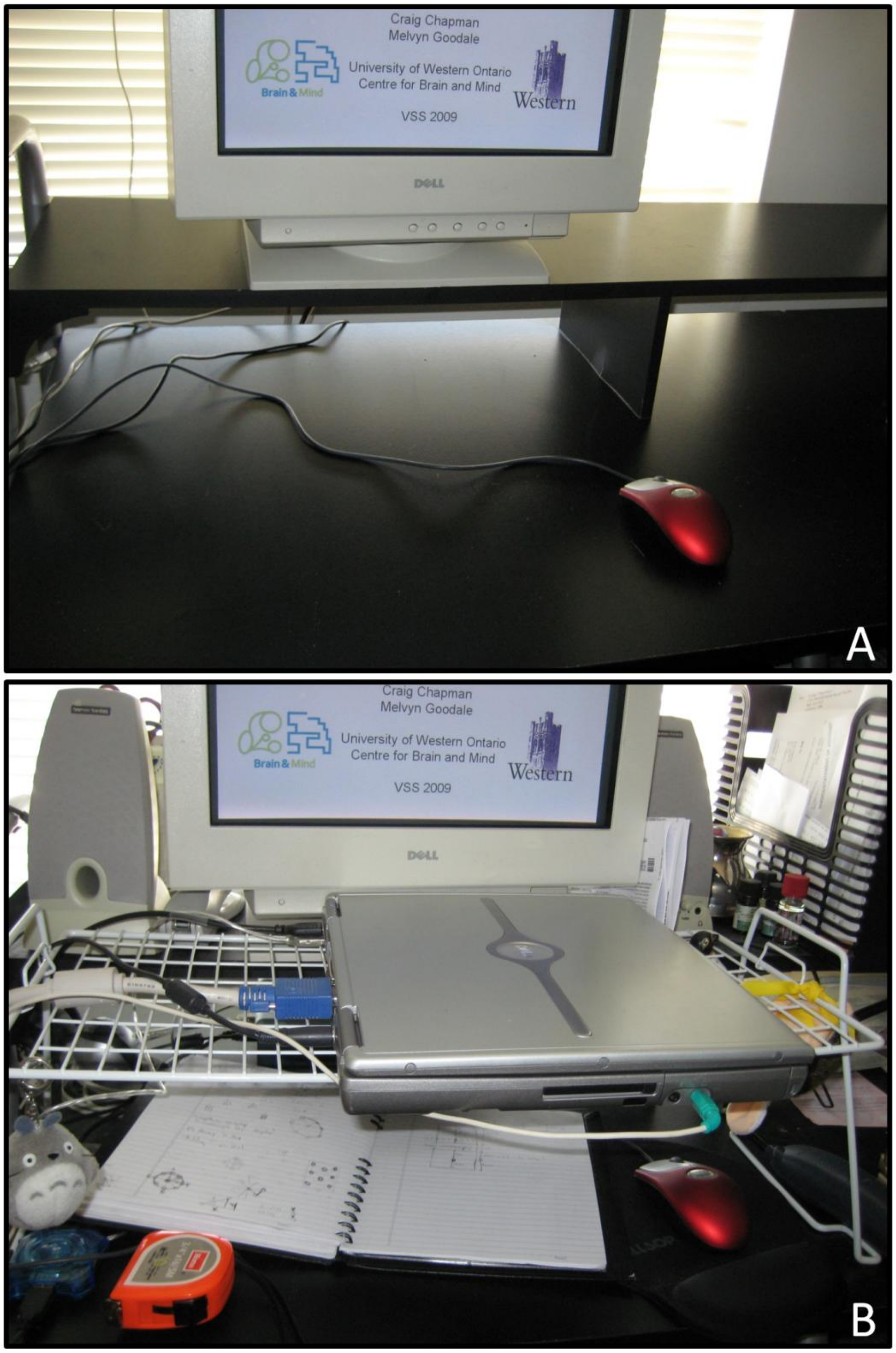

Figure 1.1. Comparative photographs of my desk. (A) An environment where the target object (red computer mouse) is presented in isolation, representative of how visuomotor experiments are usually conducted. (B) A more realistic cluttered environment, where objects other than the target compete for selection and can function as obstacles.

Consider the photograph of my desk shown in Figure 1.1a. Imagine that I want to reach out and grab the red computer mouse. It is presented in relative isolation (though the edge of the desk and the computer monitor are obviously other objects in the environment that could shape my behaviour). But my desk is never that clean (unless I clear it to take a photograph). Instead, my desk usually appears as it does in Figure 1.1b. Admittedly, my desk is messy, but the introduction of even the mouse pad, or just the lab book, completely changes the type of reaching movement I can make toward the red mouse. But when moving in our environments, we rarely consider the targets of our action (the red mouse) let alone all the other objects that surround them and affect our movements. This suggests two critical and related features of the visuomotor system. First, it demands that multiple objects be processed automatically and in parallel. The simple fact that a reach toward a target object is different than a reach toward a target object *when a second object is present* is strong evidence of parallel processing. Second, by extension, the fact that there is simultaneous encoding of multiple objects requires that the visuomotor system select and specify targets from non-targets. Consider again my cluttered desk in Figure 1.1b. The target red computer mouse actually shares many features (similar size and shape, and similar colour) with the orange tape measure to the left. Given that both objects obviously give rise to a visual response, but only the mouse is the target of my action, the visuomotor system must selectively process the mouse rather than the tape measure. Visuomotor selection, then, lies at the heart of target-directed reaching, and by extension, determines the role and influence of non-selected objects in the workspace (for which one label is obstacles). Therefore, I start my Introduction with a review of three theoretical frameworks that speculate on how visuomotor selection might be implemented and provide evidence for some of their most important claims. That section ends with a summary of how the critical points from these frameworks directly pertain to obstacles, and how this shaped the current thesis, including the remainder of the Introduction.

1.2. Theoretical frameworks of visuomotor selection

Obstacles are an interesting category of objects in our environment. They must certainly demand attention (the repercussions of colliding with a dangerous object could be dire) yet, unlike other objects in our environment which automatically capture attention and compete for selection, they cannot act as attractors to movement. Moreover, it may not be enough to simply ignore an obstacle, or treat it as if it were not there, since it must be avoided. This implies some sort of active inhibition of obstacles. Active inhibition, however, may not be as complicated as it sounds. If one imagines that all objects – and potential motor plans for that matter – compete for selection (or execution in the case of motor plans), then for one object to be actively inhibited it means only that the ‘strength’ of its representation needs to be less than all other objects currently represented. That is, selection and inhibition are relative. Consider the simple case of reaching toward one object in the presence of a second non-target object. Both objects will initially be coded with some positive activation (a virtue of being an identifiable visual object). Should both objects act as potential targets even until movement execution, then this would result in a reach trajectory at the midpoint between the two objects (as we have recently shown, C. S. Chapman, Gallivan et al., 2010a). If prior to movement onset, however, one of the targets is clearly selected as the target for action, then the neural activity associated with its representation will be increased, leading to a hand path that is attracted (or moves straight toward) the position of that object. Importantly, if one of the objects is identified as a potential obstacle prior to movement onset, then the neural activity associated with its representation will be suppressed, leading to the avoidance of its position. Notice that the coding of the obstacle location could still be above baseline; i.e., its representation need be reduced only relative to that of the other in order for that object to be avoided.

Underlying this explanation of avoidance is the premise that the representation of objects (and motor plans) compete for selection (and specification). Here I outline three theoretical frameworks which have recently been advanced that describe how and where competitive representations might be implemented in the brain, and describe evidence for this competition in a variety of domains. While only the last framework (attentional landscapes hypothesis, section 1.2.3) specifically describes evidence from tasks involving obstacles, all three raise issues important to understanding how obstacles and other objects in our cluttered environments compete for neural resources and ultimately affect behaviour.

1.2.1. Biased competition hypothesis

One of the most formal descriptions of competitive interactions in the brain comes from John Duncan and Robert Desimone's account of selective attention as the result of 'biased competition' (also referred to as integrated competition) between sensory information (for reviews, see Desimone, 1998; Desimone & Duncan, 1995; Duncan, 1996, 1998, 2006). The majority of the examples they discuss come from the domain of selective *visual* attention, which will also be the focus here. A recent review of the theory integrating new neural evidence has also been written (Beck & Kastner, 2009). The problem which motivated the development of this framework is best summarized by Duncan:

> "Vision is selective: at any given moment, only a small fraction of the total available visual input can be consciously identified or used in the control of behaviour. Subjectively, attention is paid to some things but withheld from others. How is selectivity implemented in the multiple brain systems activated by visual input?" (1996, p. 551)

This led Duncan to propose three tenets (which I have reordered to improve the coherence of my argument) at the core of the biased competition hypothesis:

> "1. Of the many brain systems responding to visual input, perceptual and motor, cortical and subcortical, many and perhaps most are *competitive* (Rizzolatti and Camarda 1987). Within each system, a gain in activation or representation for one object is bought at a loss to others; for example, representations of different objects may be mutually inhibitory.
>
> 3. Competition is *controlled*…by advance priming of units responding to one kind of object rather than another (see Harter and Aine 1984; Walley and Weiden 1973). Suppose, for example, that the animal searches for fruit of a particular colour. Units selectively responsive to that colour are preactivated in one or more brain systems in which colour is coded. Inputs with the desired colour gain a competitive advantage in the primed system; as such an input gains ascendancy in that system, it tends also to take control of others.
>
> 2. Between systems…competition is *integrated*. As an object gains ascendancy in one system, this ascendancy tends also to be transmitted to others. "Attention" is the state that emerges as different brain systems converge to work on the same dominant object (e.g., Duncan 1993; Farah 1990; Kinsbourne 1987)…" (Duncan, 1996, pp. 551-552).

It is important to note that each of these three components is crucial to understanding how obstacles are encoded in the brain: first, that the neural coding of obstacles competes with the neural coding of other objects in the environment, and the inhibition of obstacle-related activity could facilitate the selection of other objects or targets; second, that the inhibition of obstacle codes could be generated from other (top-down) signals in the brain and that this inhibition would be contingent on the obstacle's task relevance (in this case, task relevance could directly correspond to the amount an obstacle interfered with a desired movement); and third, that the inhibition of obstacle codes could propagate throughout brain networks resulting in avoidance during motor execution.

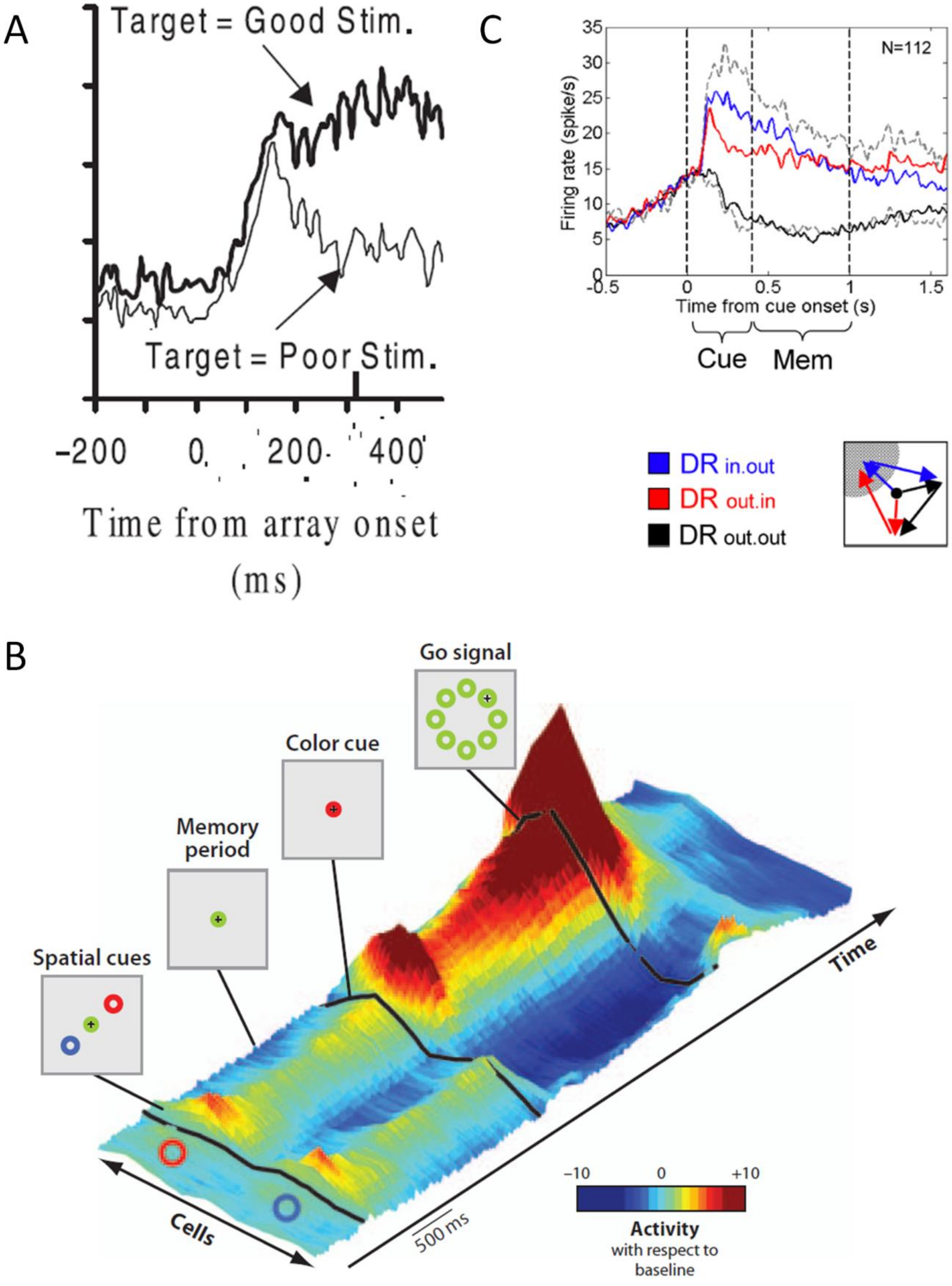
A
Target = Good Stim.
Target = Poor Stim.
-200
0
200
400
Time from array onset (ms)
C
35
30
25
20
15
10
5
0
Firing rate (spike/s)
N=112
-0.5
0
0.5
1
1.5
Time from cue onset (s)
Cue
Mem
DR in.out
DR out.in
DR out.out
B
Go signal
Color cue
Memory period
Spatial cues
Time
Cells
500 ms
−10
0
+10
Activity
with respect to baseline

Figure 1.2. Examples of competitive parallel encoding of objects from the three attentional frameworks discussed in section 1.2. (A) Biased competition hypothesis (from Desimone, 1998): Recordings from 88 cells in macaque IT cortex initially respond equally to two complex objects (e.g. a flower). After 170 ms the ‘Good’ stimuli response is enhanced and the ‘Poor’ stimuli response is reduced. This selection occurs prior to the eye-movement response (short vertical bar on x-axis). (B) Affordance competition hypothesis (from Cisek & Kalaska, 2010): Population encoding across 100 dorsal premotor cells in macaque monkeys. Two possible reach targets (Spatial cues) are encoded across a delay (Memory period) even in the absence of a visual target. When one is selected (Colour cue) its corresponding activity is enhanced while the activity for the non-selected target is reduced. Premotor cells are also heavily recruited during the movement (after the Go cue). (C) Attentional landscape hypothesis (from Baldauf, Cui, & Andersen, 2008): Recordings from 112 PPC cells in macaque monkeys. Targets within the receptive field of the cell gave rise to a significant increase in activity (maintained across a memory delay) whether they were the first (blue trace) or second (red line) target in a rapid reach to two consecutive locations. Targets outside the receptive field (black line) showed no enhancement (dashed grey lines show activity on single target trials where the target is inside or outside the receptive field of the cell).

While a discussion of all of the evidence supporting the three major tenets is beyond the scope of this thesis, a summary of some of the key findings and their implications to obstacle representations is useful. First, in support of the notion of *competition* between visual objects both neurophysiological recordings in monkeys (e.g. Chelazzi, Duncan, Miller, & Desimone, 1998; Chelazzi, Miller, Duncan, & Desimone, 1993) and neuroimaging in humans (e.g. Kastner, De Weerd, Desimone, & Ungerleider, 1998) demonstrates that presenting two or more objects simultaneously (especially within the receptive field of a cell) reduces the visual response (from primary visual cortex (V1) through to inferior temporal (IT) cortex) when compared to activity generated by a single object (though the response to multiple objects is still positive). This is taken as evidence of the suppressive effects of competition. Moreover, after an initial rise to this level of competitive activation (objects are mutually suppressed and equally weighted), when one of the objects is selected, its neural activity continues to rise to a level comparable to the response generated when it is presented in isolation. Importantly for this thesis, the activity of the non-selected target is now significantly suppressed, evidence that the selection of one target is accompanied by the inhibition of another (see Figure 1.2a). Desimone summarizes this process as "…an initial parallel activation of cortical representations by several stimuli in the visual field, and the ultimate suppression of response to the behaviourally irrelevant distractor" (1998, p. 1248).

Evidence for the *control* of competitive bias (i.e. top-down selection of some task-relevant object features over others) is an expansive topic in and of itself (e.g. Corbetta, Patel, & Shulman, 2008; Corbetta & Shulman, 2002). For the purposes of the current thesis, it is enough to say that studies have demonstrated that a cue which precedes the onset of a stimulus activates visual areas in the brain which are sensitive to that cue (e.g. complex shape in monkey V4/IT neurophysiology (Chelazzi et al., 1998) or spatial location in human neuroimaging of V1-V4 (Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999)), and that this activity persists even after the cue is gone – anticipating the upcoming stimulus and biasing future neural events. Duncan makes one remark regarding the control of bias that is particularly relevant to the current thesis, "Perhaps the most important point is its flexibility – potentially, any type of object can be relevant to behaviour, and, correspondingly, there are many ways to direct attention to targets"

(2006, p. 5). One could imagine that, in one task, tall grey objects are the targets of action, and thus areas in the brain selecting for colour and shape would show a bias for those features. However, in a different task (like those described in this thesis) tall grey objects could act as obstacles, and never be selected as targets. In these cases, the relevance of the tall grey object might be determined by its position with respect to the current movement goal, and the attention it receives may be generated from areas in the brain that are specifically involved with generating and maintaining movement plans.

One final issue regarding the control of competitive bias is the 'source' of the biasing signals. I use the word source tentatively since Duncan argues that, "integrated competition does not sit well with a firm site-source distinction…bias can begin at any part of the system, spreading both to "higher" and "lower" levels" (2006, p. 21). He does suggest, however, that "flexibility and selectivity…may reach their peak in regions of frontal and parietal cortex" (2006, p. 14). This identification of a frontoparietal network implicated in the control of attention (or selective bias) fits well with a substantive literature providing evidence for that claim (Beck & Kastner, 2009; Corbetta et al., 2008; Corbetta & Shulman, 2002; Kastner & Ungerleider, 2000; Pessoa, Kastner, & Ungerleider, 2003; Riddoch et al., 2010; Serences & Yantis, 2007). Moreover, many of these studies demonstrate that this frontoparietal network can modulate the visual cortical representation of objects – enhancing activity at attended locations and suppressing activity at unattended locations in retinotopic cortex. The most relevant of these studies, those specifically dealing with the suppression of a signal at a location corresponding to a distracting stimulus are discussed in section 1.3.

Finally, the tenet of the biased competition hypothesis that has received the least experimental evidence is for the *integration* of representations across systems. That is, as Duncan puts it, "…effective behaviour will require selective focus on particular sensory inputs, on particular action goals, on particular information from semantic memory and so on; usually, we "attend" to all these things as a coherent whole" (2006, p. 21). Two lines of evidence do suggest that integration does occur. First, with improved detection of retinotopic maps extending into frontal and parietal cortex (e.g. the frontal eye fields (FEF) and intraparietal sulcus (IPS)), it has been shown that attention to a specific quadrant of the visual field led to an enhanced signal in that field across the nearly 20 maps identified throughout the frontoparietal network (Beck & Kastner, 2009). Second, when participants were asked to attend to only one feature of an object (say the colour of a patch of moving dots), selective biases also developed in regions responding to an orthogonal dimension (e.g. motion areas were also selectively biased, McMains, Fehd, Emmanouil, & Kastner, 2007); this speaks to the integration of object encoding across several areas of cortex (O'Craven, Downing, & Kanwisher, 1999). In the current thesis, we are specifically interested in the integration of object encoding that is relevant because of its implications to an upcoming action. That is, if an object obstructs a ‘particular action goal’ (as Duncan remarked) would its neural representation be selectively biased at other points in the brain? The two additional theoretical frameworks discussed next address this point in more detail.

1.2.2. Affordance competition hypothesis

First outlined by Paul Cisek in 2007 and recently presented more broadly with additional accompanying evidence (Cisek & Kalaska, 2010) the affordance competition hypothesis argues that the competing representations in the brain occur between the potential actions afforded by the environment. In many ways, the affordance competition hypothesis operates on the same principles as the biased competition hypothesis, a point Cisek and Kalaska acknowledge, “…models of action selection…are functionally equivalent to the biased competition model used to explain data on visual attention” (2010, p. 283). The critical difference emerges in that the affordance competition hypothesis is completely grounded in an ethological and evolutionary explanation. As I have already quoted, but will repeat since I firmly believe it is a point worth repeating, Cisek and Kalaska state, “One of the most important facts we know about the brain is that it evolved” (2010, p. 275). Moreover:

> “Continuous interaction with the world often does not allow one to stop and think or to collect information and build complete knowledge of one’s surroundings. To survive in a hostile environment, one must be ready to act at short notice, releasing into execution actions that are at least partially prepared. These are the fundamental demands which shaped brain evolution. They motivate animals to process sensory information in an action-dependant manner to build

> representations of the potential actions which the environment currently affords" (Cisek, 2007, p. 1586).

Thus, the selective biases that develop in the brain are selective of and biased toward actions. Ultimately, task relevance must be dictated by actions, since the task (from an evolutionary perspective) is always to perform the most beneficial action and thus the relevance of any object is intrinsically tied to how it shapes movements. From this perspective, it is clear that obstacle objects (which clearly impact actions) are an important component of the competitive framework.

Since the key difference between the biased competition and affordance competition hypotheses is the nature of *what* is being represented in the brain (which is difficult to test experimentally), not *where* and *how*, the evidence for both hypotheses is similar. That is, like Duncan, Cisek argues that, "the competition between potential actions plays out in large part within the reciprocally interconnected fronto-parietal system" (Cisek, 2007, p. 1588). One study by Cisek and Kalaska, which therefore could support both frameworks of competition, involved recording activity from the premotor cortex of a monkey performing a delayed reach task (Cisek & Kalaska, 2002, 2005). Here, the monkey was shown a simple display with two differently coloured targets (a red and blue circle equally eccentric from a central fixation) either of which could be the target of a reach action on a given trial. After a delay, a colour cue presented at fixation indicated to the monkey which target to reach for. The critical finding was that, during the delay, across a population of neurons in the premotor cortex, two discrete peaks of activity were recorded – one for each of the two potential target locations (see Figure 1.2b). Importantly, once the colour cue indicated which target was to be acted on, the activity corresponding to that target location increased dramatically, while activity corresponding to the non-selected location was reduced to baseline. Equally importantly, the same premotor neurons that were active during the delay and showed selectivity for the target with the presentation of the colour cue were also robustly active *during the movement*. This provides critical evidence that the final reach target was not just selected but was specifically selected *for action*. The fact that the same neurons were responsible from the visual specification of both targets, through the selection of one target and, critically, during the movement execution toward that target, favours an interpretation that competitive neural representations are ultimately there to shape action. Given this hypothesis – which favours an interpretation of attentional distribution based on an object's relevance to the planned action – we would predict that obstacle objects should show competitive / selective effects comparable to other task / action relevant objects. One aspect of this hypothesis regarding obstacles is tested and described in the third and final framework discussed below.

1.2.3. Attentional landscapes hypothesis

Recently put forward by Baldauf and Deubel (2010), the attentional landscapes hypothesis represents a sort of compromise between the biased competition hypothesis (which is primarily concerned with visual selective attention) and the affordance competition hypothesis (which is primarily concerned with the implications of competitive representations of motor plans). In their review, they introduce a concept called visual preparation, "the spatially selective, action-specific extraction of motor-relevant information from the visual scene by means of attentional mechanisms" (Baldauf & Deubel, 2010, p. 999). They go on to argue that,

> "Visual preparation involves the top-down weighting of incoming visual information via feedback routes from action planning areas of the brain. We suggest that any kind of goal-directed action preparation is accompanied by a visual preparation process and that the top-down signals that weight visual information at early processing stages may therefore have various possible sources, depending on which motor system is in use. Although understood as a top-down weighting of visual input, the process of visual preparation is automatic in the sense that it is a mandatory component of preparing a goal-directed action" (2010, p. 999).

Baldauf and Duebel conceptualize the resulting allocation of visual attention as an 'attentional landscape' with peaks of activation facilitating the visual representation of task relevant objects (from a goal directed motor sense) and valleys of activation inhibiting the representation of irrelevant, distracting or interfering objects. Among the many examples of experimental evidence presented in their review (Baldauf & Deubel, 2010), several of the studies deserve specific attention in the current thesis. A group of the studies have used a similar paradigm to demonstrate how the allocation of visual attention is linked to the planning of movements. Specifically, participants are required to perform two tasks: the first is a target directed action (here I restrict myself to a discussion of reach movements, but similar work has been done with eye movements, Baldauf & Deubel, 2008; Deubel & Schneider, 1996; Schneider & Deubel, 2002) and the second is a perceptual identification (see Figure 1.3). The perceptual identification requires participants to indicate whether a target briefly (~100ms) presented among distractors, then immediately masked, was an ‘E’ or was a reverse E (similar to a digital ‘3’). The target is presented after the participants are cued to make a movement but before the movement has been initiated. The critical comparison examines identification performance when the target is presented at action-relevant (i.e. the goal of an action) or action-irrelevant locations. Several studies using this paradigm provide insight that is significant to the current thesis. First, it was found that the preparation of a reach movement to a target position facilitated detection specifically at that location (Duebel, Schneider, & Paprotta, 1998). Second, impressively, this finding extended to cases where participants were making sequential movements (Baldauf, Wolf, & Deubel, 2006). In this study, participants planned movements where they reached to an initial target position and then to a target position one removed in a clockwise direction (equivalent to pointing to the 1 and then the 3 on a standard clock). Identification at *both* movement goals was enhanced. Moreover, when participants were required to extend the movement to include a 3rd location (either once more removed from the second target (like 1, 3, 5 on a clock), or directly across the circle (like 1, 3, 9 on a clock)) the identification enhancement was seen at all three locations. Importantly, the enhancement at multiple locations did not come at a cost to the enhancement at a single location – that is, participants were as good at detecting targets at the first movement goal regardless of whether it was the only target, or the first of three targets. This finding provides strong evidence for the parallel specification of movement goals and the attentional enhancement at multiple points in the attentional landscape – likely a necessary requirement when avoiding an obstacle while reaching to a specific target.

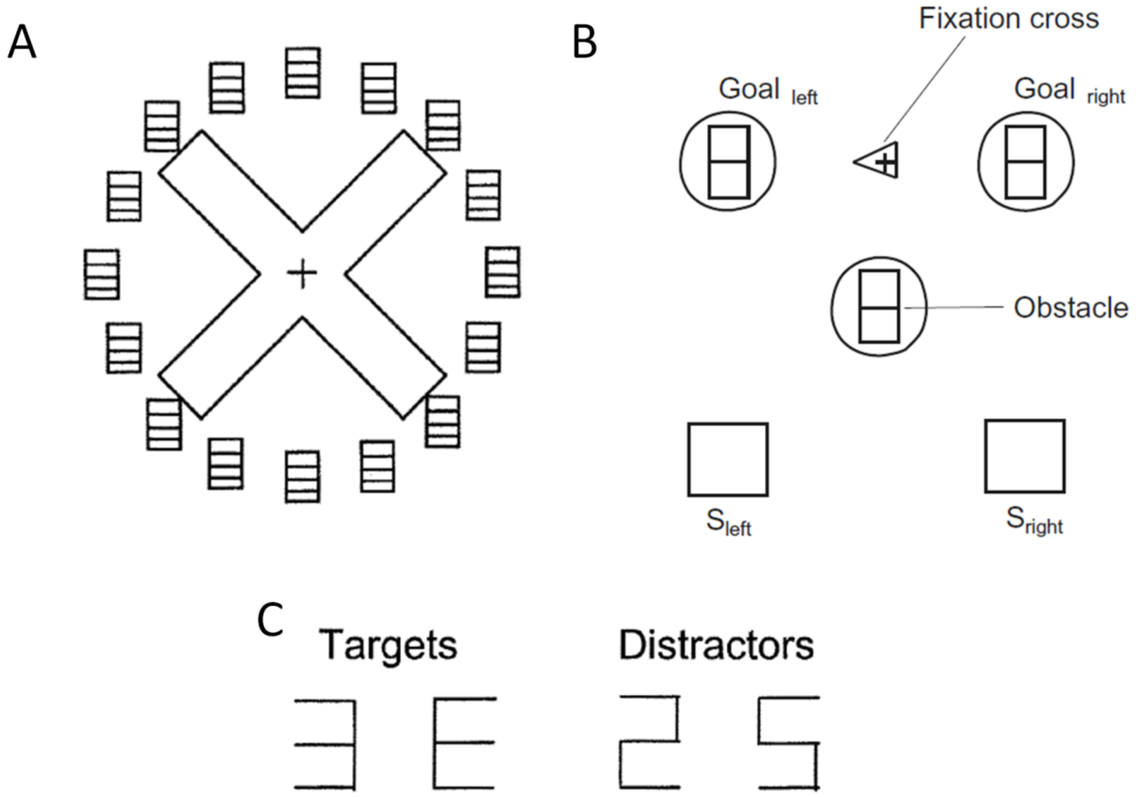

Figure 1.3. Stimuli arrangement for two studies using the dual-task perceptual identification / reaching paradigm (A) From Shiegg et al. (2003): A cross could be grasped with the thumb and forefinger at opposite ends of either cross-beam. Targets and distractors could be presented at one of 16 locations, some of which aligned with the grasp points. (B) From Duebel and Schneider (2004): Participants made reaches with either their left or right hand (starting at S_{left} or S_{right} respectively) to one of two goal targets (aligned directly ahead of the left and right start positions). An obstacle was sometimes present in the middle of the workspace. Targets and distractors could be presented at either of the goal locations or at the obstacle location. (C) Example of targets and distractors used for the perceptual identification.

Two additional studies are particularly relevant to the current thesis. The first (of consequence to the experiment described in Chapter 4, C. S. Chapman, Gallivan, Culham, & Goodale, 2010) showed that when participants planned a grasp toward an object shaped like an ‘X’ (finger and thumb on opposite ends of one arm of the ‘X’) identification enhancement was seen for targets presented at both the index finger and the thumb targets, but not at the ends of the other arm of the ‘X’ (see Figure 1.3a, Schiegg et al., 2003). This suggests that grasping also requires the parallel processing of multiple target positions, in this case both the finger and thumb goals. Finally, most relevant to the current study, these researchers examined the allocation of attention in a task requiring the avoidance of an obstacle (Deubel & Schneider, 2004). In this study participants made reaches with either their left or their right hand, each of which started from its own start position (see Figure 1.3b). Reaches with either hand could be toward one of two targets – straight ahead or across the workspace (to the straight-ahead target for the opposite hand). On half the trials, an obstacle was placed in the middle of the workspace (midpoint of the square formed by start and target positions). Identification was tested at three locations – the two target locations and the location of the obstacle. Of most interest, identification performance was enhanced at the obstacle location only when an obstacle was present *and only when an across-workspace reach was required*. That is, on straight ahead reaches with either hand (where avoidance was not required and trajectory deviations were not observed) there was no perceptual enhancement at the obstacle location. In comparison, on trials when the arm crossed the workspace, and deviations were required in order to avoid the obstacle, perceptual enhancement was seen at the obstacle location. Critically, this finding suggests that the obstacle position was automatically coded (as measured by attentional enhancement) prior to movement onset, and that this enhancement was specifically tied to the current movement goal and level of interference provided by the obstacle.

Finally, two recent studies by the same research group have examined the neural correlates of this attentional enhancement at action-relevant locations. Using the known event related potential (ERP) response difference to flashed items at attended versus unattended locations (known as the dot-probe paradigm), Baldauf and Duebel (2009) demonstrated that attention was preferentially allocated to both of the upcoming targets in a sequential pointing task. While source localization is a difficult problem with ERPs, these researchers speculated that the prefrontal cortex and posterior parietal cortex (PPC) were likely involved. The involvement of the PPC was directly tested using neural recordings from the PPC of behaving monkeys (Baldauf et al., 2008). The majority of cells with a preferred reach direction showed an enhanced response when either the first or second of the sequential targets was present in their receptive field, and this enhancement persisted across a delay period (see Figure 1.2c).

Several principles can be extracted from the attentional landscape hypothesis that resonate with the two previously discussed frameworks and that have important implications for the current thesis and obstacle representation in general. First, as with both the biased competition and affordance competition hypotheses, the attentional landscape hypothesis argues for the parallel representation of multiple visual objects (or parts of objects, as is the case in grasping). While the attentional landscape hypothesis does not make a direct claim for competition, parallel encoding when (usually) only one target is selected implies a competitive interaction. Second, and more akin to the affordance competition hypothesis, the peaks of facilitation within an attentional landscape are intrinsically bound to action goals. Third, a frontoparietal network is implicated in the control (or manifestation) of selective biases, with potential effects visible in the early visual cortical representation of selected or inhibited objects. Finally, and specific to the evidence presented for the attentional landscape hypothesis, the representation at obstacle locations is enhanced prior to movement onset and is contingent on the level of interference the obstacle presents to the current reach movement.

1.2.4. Conclusions from frameworks

Here I summarize three key points of convergence across the three frameworks described above. For each point, how it specifically affects our understanding of obstacles, and how it motivated the current thesis is discussed.

Suppression of non-target objects

At the start of this section I proposed that one way obstacles might influence action is for their neural coding to be actively inhibited relative to the encoding of a target object. This proposal requires that there is an initial positive coding for both the target and obstacle object, followed by the inhibition of the obstacle-related activity and a corresponding boost to the target-related activity. Studies that have been motivated by all three frameworks provide evidence supporting the notion of an initial parallel encoding of objects, where an initial response to two or more objects in the workspace has been demonstrated (see Figure 1.2). Both the competitive bias and affordance competition hypotheses have argued that the activity associated with non-target objects (but not necessarily obstacles) is suppressed once a target is specified. What is still unknown is whether or not the neural encoding of obstacles will show the same suppression as the neural encoding of non-selected objects; that is, if an obstacle's non-target status is implied, rather than cued, will there still be evidence for suppression? That is one of the specific questions tackled in the current thesis.

Dynamics of non-target representations – from planning to execution

Another feature uniting all three frameworks is the evidence that parallel selective biases develop *prior* to movement initiation. This indicates that parallel object/motor-plan specification develops and is maintained across delays during movement planning – an aspect that will become important both when we consider the obstacle effects in neuropsychological patients discussed in section 1.6 and the design of the functional magnetic resonance imaging (fMRI) study discussed in Chapter 4 (C. S. Chapman, Gallivan, Culham et al., 2010). Furthermore, the idea of the dynamics of the obstacle representation (i.e. how they evolve during movement execution) – a relatively unexplored aspect of non-target representations – also provided the motivation for the behavioural studies (C. S. Chapman & Goodale, 2010a, 2010b) conducted in the current thesis.

Frontoparietal (dorsal stream) control of visuomotor bias

A final point of commonality between the three frameworks that is significant to the current thesis is the notion that visuomotor biases are developed and maintained in a frontoparietal network. This network is putatively responsible for the flexible selection of action relevant objects and inhibition of objects that are irrelevant or interfere with movements. As will be discussed in section 1.6, frontoparietal circuits are also part of the dorsal visual stream, known to carry and transform visual information important for the control of action and implicated in obstacle avoidance in neuropsychological populations. In the current thesis, I aim to specifically test the involvement and capabilities of the dorsal stream in obstacle avoidance both behaviourally and through neuroimaging.

The remainder of the Introduction loosely follows the order of the three topics presented above. First, I review experimental evidence in support of the suppression of non-target (or distractor) visual information in both neuroimaging and behavioural work. Since the current thesis presents the first neuroimaging experiment directly looking for the suppression of neural activity associated with obstacles, the neuroimaging portion of this review is restricted to an examination of the suppression of activity associated with non-obstacle distractors in predominantly non-action tasks. The behavioural portion focuses entirely on work examining the effect of distractors on reaching and grasping movements. A complementary literature in the domain of eye-movements is likely relevant, but is not discussed for the sake of brevity. The second and third topics – namely the dynamics of obstacle representation and its control by the dorsal visual stream – while distinct motivating factors for the current thesis, are largely inseparable in the relevant work that is reviewed. As such, the remaining sections in the Introduction discuss the dynamics and dorsal stream control of obstacle avoidance together. First, I review the (limited) work on obstacle avoidance in non-human animals before turning the focus to work on neuropsychological patients. I conclude the Introduction with a summary of previous behavioural work on obstacle avoidance during reach and grasp movements.

1.3. Neural correlates of distractor suppression

1.3.1. Suppression in an action task

As discussed above, within a biased competition framework, an obstacle can be conceptualized as a non-target object in the workspace whose representation must be suppressed, resulting in its avoidance during movement execution (for further speculation of the exact mechanism that might underlie such suppression, refer to section 5.3 in the Discussion). To my knowledge, prior to the work described in this thesis (Chapter 4, C. S. Chapman, Gallivan, Culham et al., 2010) only one study has examined human neural activity when performing real reach actions in the presence of real non-target objects (H. Chapman et al., 2007). In this experiment participants reached out and grasped spherical targets (attached to a rod which allowed the targets to be retracted) at one of three locations. There were two experimental conditions (run as a blocked fMRI design): 1) the target could appear in isolation prior to its location being cued, or 2) the target could appear together with identical objects at the two other locations prior to being cued (all locations had an equal likelihood of being selected as the target on any given trial). Critically in the three-target condition simultaneous presentation of multiple targets meant that potential motor plans may have been generated toward all three locations. In agreement with other neuroimaging work demonstrating an automatic response to objects within reach (Gallivan, Cavina-Pratesi, & Culham, 2009), H. Chapman et al. (2007) found greater activation for the three-target than the single-target condition in the superior parietal occipital cortex, which they label as precuneus activity. This finding is in accord with the involvement of the frontoparietal network in visual selection of and the specification of actions toward relevant objects. Given the nature of this task, however, it is unclear exactly what process was being measured. If it was a purely motor planning response, then this activity could have corresponded to an increase in the number of motor plans being specified. If it was a response selection response, however, then this activation could have corresponded to the selection of one target amongst many and/or the suppression of non-selected locations. Finally, if the response was related to motor execution then it may have been driven by the act of reaching in the presence of non-target objects, which could have functioned as obstacles (whose level of interference would have shifted with the specific location reached to, a factor not discussed in this study). Therefore, while this study suggests an important role of the PPC when performing reaches in the presence of non-target objects, other methods are required to tease out the specific components of the planning to execution continuum.

1.3.2. Suppression in visual cortex and parietal top-down control

In this vein, experiments have been conducted to examine the brain network responsible specifically for the suppression of unwanted visual information (though not in the context of action). In two studies, participants were required to respond to the angle of one of two visual stimuli, while being scanned with fMRI (Sylvester, Jack, Corbetta, & Shulman, 2008; Sylvester, Shulman, Jack, & Corbetta, 2007). Which stimulus they were required to attend to was cued with one of two auditory beeps 6-10s prior to the presentation of the visual stimuli. This pre-cue and subsequent delay allowed the researchers to measure the neural signature of the allocation of attention to both the cued and uncued target locations during this preparatory period. They found that the allocation of attention led to a correlated difference in the visual cortical representations of the attended (activity enhanced) and non-attended (activity suppressed) locations (Sylvester et al., 2007), and that the suppression of activity at non-attended locations was larger when the expected discrimination was going to be more difficult (lower contrast, Sylvester et al., 2008). These results fit well within a competitive framework where attention toward the cued location is accompanied by a suppression of activity at the non-cued location, especially when the difficulty demands even greater attentional resources. Additional findings from these studies also suggest that the modulations in preparatory activity observed in early visual cortex were generated by top-down attentional control signals from a frontoparietal network (see also Bressler, Tang, Sylvester, Shulman, & Corbetta, 2008; Silver, Ress, & Heeger, 2007). A similar result was found in another experiment (where the likelihood of the appearance of distractors was cued) which demonstrated that the amount of preparatory activity observed in visual cortex was contingent upon whether or not participants expected distractors to appear together with the targets (Serences, Yantis, Culberson, & Awh, 2004).

One neurophysiological study, where recordings were made from the IPS (specifically the lateral intraparietal (LIP) area) of rhesus monkeys during a visual search task (Ipata, Gee, Gottlieb, Bisley, & Goldberg, 2006), also provides neural evidence for the role of the parietal cortex in distractor suppression. In this experiment, search displays always contained a target that was difficult to detect amongst several distractors one of which was highly-salient and ‘popped out’. Initially, neuron responses to the pop-out distractor were higher than for non-pop-out distractors. However, with training, the responses of the neuron for the pop-out distractor became slower and smaller than the responses for the non-pop-out distractors. This was taken as evidence that with sufficient knowledge (in this case training) the representation of salient but irrelevant information in the IPS could be suppressed.

Finally, a recent set of experiments has used fMRI and transcranial magnetic stimulation (TMS) to confirm the role of the parietal cortex when human participants responded to one set of visual information while ignoring another (Mevorach, Hodsoll, Allen, Shalev, & Humphreys, 2010; Mevorach, Humphreys, & Shalev, 2005, 2006, 2009; Mevorach, Shalev, Allen, & Humphreys, 2009). Specifically, these researchers used compound letter stimuli where a larger letter is comprised of smaller elements of a different letter (e.g. a large letter ‘H’ comprised of small letter ‘D’s, see Figure 1.4). In these compound stimuli there are two orthogonal dimensions, the global, large letter and the smaller, local letters, whose salience can be varied (i.e. blurring the local elements makes the large letter more salient, while making local elements different colours makes them the more salient dimension, see Figure 1.4). Importantly, one can then contrast behaviour and neural activity on trials when participants are responding to the high-salience or low-salience dimension independent of whether that dimension is the global or local target. Brain areas responding to this contrast would then specifically be implicated in the selection (or suppression) of high- or low-salience information. Using repetitive TMS (10 min of stimulation over one site, which leads to a disruption of that area for several minutes) these researchers showed that disrupting the right PPC interfered with participants’ ability to respond to the high salient dimension (again, irrespective of whether it was global or local) while disrupting the left PPC interfered with participants’ ability to respond to the low salient dimension (Mevorach et al., 2006). The most relevant conclusion to the current thesis, that the left PPC biases selection away from the salient dimension (i.e. enabling one to ignore distracting information), was replicated and extended in two follow up studies. First, using transient TMS (where a brief burst of TMS is given at different points in a trial), Mevorach et al. (2009) showed that the deficit in responding to low-salience information after left PPC disruption was maximal with

TMS prior to stimulus onset, indicating that the suppressive response was preparatory in nature. Second, using fMRI, these researchers (Mevorach, Shalev et al., 2009) further localized the preparatory left PPC activity to the IPS.

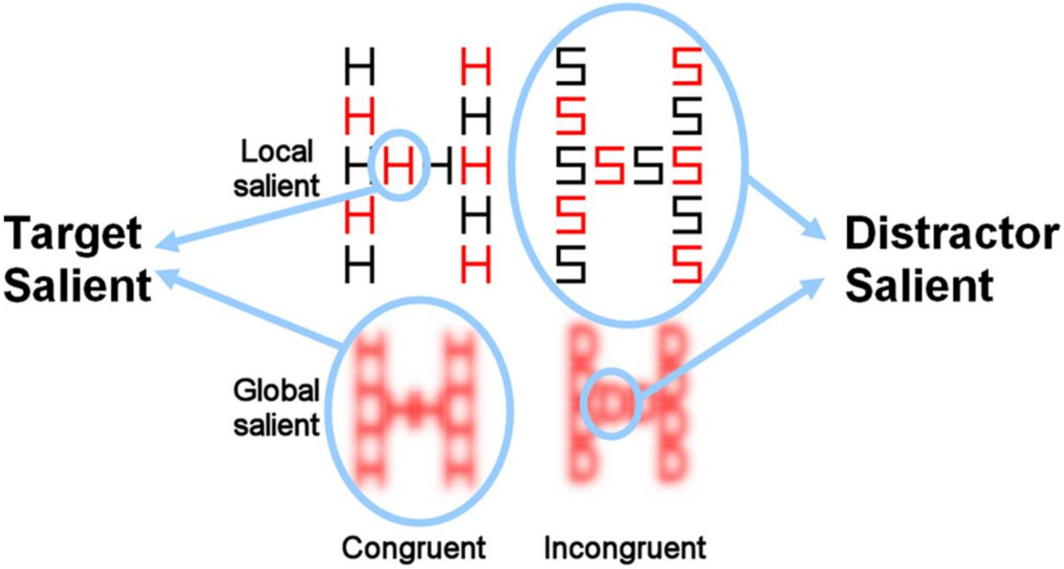

Figure 1.4. Compound letter stimuli used by Mevorach and colleagues (from Mevorach et al., 2010). A large global letter (in this case H) is made up of smaller local-element letters that are either congruent (in this case H) or incongruent (in this case S or D) with the larger letter. By providing a high resolution stimulus (top row) with different coloured local elements, the local dimension can be made more salient. By blurring the stimulus (bottom row) the global dimension can be made more salient. A contrast can therefore be made between high and low salient information that is independent of the global / local level of the information.

One recent study (Mevorach et al., 2010) brings together the work showing a suppression of visual cortex activity at the location of an anticipated distractor (Sylvester et al., 2008; Sylvester et al., 2007) and the increase in left PPC activity when suppression is required (Mevorach, Shalev et al., 2009). In this study, Mevorach and colleagues (2010) combined TMS and fMRI to specify a causal relationship between left IPS activation and visual cortex suppression. First, in a pre-TMS fMRI scan, they confirmed that the left IPS was activated more on trials where participants were required to respond to low salient, as compared to high salient information. From this data, they also demonstrated that the increased left-IPS activation was correlated with a decrease in activity in visual cortex. Finally, using repetitive TMS followed immediately by an fMRI scan (such that the disruptive TMS effects were still evident) they showed that left-IPS disruption led to an increase in the blood oxygenation level dependent (BOLD) fMRI response in visual cortex, but only when participants were required to respond to the low-salience dimension of a compound stimulus. That is, in cases where the left IPS should have been generating the suppressive response required to ignore the irrelevant high salient information, its disruption led to an increased visual response, corresponding, they argued, to a lack of suppression. Taken together, these TMS and neuroimaging studies of the suppression of distracting visual information suggest that the detection of irrelevant information is generated by preparatory activity in the PPC (specifically the left IPS) which leads to the suppression of the corresponding retinotopic location in early visual cortex.

It should be noted that there are many other tasks which likely rely on suppressive mechanisms which are similar to those described in this section, including Go/No-Go (or cancellation, e.g. Curtis, Cole, Rao, & D'Esposito, 2005) tasks (where the participant is required to countermand a planned response, e.g. Rubia et al., 2001) anti-saccade tasks (where the participant is required to make an eye movement to a location opposite a visual cue, e.g. Connolly, Goodale, Desouza, Menon, & Vilis, 2000; Connolly, Goodale, Menon, & Munoz, 2002) and, perhaps most relevantly, anti-pointing tasks (e.g. Connolly et al., 2000). Interestingly, as was the case for the distractor suppression studies described above, a frontoparietal network (in which the PPC plays a crucial role) has been implicated in all of these related tasks. Key differences between these tasks and obstacle avoidance, however, make a further discussion of them beyond the scope of this thesis. In anti-pointing and anti-saccade tasks, while a movement to the visual cue must be suppressed, there is also considerable remapping required to generate a movement to the new anti-location, which is not required in an obstacle task where no target remapping is needed. For Go/No-Go tasks neural activity resulting from the complete cancellation and corresponding lack of response is likely to be very different from obstacle tasks where an action is always performed, and only a single object, and not an entire action, must be suppressed.

1.3.3. Conclusions from distractor suppression

As predicted by the frameworks described in section 1.2, acting in the presence of distracting objects or attending to one visual stimulus (or one dimension of stimulus) in the presence of a second stimulus (or dimension) recruits a frontoparietal network – specifically, the PPC. Interestingly, in these tasks a suppression signal can result in changes to the early visual response – enhancing activity at attended locations and suppressing activity at unattended or irrelevant-object locations. None of these studies, however, has looked at the neural activity and possible suppression related to obstacles, a key component of the current thesis.

1.4. Distractor interference in reaching tasks

Work examining the effect of non-target objects on reach behaviour was borne out of the same ideas that drove researchers to examine selective attention. That is, just as it is necessary to filter the overwhelming influx of visual information that constantly arrives at our retina, so too is it necessary to filter the possible objects on which we might act. Of course, as has already been argued above (see section 1.2), recent theoretical frameworks posit that these two selective process are actually a unified phenomenon of a brain that has evolved to visually select action relevant objects. The described frameworks, however, were in part inspired by researchers exploring what was specifically known as “selection-for-action”. Alan Allport was one of the first to recognize the problem of selection specifically as it pertained to action, and he describes the problem as follows:

> "The action is, say, picking apples. Many fruit are within reach, and clearly visible, yet for each individual reach of the hand, for each act of plucking, information about just one of them must govern the particular pattern and direction of movements. The disposition of the *other* apples, already encoded by the brain, must be in some way temporarily decoupled from the direct control of reaching, though it may of course still influence the action, for example as representing an obstacle to be reached around, not to be dislodged, and so on." (1987, p. 396)

While Allport makes a distinction between the processes of selection and obstacle avoidance (which may in fact be part of the same competitive process) the demands of selection for action are clear – actions must be performed toward a limited (usually one) number of objects in an environment full of other distracting objects.

1.4.1. Reaching in the presence of distractors – Tipper and colleagues

In an important paper, Tipper and colleagues presented some of the first experiments looking directly at selective attention using reach responses (Tipper, Lortie, & Baylis, 1992). In these experiments, participants made reaches to buttons at different target positions signalled each trial by a light emitting diode (LED). On some trials a second target button would be signalled with a different coloured LED, which participants were told to ignore. The results showed that the cuing of non-target locations interfered with reaches to target locations, indicated by slower response times. This pattern of interference indicated that non-target locations in the path of the reach (or, in a slightly modified version, non-targets closest to the hand, Meegan & Tipper, 1998) interfered the most, while non-targets presented past the reach target showed reduced interference (Tipper et al., 1992). That the interference effects were contingent on the anticipated reach trajectory (or position of the moving hand) provides strong support that the selective attentional effects arose from the relevance of the distractors to the action. In several follow-up studies, the trajectories of reaching movements were monitored in a similar task (Howard & Tipper, 1997; Tipper, Howard, & Houghton, 2000). It was found that trajectories deviated both toward (Tipper et al., 2000) and away (Howard & Tipper, 1997) from distractor locations. This somewhat confusing result is discussed in further detail in below.

The results described above were restricted to examining the effects of LED distractors. Thus, to extend their investigations, in one study Tipper and colleagues (Tipper, Howard, & Jackson, 1997) examined reach-to-grasp movements directed toward coloured cubes in the presence of other non-target cubes. Target and distractor cubes were placed in one of four spots, arranged in a square on a table (resulting in 'far' and 'near' positions in combination with 'right' and 'left' positions) and the trajectory of the hand through space was measured (see Figure 1.5). When reaching for a 'near' cube, with a distracting cube in one of the 'far' positions slight deviations toward the non-target cube were observed (see Figure 1.5a), while reaches to 'far' cubes with a distracting object in one of the 'near' positions had deviations away from the non-target cube (see Figure 1.5b). In this study, it was acknowledged that the 'near right' non-targets likely functioned as obstacles and this accounted for some of the observed deviations. However, the researchers claimed that objects in the 'near left' location did not physically obstruct the movement; thus deviations away from this distractor did not represent avoidance. In contrast to this, I would argue that all of these 'near' deviations can be attributed to obstacle effects (Tresilian, 1998; 1999, makes the same argument) since, as we have shown in a number of studies (C. S. Chapman & Goodale, 2008, 2010a, 2010b), an obstacle does not need to physically impede a movement to induce avoidance. The demonstration of the (very slight) deviation toward 'far' distractors likely represents those objects functioning as competing targets, a point of distinction we return to later in this section.

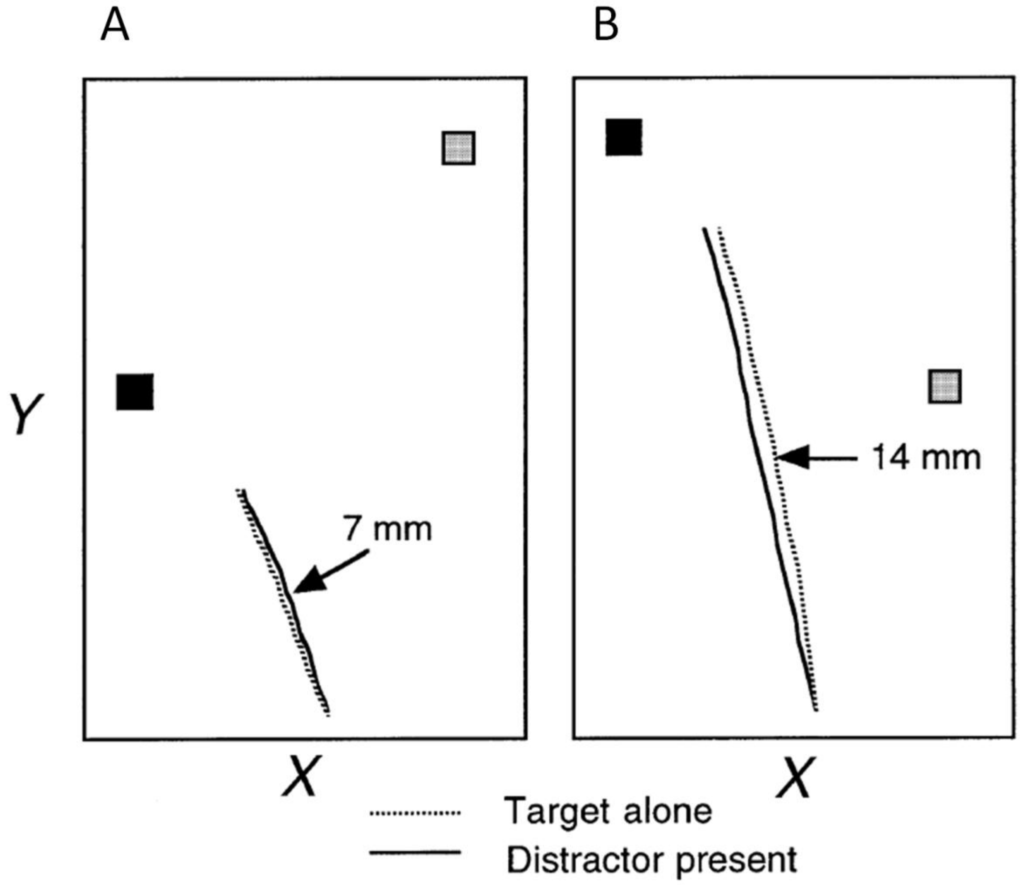

Figure 1.5. Overhead view of reach trajectories showing the effects of distractor interference in the Tipper reach-to-grasp task (Figure from Tipper, Howard, & Houghton, 1998; Results from Tipper et al., 1997). Reaches to targets (black squares) in the presence of distractors (grey squares) deviated slightly (7 mm) toward far distractors (A) or away (14 mm) from near distractors (B). Solid lines correspond to reaches with a distractor present, dashed lines correspond to reaches with only a target present.

One of the striking parts of the above study involving the grasping of cubes (Tipper et al., 1997) was the researchers' treatment of distractors and obstacles as being separable phenomena. In a follow-up review article they state, "…hand deviations away from distractors may not reflect inhibitory mechanisms so much as the avoidance of a collision between the reaching hand and the distractor" (Tipper et al., 1998, p. 1390). Unlike what I have been arguing – namely that obstacles, like distractors, are in some sense to-be-ignored stimuli – this statement appears to argue that the avoidance of obstacles lies outside the domain of inhibition / suppression (though no description of how obstacles are avoided is ever offered). Their stance on this issue is confirmed in two more recent studies (Meegan & Tipper, 1999; Tipper, Meegan, & Howard, 2002) where an obstacle was used to modulate the level of distractor interference. That these researchers use an obstacle to *independently* alter distractor effects implies that they believe obstacle avoidance and distractor interference are not related processes. Specifically, they adapted the LED-distractor paradigm described above (Tipper et al., 1992) by placing a transparent obstacle in front of one of the target locations (Meegan & Tipper, 1999). In general, they found that distractors behind transparent obstacles interfered with reaches (measured only by response time) to other locations less than distractors that were not behind obstacles. This reduction of distractor interference at obstacle locations was accompanied by longer response times when participants were asked to act at the obstacle location (with no distractors present). They argued that, "The obstacle successfully decreased motor processing efficiency (i.e. increased response time)…As predicted by the visuomotor processing hypothesis, this decreased motor processing efficiency also produced a decrease in interference from a distractor…" (Meegan & Tipper, 1999, p. 1355). What they do not consider is *why* the motor efficiency would be reduced at the obstacle location. Of course, as I have argued, the representation of the obstacle might itself be suppressed, which in turn could account for the distractors reduced effect. It is quite surprising that they neglect the potential evidence for the suppression of an obstacle that their own reaction time measure of interference indicates.

1.4.2. Reaching and grasping in the presence of distractors – other work

Other research groups have also examined distractor effects in movement tasks. This remaining work can fall into roughly two categories: studies examining the influences of distractors on grasping movements (Ansuini, Tognin, Turella, & Castiello, 2007; Bonfiglioli & Castiello, 1998; Castiello, 1996, 1998, 1999, 2001; Castiello, Badcock, & Bennett, 1999; Gangitano, Daprati, & Gentilucci, 1998; Jackson, Jackson, & Rosicky, 1995; Kritikos, Bennett, Dunai, & Castiello, 2000; Kritikos, Dunai, & Castiello, 2001) and studies examining the influences of distractors on reaching movements (Chang & Abrams, 2004; Fischer & Adam, 2001; Keulen, Adam, Fischer, Kuipers, & Jolles, 2002, 2003; Kurniawan et al., 2010; Song & Nakayama, 2006, 2009; Trommershauser, Landy, & Maloney, 2006; Trommershauser, Maloney, & Landy, 2003a, 2003b; Trommershauser, Mattis, Maloney, & Landy, 2006; Weir et al., 2003; Welsh & Elliot, 2005; Welsh & Elliott, 2004; Welsh, Elliott, & Weeks, 1999; Welsh & Zbinden, 2009). Obviously it is beyond the scope of the current thesis to describe the results from all these studies in any detail, but a few important results are highlighted. Focussing on grasping studies, the bulk of the research comes from the research group led by Umberto Castiello. A theme across the majority of their studies is having participants make reaches to more ecologically relevant stimuli, specifically fruits, in the presence of related non-target objects, usually the same or different types of fruit (Bonfiglioli & Castiello, 1998; Castiello, 1996, 1998, 1999, 2001; Castiello et al., 1999; Kritikos et al., 2000; Kritikos et al., 2001). Across studies, these researchers find consistent evidence for the automatic processing of distractor features in a way that interferes with reach-to-grasp movements – but only when attention is directed toward the distractor. For example, in one experiment, Castiello had participants reach toward an apple that could be presented alone, with a three dimensional (3D) fruit distractor (apple or cherry), or with a two dimensional (2D) photograph of the fruit distractor (Castiello, 2001). Here, he reports that attention needs to be drawn to the distractor (by sudden illumination) in order for it to influence the reach, and when the distractor does interfere, it does so in a manner that is task relevant. That is, when the distractor is 3D, it impacts both the reach and grasp components of the movement, while a 2D distractor only influences the reach component.

This, Castiello argues, supports the notion that automatic processing of distractor features is specific to those features that are relevant to the intended action; since 2D photographs can be pointed at but cannot be grasped, their interference is seen only in reaching, and not grasping (Castiello, 2001). Most commonly, distractor effects in these studies suggest that parameters from the attended distractor leak into the motor execution toward the target – for example, reaching for an apple in the presence of a cherry leads to smaller grip apertures than reaching toward the apple alone. These size effects are not consistent (Jackson et al., 1995), however, indicating the exact nature of the distractor interference in these tasks remains unclear.

As was already noted above in discussing the work from Steve Tipper’s group (section 1.4.1), a similar inconsistency in results is found in the reaching literature. Specifically, reaches toward targets can deviate either toward distractors (Chang & Abrams, 2004; Keulen et al., 2002; Welsh & Elliot, 2005; Welsh & Elliott, 2004; Welsh et al., 1999) or away from them (Fischer & Adam, 2001; Keulen et al., 2002; Welsh & Elliott, 2004). One possible interpretation for deviations toward distractors is that they are coded as potential targets, and thus, in a competitive framework, some biasing toward their location is noted during reaching. We have developed a novel rapid-reaching paradigm that has directly tested this idea (C. S. Chapman, Gallivan et al., 2010a, 2010b; Gallivan et al., 2010) and found convincing evidence for the encoding of multiple targets which results in profound shifts in reach trajectory (most notably initial trajectories which aim directly toward the midpoint of two potential targets, prior to one of them being selected in-flight). By forcing participants to treat all visual stimuli as potential targets, rather than presenting only one target among some distractors, our work improves upon the explanatory power of other rapid reaching tasks (for review see Song & Nakayama, 2009) where distractor effects were seen to ‘leak’ into movement execution (akin to the effects described above during grasping tasks). This thesis, however, is concerned with non-target objects that function as obstacles, and I will not discuss the literature on distractors that attract movements in any more detail.

This leads to a discussion of cases where reaches deviate away from distracting stimuli, an area of research that is likely to be more relevant since these deviations would appear to mirror the behaviour that occurs when someone avoids a physical obstacle. The two groups that have noted reach deviations away from distractors both have hypothesized that the deviations away are the result of a distractor whose representation has been inhibited and pushed below baseline (Houghton & Tipper, 1999; Tipper et al., 1998; Welsh & Elliott, 2004; Welsh et al., 1999). These researchers also believe that deviations toward distractors represent inhibitory processes – just ones that are weak (Houghton & Tipper, 1999; Tipper et al., 1998) or have not had sufficient time to develop (Welsh & Elliott, 2004) [Note that this explanation of deviations toward distractors does not exclude the interpretation of these deviations being representative of multiple target encoding. It is just that, at some point, the non-targets must be inhibited, and that this inhibition can be incomplete.] From this explanation, then, the representation of obstacles and distractors could have a shared fate – namely that inhibition of their representation is required and as a result the hand and arm deviate away from that position (for further speculation regarding the details of obstacle inhibition, see section 5.3). Of course, the amount a given distractor or obstacle interferes with a reach (and thus the amount of inhibition it receives and deviation it results in) is likely to be tied to factors other than its location. In several studies, Julia Trommershauser, and colleagues (Kurniawan et al., 2010; Trommershauser, Landy et al., 2006; Trommershauser et al., 2003a, 2003b; Trommershauser, Mattis et al., 2006) have demonstrated that this is indeed the case. In these studies, target areas and penalty areas are displayed on a computer screen and each is given a point value (positive for target and negative for penalty), with the task being to rapidly point to the screen on each trial and accumulate as many points as possible. By varying the position and value of the two areas, the experimenters have shown that participants accurately adjust their reaches to maximize point gain, and do so without changing their reaction times. In one recent study, the negative consequence assigned to penalty regions was a mild pain stimulus delivered to the non-acting hand (Kurniawan et al., 2010) and similar results were found. In all cases, participants do not merely adopt a strategy in which they simply avoid penalty regions, but rather their deviations away from penalty regions scale precisely with the location and negative value (or relative pain) assigned to both the penalty and target. This parallels the way that deviations around obstacles scale precisely to the location and degree of interference (e.g.

size) of each obstacle (C. S. Chapman & Goodale, 2008, see section 1.7) and suggests that the notion of negative consequences may be important when interpreting obstacles as inhibited distractors.

1.4.3. Conclusions from distractor interference

Earlier I argued that obstacles could be conceptualized as a special class of distracting stimuli that needed to be actively ignored and avoided. Behaviour from studies examining reaching and grasping in the presence of distracting visual stimuli (that are not usually physically obstructing the reach) indicate that this might be true, though the evidence is contradictory. That is, if deviations away from obstacles are the behavioural hallmark of avoidance (as described in section 1.7) then only some studies report deviations away from distractors. More studies suggest that rather than having a repulsive effect, distractors act as attractors – or more generally, distractor properties (of which only one is location) influence reaches and grasps by ‘leaking’ into the movement, causing it to become a sort of hybrid movement with parameters from both the target and distractor. Perhaps these apparently discrepant results demonstrate that there are different types (or degrees) of distracting stimuli. Thus, it may be necessary to think of distractors along a continuum from those that are perceptually similar to the target and compete as potential targets, to those that are easily distinguished from the target and thus easily ignored, to those that are clearly not targets and have negative consequences requiring avoidance. It is critical to remember, however, that regardless of the exact nature of a distracting stimulus, it will initially generate a positive visual response. From the theoretical competitive frameworks described earlier (section 1.2), this neural encoding of the distractor automatically competes for visuomotor attentional selection. Ultimately, since an action toward the distractor location is not selected, its neural representation must have lost out, indicating that, relative to the target, its neural activity was inhibited. One goal of the current thesis was to test the prediction that the neural encoding of obstacles would result in suppression effects.

1.5. Obstacle encoding in non-human animals

1.5.1. Obstacle avoidance in monkeys

I now shift the focus of the Introduction from a review of the effects of non-targets as distractors to a review of the effects of non-targets as obstacles. Like research exploring obstacle avoidance in humans (see section 1.7), the study of obstacle avoidance in non-human species is remarkably sparse. Nonetheless, the few studies that have examined movements of non-human animals in cluttered environments are revealing. In one behavioural study examining the reaching behaviour of macaque monkeys (Torres & Andersen, 2006), the researchers were interested in how hand path deviations around obstacles evolved with learning. Impressively, the spatial trajectory of the monkey’s hand around the obstacle emerged on the very first reach and remained almost identical across months of training. The temporal characteristics, however, showed evidence of learning, eventually converging on an optimal spatiotemporal trajectory that became ‘second nature’ to the animal. Overall, Torres and Andersen (2006) conclude that an ideal spatial path is automatically available during perceptual planning and that the consistency of the spatial path allows for the observed temporal learning to take place.

One older study examined the effects of various lesions on complex reaching tasks in macaque monkeys (Haaxma & Kuypers, 1975). While the details of all the experiments and lesion sites explored in this study are not relevant to this thesis, one particular finding is. Specifically, in one set of 10 monkeys, the researchers performed a unilateral leucotomy of the white matter in the parietal lobe with the aim of disrupting all intrahemispheric connections within the parietal lobule. One comment regarding the resulting behaviour is especially illuminating,

> “Yet, in all the leucotomized animals one phenomenon persisted, which was also observed in the occipital lobectomized and commissurotomized animals. When food was held in front of the cage the intact arm and hand, after a few trials, reached swiftly for the food through a 10 cm by 10 cm opening in the cage front, 15 cm above the cage floor. However, the contralateral arm and hand were much less inclined to follow this strategy and generally kept trying to reach straight forward through the spaces between the cage bars.” (Haaxma & Kuypers, 1975, p. 247).

This comment specifically identifies that the most persistent deficit in animals with white matter lesions in the parietal lobe was an inability to integrate the movement restrictions imposed by the environment into the goal-directed reaching of the contralesional arm. These monkeys could successfully identify the target and execute a reach toward it, but, put simply, they could not avoid obstacles. A follow-up study (Moll & Kuypers, 1977) found similar results in monkeys with unilateral ablations of the premotor cortex, leading the authors to conclude, “ablation of these frontal areas impairs the capacity of the animals to reach around an obstacle with the contralateral arm in order to obtain a visible food reward, and results in a tendency of this arm to reach straight to where the food is visible.” (Moll & Kuypers, 1977, p. 317).

1.5.2. Obstacle avoidance in cats

Recent studies of the locomotion of cats provides strong evidence for obstacle encoding in this species (Andujar, Lajoie, & Drew, 2010; Grahn & Owen, 2006; Lajoie, Andujar, Pearson, & Drew, 2010; Lajoie & Drew, 2007; McVea & Pearson, 2006, 2007; McVea, Taylor, & Pearson, 2009) and a role for the PPC in controlling the subsequent avoidance. In one paradigm, cats were required to step over an obstacle with their front paws before being distracted with food. While the cat ate, the straddled obstacle was removed. After a variable delay, the cat resumed walking, and the hind legs were lifted to a height that cleared the now-absent obstacle (McVea & Pearson, 2006). Impressively, this hind leg ‘avoidance’ persisted over delays as long as 10 minutes and was sensitive to the size and position of the obstacle. In a second study, McVea et al. (2009) demonstrated that bilateral lesions to area 5 (in cat PPC) disrupted this obstacle encoding such that the delayed hind limb avoidance was diminished or absent after delays longer than 1.5 seconds. Immediate avoidance by the hind limbs (no delay) was preserved. In addition to another result suggesting that the act of stepping over the obstacle with the front limb is critical to the encoding of obstacles (McVea & Pearson, 2007) these researchers argue that area 5 in the cat PPC is crucial for integrating recently experienced motor events with recently viewed visual objects into a neural code for the obstacle that it then maintains.

In a second paradigm examining the avoidance of obstacles during cat locomotion, researchers had cats walked on a treadmill with obstacles that moved at a speed that matched their walking speed or was different (Andujar et al., 2010; Lajoie et al., 2010; Lajoie & Drew, 2007). In cats with lesions to area 5, obstacles were not successfully avoided, often leading to collisions (Lajoie & Drew, 2007). This was especially true when the speed of the obstacle was slower than the speed of walking, leading to the conclusion that:

> "… despite the extent of the damage…none of the three cats showed any overt behavioural deficits in their regular overground locomotor behaviour in the laboratory. This suggests that the deficits that we observed in our locomotor task reflect an important contribution of the PPC in situations in which there is a need to integrate visual information with information about self-motion and are not the result of generalized problems of motor behaviour." (Lajoie & Drew, 2007, p. 2350).

To further specify the role of the cat PPC in encoding obstacles, another similar experiment was conducted while neurophysiological recordings were made from area 5 (Andujar et al., 2010). This study demonstrated that a subset of cells in this area fired specifically when the cat stepped over an obstacle (called step-related cells) confirming the PPC's role in the control of movements affected by obstacles. Interestingly, a larger set of cells responded to the presence of the obstacle well in advance of the cat having to step over it (called step-advanced cells). The researchers argue that this activity is not a purely visual response (since it was contingent on the proximity of the obstacle to the cat, and not on the mere presence of the obstacle) but rather must reflect the planning response when the gait needed modification. This suggests the role of the PPC is to integrate the visual information with the motor execution information to encode obstacles only when they actually interfere with the movement of the cat.

1.5.3. Conclusions from animal obstacle avoidance

These studies in non-human animals reveal several properties of obstacle encoding that are important to this thesis. First, that the encoding of obstacles is a completely automatic process, and critically, that a desired trajectory (that persists across time) is automatically afforded by the visual apprehension of the arrangement of objects in the workspace. Second, that a parietal-frontal circuit is largely responsible for the encoding of obstacles in both monkeys and cats. Third, that the neural encoding of obstacles is complex (have information about size and position) and can persist across long delays. Fourth, that the neurophysiological effects of obstacles are independently present in both the planning and the online control of a movement. Finally, fifth, that objects in the environment are only coded as obstacles when they interfere with a movement, suggesting a crucial role of the PPC is to integrate visual information with motor intention to code the task relevant level of interference of non-target objects.

1.6. Obstacle avoidance in neuropsychological patients

1.6.1. Two visual streams hypothesis

Before entering into a detailed summary of the specific neuropsychological evidence for the role of the PPC in the control of obstacle avoidance, it is useful to describe the theoretical motivation for this work. While in this thesis I put sequential precedent on describing three selective attention frameworks, historically work on the anatomical and functional flow of visual information came first. Originally, Ungerleider and Mishkin (1982) assembled anatomical and experimental evidence to demonstrate that there were two parallel pathways that visual information followed in the brain. In brief, after arriving at the retina, the majority of visual information is relayed through the lateral geniculate nucleus (LGN) to V1. After V1 (or even within different layers of V1 and the LGN), visual information is split into two streams of information, which Ungerleider and Mishkin separately called the ‘what’ and ‘where’ pathways. The ‘what’ stream flows from V1 ventrally into IT cortex where the processing of complex object shape ultimately allows for object identification (this matches well with the findings from Chelazzi et al., 1998; Chelazzi et al., 1993 showing competitive biases developing in IT cortex responsive to complex shape, see section 1.2). The ‘where’ stream flows from V1 dorsally to PPC, and thus is anatomically the same network that is implicated in the control of biased visuomotor attention (see section 1.2 on theoretical frameworks). The Ungerleider and Mishkin (1982) definition of the ‘where’ stream, however, lacked what has become acknowledged as a crucial component of the visual information in the dorsal stream – namely that this information, while carrying a spatial component, is primarily used to define *how* visually guided actions are planned and executed. This modified theory of the two visual streams – a ventral vision-for-perception and dorsal vision-for-action stream – was postulated by Goodale and Milner (Goodale & Milner, 1992; Milner & Goodale, 1995, see Figure 1.6). Of course, the fact that the PPC (and the rest of the frontoparietal network) is primarily encoding actions and action relevant targets is a key component of both the affordance competition hypothesis and the attentional landscapes hypothesis (see section 1.2).

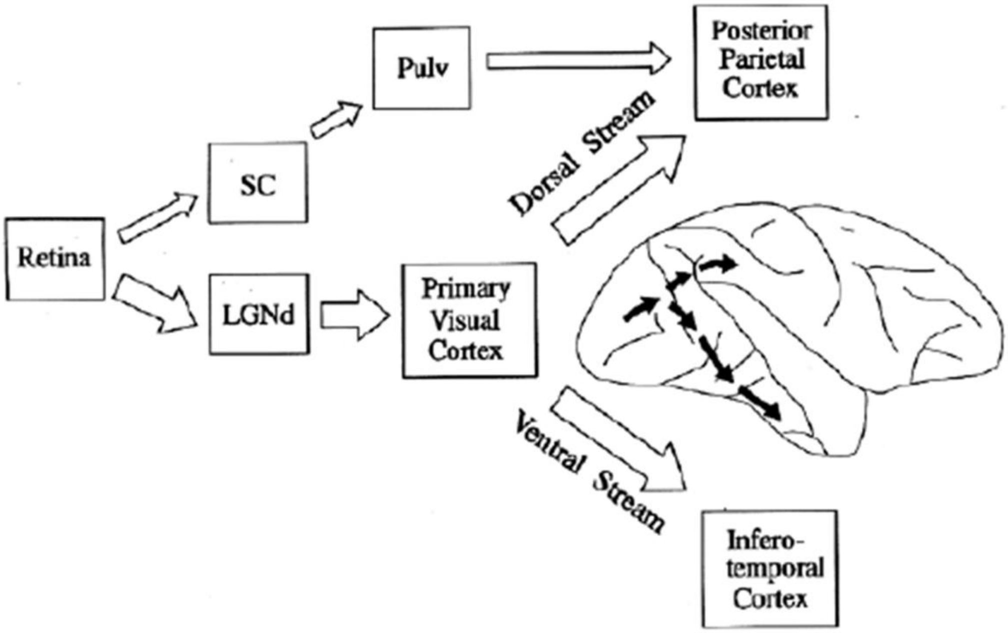

Figure 1.6. A Schematic diagram of the two visual streams (from Milner & Goodale, 1995). Visual information from the retina primarily projects through the LGN to V1. From there it splits into two streams, one dorsal that flows into PPC and one ventral that flows into IT cortex. A secondary route for vision to reach the PPC from the retina is through the superior colliculus (SC) and pulvinar (Pulv). The secondary route is thought to be evolutionarily older and provide the mechanisms for some residual sight in patients with damage to V1.

Perhaps the most compelling evidence for Goodale and Milner's characterization of the two visual streams came from work with patients who had specific brain lesions to one of the two visual streams. In the case of damage to the dorsal stream (e.g. lesions to the PPC) patients are likely to develop optic ataxia (OA), a condition associated with visuomotor deficits. Patients with damage to the ventral stream (e.g. lesions to the lateral occipital complex in IT cortex) often develop visual form agnosia (VFA), a condition associated with impairments in identifying visual objects (from complete reviews, see Goodale & Milner, 2004; Goodale & Westwood, 2004; Milner & Goodale, 1995). As a specific example, patient D.F., with profound VFA was unable to identify the orientation of a slot in front of her. However, when asked to put a card into the slot (as though she were mailing a letter) she accurately grasped the card and rotated it to the correct orientation (Goodale, Milner, Jakobson, & Carey, 1991; Milner et al., 1991). In comparison, patients with OA tested on the same task (Perenin & Vighetto, 1988) were able to correctly identify the orientation of the slot when asked to give a verbal report, but when asked to insert the card into the slot their actions were clumsy – missing the slot entirely or rotating the card to the wrong orientation. Given the dissociation of deficits and areas of brain damage (for neuroanatomical images of patient D.F. and an OA patient I.G. see Figure 1.7) in VFA compared to OA patients these populations provide an interesting test for theories postulating the role of the frontoparietal (i.e. dorsal) network in selective visual attention. For succinctness, here I review only the pertinent literature on the performance of these neuropsychological patients on an obstacle avoidance task.

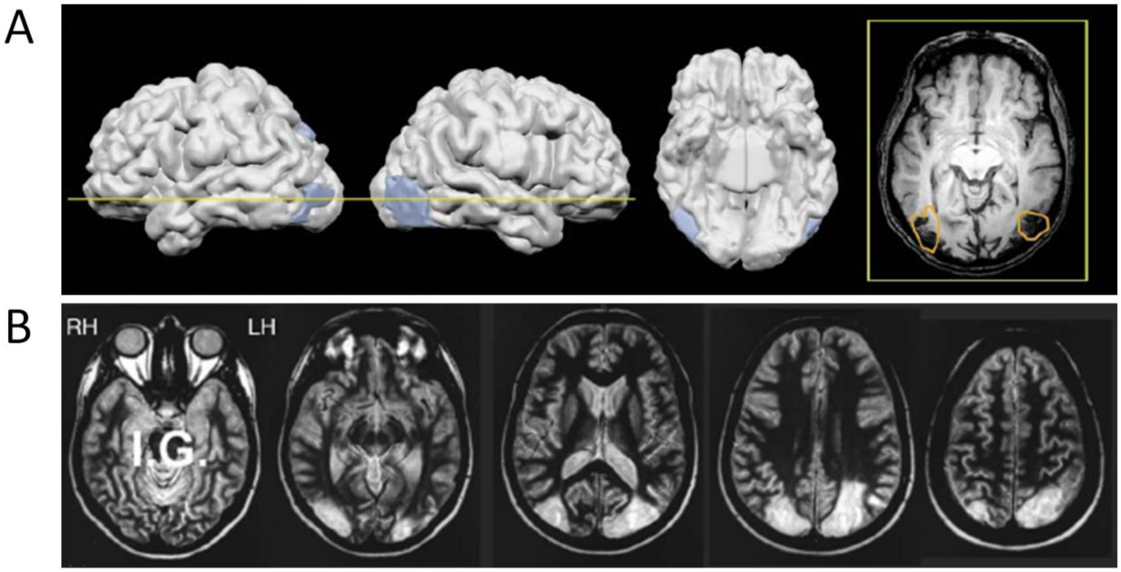

Figure 1.7. Comparison of neuroanatomy of patients with VFA vs. OA. (A) From (James, Culham, Humphrey, Milner, & Goodale, 2003): A 3D reconstruction of the brain of VFA patient D.F., with lesions coloured in blue. The rightmost image shows a slice through the lesions, outlined in orange. Note that these lesions fall along the ventral stream. (B) From (Rossetti et al., 2005): MRI scans of OA patient I.G. Lesions appear white on these images; note that they fall along the dorsal stream.

1.6.2. Impaired obstacle avoidance in patients with dorsal stream damage

In an experiment testing patients with bilateral OA (Schindler et al., 2004), participants were required to make reaches from a start button, pass their hand between two obstacles, and touch anywhere on a strip 45cm away (see Figure 1.8a). Notably, vision of the hand was occluded at movement onset, meaning that participants were reaching in visual open-loop. What varied between trials was the position of the two obstacles. On some trials, they were placed an equal distance from midline on either side (i.e. symmetrical, either close to midline (both-in) or further from midline (both-out), Figure 1.8b). On other trials, the object on one side was further from midline, while the other was close (i.e. asymmetrical, either the right object was further away (right-out) or the left object was further away (left-out), Figure 1.8b). When testing normal participants, reaches between asymmetrically aligned objects were always shifted to the side away from the closer object. When testing patients with OA, however, hand paths across the different obstacle configurations were virtually identical (see Figure 1.8c). This finding was replicated in a follow up study on a second patient who suffered from unilateral OA (Rice et al., 2008). In this case, unilateral damage to the patient’s left PPC led to a specific reaching deficit with their right hand with objects in the right visual field. On the same task, this patient showed no sensitivity to obstacle position changes occurring on the right side of space. These findings suggest that the patients with damage to their PPC (resulting in OA) were not sensitive to (or were not encoding) the position of the obstacle contralateral to the damaged hemisphere, thus supporting the hypothesis that the PPC is critical to obstacle avoidance.

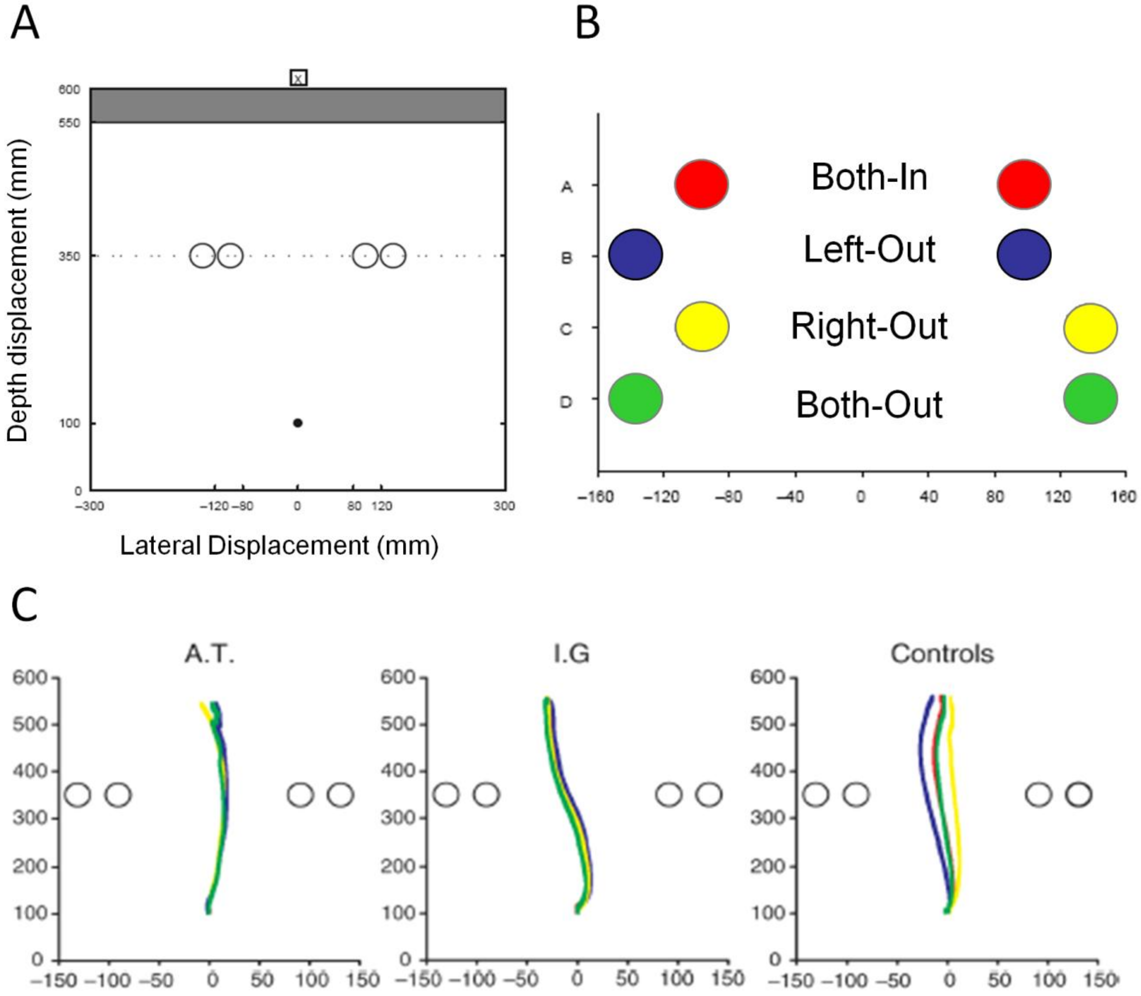

Figure 1.8. Experimental setup and results from obstacle avoidance experiment in OA patients and control participants (Schindler et al., 2004). (A) Overhead view of experimental apparatus. Small black circle is reach start point, grey strip is reach target, open circles are possible obstacle locations, cross is fixation. (B) Possible obstacle configurations. Two symmetrical and two asymmetrical (Left-Out and Right-Out). (C) Overhead views of reach trajectories under each obstacle configuration. Two left graphs are OA patient data. Rightmost graph is an average of control participants. OA patients do not show sensitivity to obstacle configuration while control subjects do.

1.6.3. Spared obstacle avoidance in patients with ventral stream damage

While patients with OA show impaired obstacle avoidance, several different patient populations show preserved avoidance. Most notably, when patient D.F. – who suffers profound VFA after localized damage to her ventral stream – was asked to perform the same task as described above, her hand path trajectories were sensitive to the position of obstacles (Rice et al., 2006). Thus, despite impairments in the ability to consciously report the obstacle locations, D.F. nonetheless took those obstacles into account when performing visually guided reach actions. It is worth mentioning that D.F. also shows preserved obstacle avoidance during locomotion (Patla & Goodale, 1996). The question of obstacles and locomotion is another area of active research (e.g. Fink, Foo, & Warren, 2007; Marigold, Weerdesteyn, Patla, & Duysens, 2007) but for succinctness I restrict this review and the review of behavioural work (see section 1.7) to reaching and grasping tasks. Other evidence of preserved obstacle avoidance in neuropsychological patients comes from studies of patients with hemi-spatial neglect (McIntosh, McClements, Dijkerman, Birchall, & Milner, 2004; McIntosh, McClements, Schindler et al., 2004; Milner & McIntosh, 2004). Patients who suffer from visuospatial neglect have difficulty directing their attention to one of their visual hemi-fields. This disorder almost always results from right hemisphere brain damage leading to neglect of the left visual field. In some cases, this disorder can be accompanied by a symptom known as visual extinction, where two simultaneously presented stimuli, one to each visual field, will result in the contralesional stimuli (again, almost always on the left side) not being perceived. Despite these problems attending to and perceiving stimuli in contralesional space, neglect patients, including those with extinction, show sensitivity to obstacles (McIntosh, McClements, Dijkerman et al., 2004; McIntosh, McClements, Schindler et al., 2004; Milner & McIntosh, 2004). Specifically, on the same task used for the VFA and OA patients, neglect patients show patterns of deviation to obstacle asymmetries that match control subjects (McIntosh, McClements, Dijkerman et al., 2004; Milner & McIntosh, 2004). In a related test with a patient who showed visual extinction, obstacles could be presented alone or in pairs (always symmetrical when paired). When presented in pairs this sometimes led to the patient reporting only one obstacle; their reach trajectory, however, was identical regardless of whether they perceived both obstacles or not (McIntosh, McClements, Schindler et al., 2004; Milner & McIntosh, 2004). This sensitivity to obstacles without conscious awareness again provides evidence for dorsal stream control over obstacle avoidance. One additional experiment demonstrating preserved obstacle avoidance in a neuropsychological population actually comes from the study described above with the unilateral OA patients (Rice et al., 2008). As was noted above, when asked to perform the obstacle task under normal circumstances, avoidance was impaired in the patients with OA. However, when the researchers introduced a 5s delay between the presentation of the obstacles and the cue to reach (note during the delay, vision was absent, as it was during the reach in the non-delay task) the avoidance performance of the OA patients returned to normal. Introducing a delay without visual feedback is thought to shift the representation of the workspace from brain areas in the dorsal stream – which code, in real-time, the visuomotor relevance of objects – to brain areas in the ventral stream – which are responsible for the perceptual encoding of objects that are retrieved (and stored) in memory (Milner, Paulignan, Dijkerman, Michel, & Jeannerod, 1999). Thus, when the workspace representation was shifted from the dorsal stream to the ventral stream in this study of OA patients (Rice et al., 2008) a sensitivity to obstacle position emerged.

Finally, one recent study that we conducted (Striemer, Chapman, & Goodale, 2009) also speaks to the representation of obstacles by the dorsal stream. In this study, we tested a patient with extensive damage to his primary visual cortex in the right hemisphere, resulting in a dense left visual field hemianopia. We used a task similar to the one described above (see Figure 1.8a) but included trials where only a single object appeared (at each of the four different locations). In addition, we asked our participant to provide a verbal report of the location of any obstacles he saw after each reach trial was completed. In the first experiment, the participant performed the task without a delay between the visual presentation of objects and the reach. In this immediate reach condition, our patient showed a preserved sensitivity to obstacle position in both his good right visual field *and* his blind left visual field (where he never reported seeing objects). In a second experiment, however, in which we introduced a 2-s no-vision delay between the presentation of the obstacles and the initiation of the reach, the sensitivity to obstacles was observed only when the obstacles were located in the right visual field. The patient showed no sensitivity to obstacles located in his left (blind) field. Taken together, these results suggest that in this patient, visual input into the dorsal stream from his blind field was somehow mediating his real-time obstacle avoidance while visual input to his ventral stream from his blind field was not available, leading to a failure in the avoidance of obstacles in delay. But, if vision flows through occipital cortex before being separating into the parallel dorsal and ventral processing pathways, why do we see any preserved avoidance? We speculate that information from this patient's blind visual field is still reaching dorsal-stream visuomotor networks in the PPC via the retino-tectal-pulvinar pathway (Kaas & Lyon, 2007; Lyon, Nassi, & Callaway, 2010, see Figure 1.6 for schematic diagram). This evolutionarily older pathway bypasses primary visual cortex and has been implicated in other studies demonstrating preserved visual ability in blind participants (termed 'blindsight', see Cowey, 2010 for recent review).

1.6.4. Conclusions from the neuropsychological studies of obstacle avoidance

The evidence from patients with impaired obstacle avoidance and damage to the dorsal stream and those with preserved obstacle avoidance and damage outside the dorsal stream confirms that frontoparietal circuitry is indeed necessary to successfully avoid obstacles. The task that was used in these studies also supports the claim that the observed obstacle encoding deficits are largely the result of impairments in visuomotor planning. That is, since vision of the limb was never available in flight, participants were not able to use vision to correct their movements. Thus, the trajectory deviations observed in the presence of obstacles must reflect deviations that were generated prior to movement onset. Motivated by the work outlined above we sought to specifically quantify what properties of obstacles were important to their avoidance in normal participants' reaching behaviour (C. S. Chapman & Goodale, 2008). The results of this study are described in the next section, which also includes a discussion of other related behavioural work involving the avoidance of obstacles while reaching and grasping.

1.7. Obstacle avoidance in healthy individuals

1.7.1. Obstacle avoidance in reach-to-grasp movements

The first study to directly test how arm and hand movements were affected by the placement of obstacles was conducted by James Tresilian (1998). In this experiment, participants made reach-to-grasp movements toward a tall rectangular block in the presence of a similarly sized cylindrical block. The cylindrical obstacle could be positioned to the sides of the rectangular target, directly behind the target, or in front and to the side of the target (see Figure 1.9). The type of grip on each trial could change, with participants cued to grasp with their thumb and forefinger opposing each other on the front and back of the rectangle, or on the left and right of the rectangle. Tresilian (1998) found that when making front and back grasps obstacles behind the target interfered with the movement, while side to side grasps were interfered with by objects beside the target. This interference was manifest as smaller grip apertures and slower movement times as compared to the trials without interference. In this study, it was also noted that the presence of obstacles, particularly in front of the target caused slower reach trajectories and deviations in the reach path around them. In a later study, the effect of obstacle position, as well as the effect of the number of obstacles was further quantified (Mon-Williams, Tresilian, Coppard, & Carson, 2001). Here, one or two obstacles could appear to the side or to the side and in front of the reach-to-grasp target. It was found that obstacles close to the target interfered with grip aperture more than those further away, while obstacles in front of the target had the largest effects on the transport phase of the reach (i.e. deviations of the entire hand path). Further, two obstacles caused significantly slower movements than one, suggesting that obstacles avoidance was sensitive to the constraints across the entire workspace (Mon-Williams et al., 2001). Other studies have used the obstacle avoidance paradigm to examine different accounts of the control of prehension (digit channel hypothesis, Biegstraaten, Smeets, & Brenner, 2003; visumotor account, Mon-Williams & McIntosh, 2000) as well as to look at the development of visuomotor behaviour (Tresilian, Mon-Williams, Coppard, & Carson, 2005). It should be noted that obstacles have been used as a *tool* in other research tasks (most notably to increase the duration, shape or complexity of a movement, Jax & Rosenbaum, 2007; Liu

& Todorov, 2007; Saling, Alberts, Stelmach, & Bloedel, 1998) but these studies were not designed specifically to examine obstacle effects. Similarly, motor control theorists have used the problem of obstacle avoidance as a method of introducing constraints into their models of reach behaviour, and then tested their models against human participants' actual avoidance behaviour (Dean & Bruwer, 1994; Hamilton & Wolpert, 2002; Rosenbaum, Meulenbroek, Vaughan, & Jansen, 1999; Sabes & Jordan, 1997; Sabes, Jordan, & Wolpert, 1998; Vaughan, Rosenbaum, & Meulenbroek, 2001). Again, while interesting and related to obstacle avoidance, these models were not specifically interested in the representation of obstacles and their subsequent effects (that is, the obstacle was not the variable of interest), but rather in their usefulness in shaping behaviour. Therefore, for the sake of space, these studies are not reviewed here.

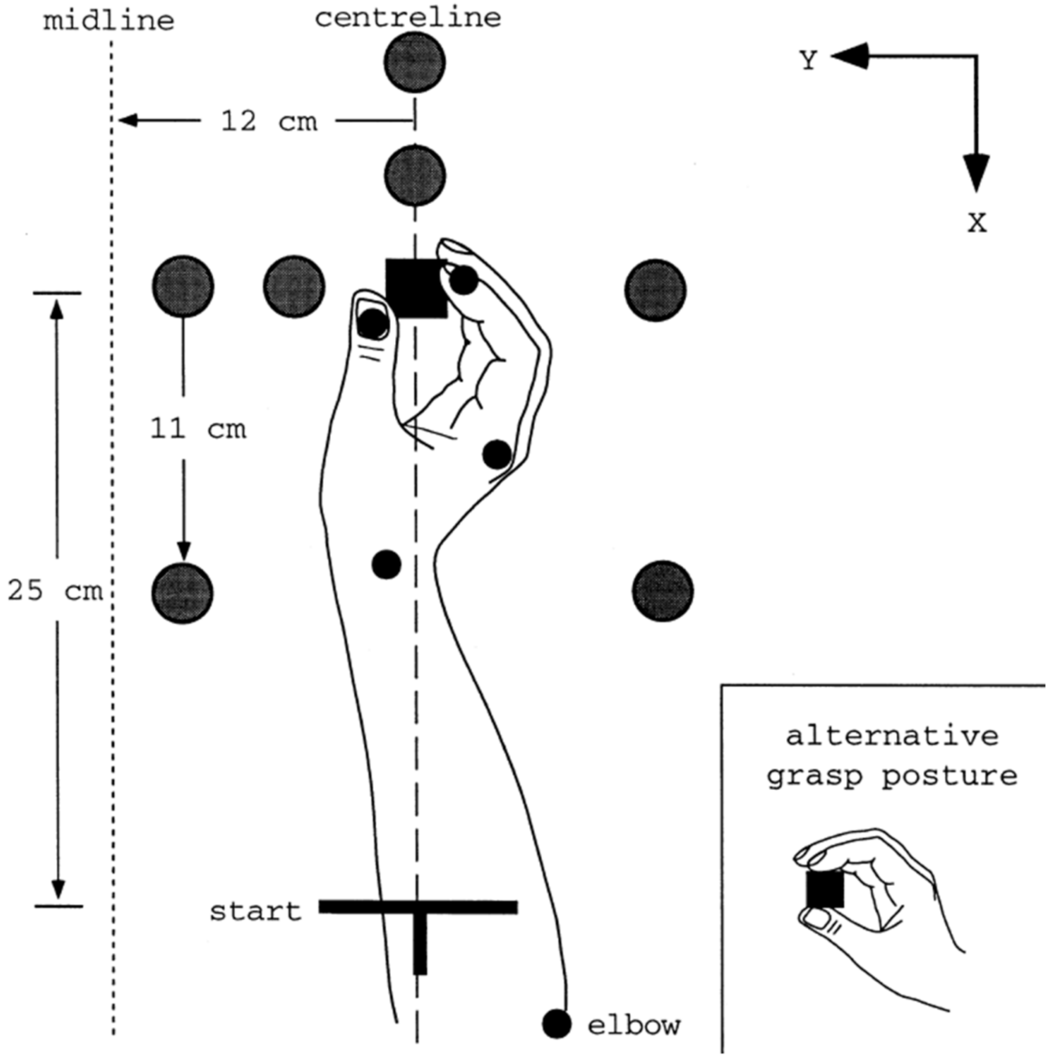

Figure 1.9. Experimental setup for the obstacle avoidance while grasping task (from Tresilian, 1998). Participants reached for and grasped a target object (black square) using one of two wrist postures: with the wrist extended (as shown in main figure, leading to the placement of the thumb to the side of the target) or wrist flexed (as shown in inset, leading to the placement of the thumb to the front of the target). Five IRED markers (small black circles) tracked the motion of the arm and hand. A single obstacle presented on each trial could be placed in one of seven locations (large black circles). This setup was adapted for use in the fMRI experiment described in Chapter 4.

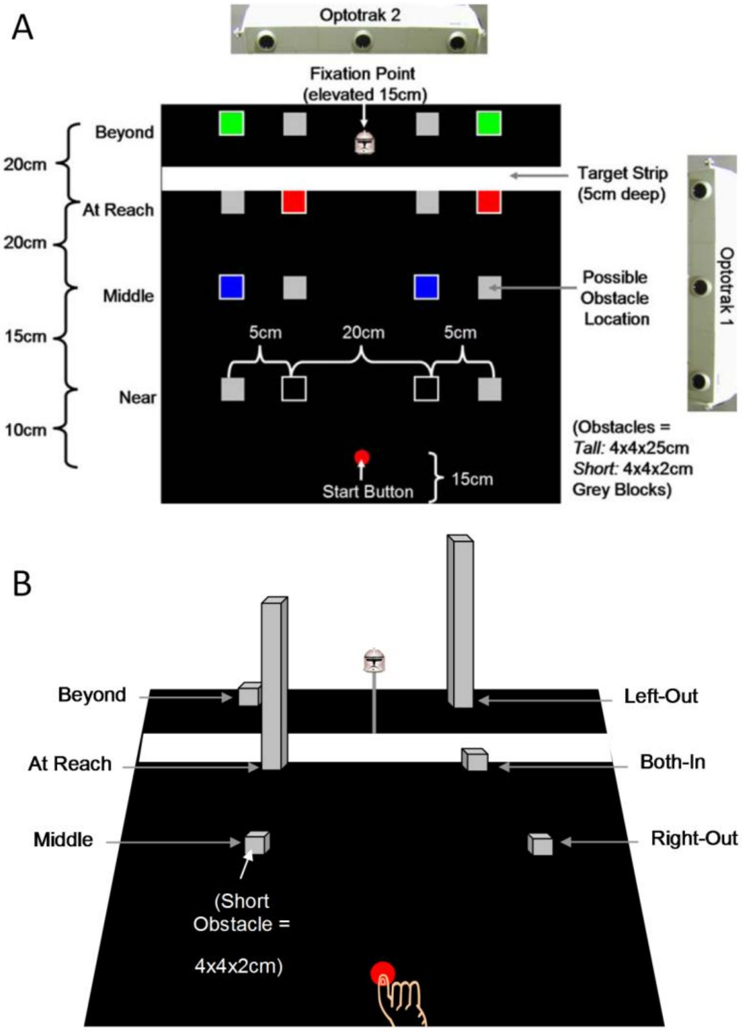

Figure 1.10. Experimental setup from obstacle avoidance while reaching task (from C. S. Chapman & Goodale, 2008). (A) In Experiment 1, participants made reaches from the start button to the target strip while fixating on an elevated fixation point. When obstacles were present, one was to either side of midline at the same depth. All possible obstacle locations are shown (squares), indicating they could appear at 4 depths and in 4 configurations: Depths = Near (10cm), Middle (25cm), At Reach (45cm), Beyond (65cm); Configurations = Both-In (Black), Left-Out (Blue), Both-Out (Green), Right-Out (Red). Movements were recorded using two OPTOTRAK cameras (one right, one in front) at 100hz. (B) In Experiment 2 similar methods (minus the Both-In configuration and Near depths) were used with the addition of the size of the object as a factor. Object pairs could now be Both-tall, Both-short or One-short / One-tall.

1.7.2. Obstacle avoidance in reach-to-point movements

In our own work, as mentioned above, we adapted the obstacle paradigm used in neuropsychological testing (e.g. Schindler et al., 2004) to quantify the effect of two obstacle parameters – namely their position and size (C. S. Chapman & Goodale, 2008). Notably, this paradigm differs from that used by Tresilian (1998) and Mon-Williams et al. (2001) in that we were interested in obstacle effects on reach-to-point rather than reach-to-grasp movements. In the first of two experiments, the layout and configurations were identical to that described by the patient work in section 1.6 with the exception that we now included the depth of the obstacles as a factor in the experiment (see Figure 1.10a). Obstacles (which could still be either absent or in one of the two symmetrical (Both-In or Both-Out) or two asymmetrical (Left-Out or Right-Out) configurations) could now be placed at one of four depths: Near (10 cm from start position), Middle (25 cm from start position) At Reach (45 cm from start position) or Beyond (65 cm from start position). The critical test in this experiment was to see if objects placed past the reach target still functioned as obstacles. The results were clear: any obstacles placed between the start and end positions of the reach significantly interfered with the reach, slowing the resulting movement and causing large deviations in reach trajectory away from the closer of two objects in asymmetrical configurations (see Figure 1.11a). By comparison, objects placed past the reach target had almost no effect on avoidance behaviour (see Figure 1.11a). This result resonates with theoretical frameworks arguing for attentional selection processes that are action specific. After all, the objects placed past the reach target were still clearly salient visual items, yet had almost no impact on the movement.

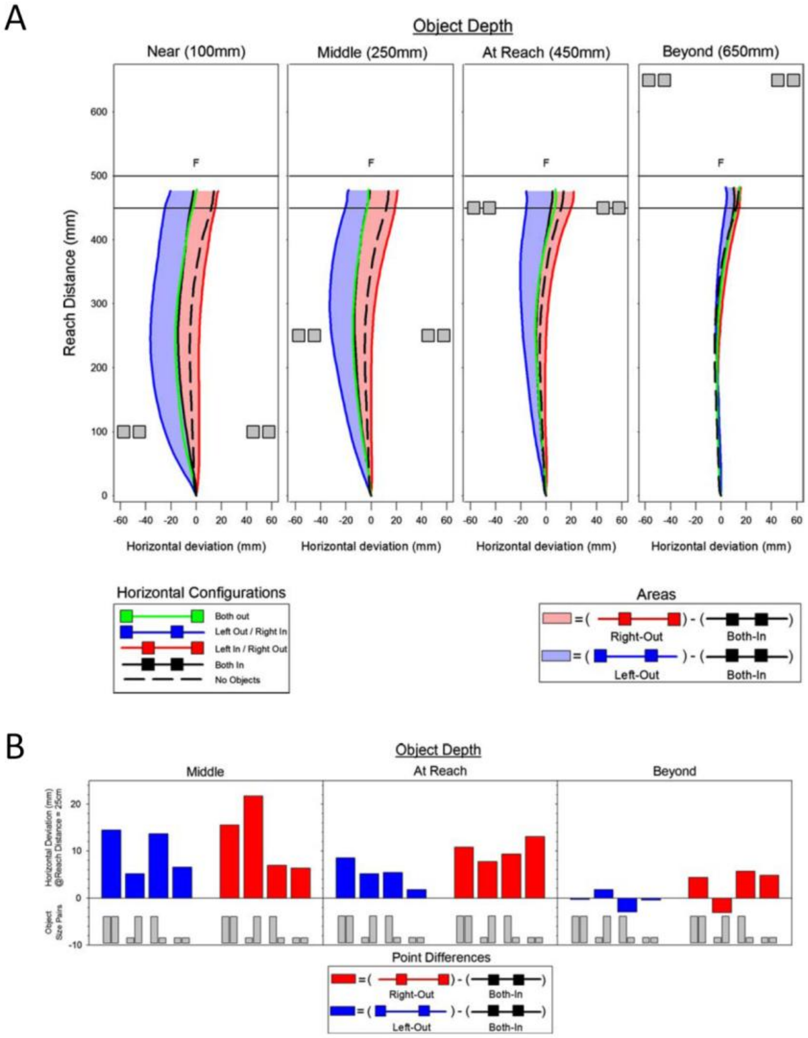

Figure 1.11. Results from Chapman & Goodale (2008) (A) Results from Experiment 1. Overhead view of average reach trajectories. Each separate plot shows configuration trajectories for a different depth. Grey squares = possible object locations, 'F' = fixation location, horizontal lines = start and end of target strip. Configuration trajectories = Both-In (Black), Left-Out (Blue), Right-Out (Red), Both-Out (Green), No Obstacles (Dashed-black). Areas = Difference between Both-In and Right-Out (Light-red), Difference between Both-In and Left-Out (Light-blue) (B) Results from Experiment 2. Mid-reach horizontal deviations caused by an asymmetric obstacle configuration to the right (Right-Out – Both-In, red bars) and left (Left-Out – Both-In, blue bars). Separate bar graphs are shown for each depth. Separate bars in each graph are for each size pair.

In the second experiment, we extended the methods to include the size of the object as a factor (see Figure 1.10b) such that now, one or both obstacles could be short or tall (we removed the Near depth and Both-Out configuration to allow for the increase in trial types). In addition to replicating our depth effect (that is, objects past the reach target had no effect on the reach movement), we now demonstrated an interesting size effect (see Figure 1.11b). All obstacles placed at the same depth as the reach target influenced trajectories similarly regardless of size (that is, reaches deviated away from the closer of two objects in the asymmetrical configurations). By contrast, obstacles placed mid-reach resulted in trajectory deviations that were sensitive both to the position and the size of the obstacles. Specifically, participants continued to avoid the closer of two asymmetrically aligned obstacles, but avoided tall objects more than short objects. These findings are intuitive: obstacles placed at the reach depth, where the hand is required to contact the table surface, should affect movements similarly regardless of height. When placed mid-reach, however, smaller obstacles are easier to avoid with the extra degree of freedom allowed by moving the hand vertically.

1.7.3. Conclusions from obstacle avoidance in healthy individuals

Together with the work of Tresilian (1998) and Mon-Williams et al. (2001) our findings (C. S. Chapman & Goodale, 2008) indicate that the visuomotor system precisely encodes the level of interference of at least two obstacles during reach planning. Moreover obstacles can interfere with both the grasp and reach component of a movement, resulting in hand or digit paths that move away from an obstacle and slower movements. Given the obstacle avoidance impairments of patients with damage to PPC, these behavioural findings in normal participants fit well within the competitive frameworks detailed in section 1.2. Obstacles appear to be encoded in parallel during reach planning, with the control of this process likely residing in the PPC.

1.8. Summary and Motivation of current thesis

As a general aim, I was interested in testing if the encoding of obstacles and the subsequent avoidance behaviour that result from reaches in their presence fits within a theory of competitive visuomotor attention. At the start of this Introduction (section 1.2)

I introduced three critical concepts (suppression of distractors, dynamics of object representations and frontoparietal control) that were distilled from the theoretical frameworks of selective visuomotor attention which shaped my thinking and were motivating factors for the current thesis. I now briefly introduce the three experiments that comprise this thesis, and describe how they were motivated from these concepts.

In Chapter 2 of this thesis, I describe an experiment in which we manipulated whether participants had visual feedback of their hand when avoiding obstacles while reaching (C. S. Chapman & Goodale, 2010b). Manipulating both the availability and predictability of visual feedback is known to influence the degree to which participants use visual information to correct their reaches in flight. While much is known about the influence of obstacles that are encoded prior to movement onset, as Baldauf and Deubel say in their review on attentional landscapes, “Unfortunately, not much is known about the dynamics of the attentional landscapes before and during goal-directed manual movements” (Baldauf & Deubel, 2010, p. 1002). Thus, this experiment was designed to examine how obstacle representations were updated while the hand was in flight. Interestingly, we found no evidence that reaching in the presence of obstacles was altered by the availability or predictability of visual information. In many ways, the experiment described in Chapter 2 was necessary to set the groundwork for the experiment described in Chapter 3, namely to quantify the effects of vision, single obstacles and targeted reaching.

Chapter 3 of this thesis describes a second behavioural study which more directly tested the possibility that obstacle representation could be accessed during movement execution. In this study (C. S. Chapman & Goodale, 2010a) participants made reaches toward an initial target that sometimes jumped to a new target position at reach onset. These so-called double-step paradigms are known to induce automatic corrections of the hand toward the new target location. Interestingly, the neural control of these automatic corrections has been localized to the PPC in the dorsal stream – the same regions thought to control obstacle avoidance. Critically, in our experiment, the corrected movement was sometimes interfered with by the position of a single obstacle. Thus, this study represents a convergence of two critical concepts: the dynamics of obstacle representations and the posterior parietal control of visuomotor tasks. We find clear evidence that obstacle representations can influence the corrected movement (with corrected reaches automatically avoiding obstacles only when they interfere), providing some of the first evidence for the dynamics of visuomotor attention during movement execution. Moreover, I believe that this result provides evidence for a close link between behaviours mediated by the PPC, namely, obstacle avoidance and online corrections.

Finally, in Chapter 4 of this thesis, I outline an fMRI experiment that was conducted to specifically examine how the planning of a grasp movement was affected by the position of an obstacle (C. S. Chapman, Gallivan, Culham et al., 2010). We were specifically interested to see if there was any evidence of the suppression of neural activity associated with the obstacle, given that previous neuroimaging studies have showed a reduced visual response at the location of a to-be-ignored stimulus. We found that an area in the left posterior IPS was more active during the planning of movements that were interfered with by an obstacle, and that this activity occurred in conjunction with an area of the visual cortex that was less active during interference trials. The visual cortical suppression was in exactly the same region that coded for the position of the obstacle prior to movement planning and thus we interpret our results as strong evidence favouring a common mechanism (or perhaps the same process) for the suppression of distractor and obstacle information. In addition to aligning with the conceptualization of an obstacle as a non-target object that gets suppressed, these results align with an account of the PPC being crucial to generating and maintaining visuomotor biases contingent on the flexibly encoded relevance of multiple objects and intended actions.

In sum, these experiments provide a richer understanding of how obstacles are encoded and affect behaviour. Specifically, after initially competing for selective visuomotor attention, the specification of an intended action toward a target marks the obstacle as interfering with the planned reach. The subsequent suppression of visual information at the obstacle location results in reaching behaviour that deviates away from this position (for complete description, see section 5.3). Moreover, since an obstacle affects automatically corrected movements, the partial suppression of an obstacle representation likely occurs any time it is present in the workspace, and can be rapidly updated with the demands of the movement. The ability to plan a reach sensitive to both a target and an obstacle indicates that the visuomotor system is capable of parallel encoding. With parallel encoding comes the difficult problem of target selection (or non-target inhibition). I believe the theoretical solution to this problem is provided by the notion of competitive visuomotor attention and that the results of the current thesis fit well within that framework.

1.9. References

Allport, A. (1987). Selection for Action: Some Behavioral and Neurophysiological Considerations of Attention and Action. In H. Heuer & A. F. Sanders (Eds.), *Perspectives on Perception and Action* (pp. 395 - 419). Hillsdale, New Jersey: Lawrence Erlbaum Associates.

Andujar, J. E., Lajoie, K., & Drew, T. (2010). A contribution of area 5 of the posterior parietal cortex to the planning of visually guided locomotion: limb-specific and limb-independent effects. *J Neurophysiol, 103*(2), 986-1006.

Ansuini, C., Tognin, V., Turella, L., & Castiello, U. (2007). Distractor objects affect fingers' angular distances but not fingers' shaping during grasping. *Exp Brain Res, 178*(2), 194-205.

Baldauf, D., Cui, H., & Andersen, R. A. (2008). The posterior parietal cortex encodes in parallel both goals for double-reach sequences. *J Neurosci, 28*(40), 10081-10089.

Baldauf, D., & Deubel, H. (2008). Properties of attentional selection during the preparation of sequential saccades. *Exp Brain Res, 184*(3), 411-425.

Baldauf, D., & Deubel, H. (2009). Attentional selection of multiple goal positions before rapid hand movement sequences: an event-related potential study. *J Cogn Neurosci, 21*(1), 18-29.

Baldauf, D., & Deubel, H. (2010). Attentional landscapes in reaching and grasping. *Vision Res, 50*(11), 999-1013.

Baldauf, D., Wolf, M., & Deubel, H. (2006). Deployment of visual attention before sequences of goal-directed hand movements. *Vision Res, 46*(26), 4355-4374.

Beck, D. M., & Kastner, S. (2009). Top-down and bottom-up mechanisms in biasing competition in the human brain. *Vision Res, 49*(10), 1154-1165.

Biegstraaten, M., Smeets, J. B., & Brenner, E. (2003). The influence of obstacles on the speed of grasping. *Exp Brain Res, 149*(4), 530-534.

Bonfiglioli, C., & Castiello, U. (1998). Dissociation of covert and overt spatial attention during prehension movements: selective interference effects. *Percept Psychophys, 60*(8), 1426-1440.

Bressler, S. L., Tang, W., Sylvester, C. M., Shulman, G. L., & Corbetta, M. (2008). Top-down control of human visual cortex by frontal and parietal cortex in anticipatory visual spatial attention. *J Neurosci, 28*(40), 10056-10061.

Castiello, U. (1996). Grasping a fruit: selection for action. *J Exp Psychol Hum Percept Perform, 22*(3), 582-603.

Castiello, U. (1998). Attentional coding for three-dimensional objects and two-dimensional shapes. Differential interference effects. *Exp Brain Res, 123*(3), 289-297.

Castiello, U. (1999). Mechanisms of selection for the control of hand action. *Trends Cogn Sci, 3*(7), 264-271.

Castiello, U. (2001). The effects of abrupt onset of 2-D and 3-D distractors on prehension movements. *Percept Psychophys, 63*(6), 1014-1025.

Castiello, U., Badcock, D. R., & Bennett, K. M. (1999). Sudden and gradual presentation of distractor objects: differential interference effects. *Exp Brain Res, 128*(4), 550-556.

Chang, S. W., & Abrams, R. A. (2004). Hand movements deviate toward distracters in the absence of response competition. *J Gen Psychol, 131*(4), 328-344.

Chapman, C. S., Gallivan, J. P., Culham, J. C., & Goodale, M. A. (2010). Mental Blocks: fMRI reveals top-down modulation of early visual cortex when obstacles interfere with grasp planning. *Neuropsychologia*.

Chapman, C. S., Gallivan, J. P., Wood, D. K., Milne, J. L., Culham, J. C., & Goodale, M. A. (2010a). Reaching for the unknown: Multiple target encoding and real-time decision-making in a rapid reach task. *Cognition, 116*(2), 168-176.

Chapman, C. S., Gallivan, J. P., Wood, D. K., Milne, J. L., Culham, J. C., & Goodale, M. A. (2010b). Short term motor plasticity revealed in a visuomotor decision-making task. *Behav Brain Res*.

Chapman, C. S., & Goodale, M. A. (2008). Missing in action: the effect of obstacle position and size on avoidance while reaching. *Exp Brain Res, 191*(1), 83-97.

Chapman, C. S., & Goodale, M. A. (2010a). Obstacle avoidance during online corrections. *J Vis, 10*(11), 1-14.

Chapman, C. S., & Goodale, M. A. (2010b). Seeing all the obstacles in your way: the effect of visual feedback and visual feedback schedule on obstacle avoidance while reaching. *Exp Brain Res, 202*(2), 363-375.

Chapman, H., Pierno, A. C., Cunnington, R., Gavrilescu, M., Egan, G., & Castiello, U. (2007). The neural basis of selection-for-action. *Neurosci Lett, 417*(2), 171-175.

Chelazzi, L., Duncan, J., Miller, E. K., & Desimone, R. (1998). Responses of neurons in inferior temporal cortex during memory-guided visual search. *J Neurophysiol, 80*(6), 2918-2940.

Chelazzi, L., Miller, E. K., Duncan, J., & Desimone, R. (1993). A neural basis for visual search in inferior temporal cortex. *Nature, 363*(6427), 345-347.

Cisek, P. (2007). Cortical mechanisms of action selection: the affordance competition hypothesis. *Philos Trans R Soc Lond B Biol Sci, 362*(1485), 1585-1599.

Cisek, P., & Kalaska, J. F. (2002). Simultaneous encoding of multiple potential reach directions in dorsal premotor cortex. *J Neurophysiol, 87*(2), 1149-1154.

Cisek, P., & Kalaska, J. F. (2005). Neural correlates of reaching decisions in dorsal premotor cortex: specification of multiple direction choices and final selection of action. *Neuron, 45*(5), 801-814.

Cisek, P., & Kalaska, J. F. (2010). Neural Mechanisms for Interacting with a World Full of Action Choices. *Annu Rev Neurosci*.

Connolly, J. D., Goodale, M. A., Desouza, J. F., Menon, R. S., & Vilis, T. (2000). A comparison of frontoparietal fMRI activation during anti-saccades and anti-pointing. *J Neurophysiol, 84*(3), 1645-1655.

Connolly, J. D., Goodale, M. A., Menon, R. S., & Munoz, D. P. (2002). Human fMRI evidence for the neural correlates of preparatory set. *Nat Neurosci, 5*(12), 1345-1352.

Corbetta, M., Patel, G., & Shulman, G. L. (2008). The reorienting system of the human brain: from environment to theory of mind. *Neuron, 58*(3), 306-324.

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci, 3*(3), 201-215.

Cowey, A. (2010). The blindsight saga. *Exp Brain Res, 200*(1), 3-24.

Curtis, C. E., Cole, M. W., Rao, V. Y., & D'Esposito, M. (2005). Canceling planned action: an FMRI study of countermanding saccades. *Cereb Cortex, 15*(9), 1281-1289.

Dean, J., & Bruwer, M. (1994). Control of human arm movements in two dimensions: paths and joint control in avoiding simple linear obstacles. *Exp Brain Res, 97*(3), 497-514.

Desimone, R. (1998). Visual attention mediated by biased competition in extrastriate visual cortex. *Philos Trans R Soc Lond B Biol Sci, 353*(1373), 1245-1255.

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annu Rev Neurosci, 18*, 193-222.

Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: evidence for a common attentional mechanism. *Vision Res, 36*(12), 1827-1837.

Deubel, H., & Schneider, W. X. (2004). Attentional selection in sequential manual movements, movements around an obstacle, and in grasping. In G. W. Humphreys & M. J. Riddoch (Eds.), *Attention in action : advances from cognitive neuroscience* (pp. 69-91). Hove, East Sussex: Psychology Press.

Duebel, H., Schneider, W. X., & Paprotta, I. (1998). Selective Dorsal and Ventral Processing: Evidence for a Common Attentional Mechanism in Reaching and Perception. *Visual Cognition, 5*(1), 81-107.

Duncan, J. (1996). Cooperating Brain Systems in Selective Perception and Action. In T. Inui & J. L. McClelland (Eds.), *Attention and Performance XVI* (pp. 549-578). Boston: The MIT Press.

Duncan, J. (1998). Converging levels of analysis in the cognitive neuroscience of visual attention. *Philos Trans R Soc Lond B Biol Sci, 353*(1373), 1307-1317.

Duncan, J. (2006). EPS Mid-Career Award 2004: brain mechanisms of attention. *Q J Exp Psychol (Colchester), 59*(1), 2-27.

Fink, P. W., Foo, P. S., & Warren, W. H. (2007). Obstacle avoidance during walking in real and virtual environments. *ACM Transactions of Applied Perception, 4*(1).

Fischer, M. H., & Adam, J. J. (2001). Distractor effects on pointing: the role of spatial layout. *Exp Brain Res, 136*(4), 507-513.

Gallivan, J. P., Cavina-Pratesi, C., & Culham, J. C. (2009). Is that within reach? fMRI reveals that the human superior parieto-occipital cortex encodes objects reachable by the hand. *J Neurosci, 29*(14), 4381-4391.

Gallivan, J. P., Chapman, C. S., Wood, D. K., Milne, J. L., Ansari, D., Culham, J. C., et al. (2010). One to four, and nothing more: Non-conscious parallel object individuation in action. *Psychol Sci*.

Gangitano, M., Daprati, E., & Gentilucci, M. (1998). Visual distractors differentially interfere with the reaching and grasping components of prehension movements. *Exp Brain Res, 122*(4), 441-452.

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends Neurosci, 15*(1), 20-25.

Goodale, M. A., & Milner, A. D. (2004). *Sight Unseen*. Oxford: Oxford University Press.

Goodale, M. A., Milner, A. D., Jakobson, L. S., & Carey, D. P. (1991). A neurological dissociation between perceiving objects and grasping them. *Nature, 349*(6305), 154-156.

Goodale, M. A., & Westwood, D. A. (2004). An evolving view of duplex vision: separate but interacting cortical pathways for perception and action. *Curr Opin Neurobiol, 14*(2), 203-211.

Grahn, J. A., & Owen, A. M. (2006). Memory: obstacle avoidance without visual cues. *Curr Biol, 16*(7), R247-249.

Haaxma, R., & Kuypers, H. G. (1975). Intrahemispheric cortical connexions and visual guidance of hand and finger movements in the rhusus monkey. *Brain, 98*(2), 239-260.

Hamilton, A. F., & Wolpert, D. M. (2002). Controlling the statistics of action: obstacle avoidance. *J Neurophysiol, 87*(5), 2434-2440.

Houghton, G., & Tipper, S. P. (1999). Attention and the control of action: An investigation of the effects of selection on population coding of hand and eye movement. In D. Heinke, G. W. Humphreys & A. Olson (Eds.), *Connectionist Modles in Cognitive Neuroscience*. London: Springer-Verlag.

Howard, L. A., & Tipper, S. P. (1997). Hand deviations away from visual cues: indirect evidence for inhibition. *Exp Brain Res, 113*(1), 144-152.

Ipata, A. E., Gee, A. L., Gottlieb, J., Bisley, J. W., & Goldberg, M. E. (2006). LIP responses to a popout stimulus are reduced if it is overtly ignored. *Nat Neurosci, 9*(8), 1071-1076.

Jackson, S. R., Jackson, G. M., & Rosicky, J. (1995). Are non-relevant objects represented in working memory? The effect of non-target objects on reach and grasp kinematics. *Exp Brain Res, 102*(3), 519-530.

James, T. W., Culham, J., Humphrey, G. K., Milner, A. D., & Goodale, M. A. (2003). Ventral occipital lesions impair object recognition but not object-directed grasping: an fMRI study. *Brain, 126*(Pt 11), 2463-2475.

Jax, S. A., & Rosenbaum, D. A. (2007). Hand path priming in manual obstacle avoidance: evidence that the dorsal stream does not only control visually guided actions in real time. *J Exp Psychol Hum Percept Perform, 33*(2), 425-441.

Kaas, J. H., & Lyon, D. C. (2007). Pulvinar contributions to the dorsal and ventral streams of visual processing in primates. *Brain Res Rev, 55*(2), 285-296.

Kastner, S., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1998). Mechanisms of directed attention in the human extrastriate cortex as revealed by functional MRI. *Science, 282*(5386), 108-111.

Kastner, S., Pinsk, M. A., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1999). Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron, 22*(4), 751-761.

Kastner, S., & Ungerleider, L. G. (2000). Mechanisms of visual attention in the human cortex. *Annu Rev Neurosci, 23*, 315-341.

Keulen, R. F., Adam, J. J., Fischer, M. H., Kuipers, H., & Jolles, J. (2002). Selective reaching: evidence for multiple frames of reference. *J Exp Psychol Hum Percept Perform, 28*(3), 515-526.

Keulen, R. F., Adam, J. J., Fischer, M. H., Kuipers, H., & Jolles, J. (2003). Distractor interference in selective reaching: dissociating distance and grouping effects. *J Mot Behav, 35*(2), 119-126.

Kritikos, A., Bennett, K. M., Dunai, J., & Castiello, U. (2000). Interference from distractors in reach-to-grasp movements. *Q J Exp Psychol A, 53*(1), 131-151.

Kritikos, A., Dunai, J., & Castiello, U. (2001). Modulation of reach-to-grasp parameters: semantic category, volumetric properties and distractor interference? *Exp Brain Res, 138*(1), 54-61.

Kurniawan, I. T., Seymour, B., Vlaev, I., Trommershauser, J., Dolan, R. J., & Chater, N. (2010). Pain relativity in motor control. *Psychol Sci, 21*(6), 840-847.

Lajoie, K., Andujar, J. E., Pearson, K., & Drew, T. (2010). Neurons in area 5 of the posterior parietal cortex in the cat contribute to interlimb coordination during visually guided locomotion: a role in working memory. *J Neurophysiol, 103*(4), 2234-2254.

Lajoie, K., & Drew, T. (2007). Lesions of area 5 of the posterior parietal cortex in the cat produce errors in the accuracy of paw placement during visually guided locomotion. *J Neurophysiol, 97*(3), 2339-2354.

Liu, D., & Todorov, E. (2007). Evidence for the flexible sensorimotor strategies predicted by optimal feedback control. *J Neurosci, 27*(35), 9354-9368.

Lyon, D. C., Nassi, J. J., & Callaway, E. M. (2010). A disynaptic relay from superior colliculus to dorsal stream visual cortex in macaque monkey. *Neuron, 65*(2), 270-279.

Marigold, D. S., Weerdesteyn, V., Patla, A. E., & Duysens, J. (2007). Keep looking ahead? Re-direction of visual fixation does not always occur during an unpredictable obstacle avoidance task. *Exp Brain Res, 176*(1), 32-42.

McIntosh, R. D., McClements, K. I., Dijkerman, H. C., Birchall, D., & Milner, A. D. (2004). Preserved obstacle avoidance during reaching in patients with left visual neglect. *Neuropsychologia, 42*(8), 1107-1117.

McIntosh, R. D., McClements, K. I., Schindler, I., Cassidy, T. P., Birchall, D., & Milner, A. D. (2004). Avoidance of obstacles in the absence of visual awareness. *Proc Biol Sci, 271*(1534), 15-20.

McMains, S. A., Fehd, H. M., Emmanouil, T. A., & Kastner, S. (2007). Mechanisms of feature- and space-based attention: response modulation and baseline increases. *J Neurophysiol, 98*(4), 2110-2121.

McVea, D. A., & Pearson, K. G. (2006). Long-lasting memories of obstacles guide leg movements in the walking cat. *J Neurosci, 26*(4), 1175-1178.

McVea, D. A., & Pearson, K. G. (2007). Stepping of the forelegs over obstacles establishes long-lasting memories in cats. *Curr Biol, 17*(16), R621-623.

McVea, D. A., Taylor, A. J., & Pearson, K. G. (2009). Long-lasting working memories of obstacles established by foreleg stepping in walking cats require area 5 of the posterior parietal cortex. *J Neurosci, 29*(29), 9396-9404.

Meegan, D. V., & Tipper, S. P. (1998). Reaching into Cluttered Visual Environments: Spatial and Temporal Infuences of Distracting Objects. *Q J Exp Psychol A, 51a*(2), 225-249.

Meegan, D. V., & Tipper, S. P. (1999). Visual Search and Target-Directed Action. *J Exp Psychol Hum Percept Perform, 25*(5), 1347-1362.

Mevorach, C., Hodsoll, J., Allen, H., Shalev, L., & Humphreys, G. (2010). Ignoring the elephant in the room: a neural circuit to downregulate salience. *J Neurosci, 30*(17), 6072-6079.

Mevorach, C., Humphreys, G. W., & Shalev, L. (2005). Attending to local form while ignoring global aspects depends on handedness: evidence from TMS. *Nat Neurosci, 8*(3), 276-277.

Mevorach, C., Humphreys, G. W., & Shalev, L. (2006). Opposite biases in salience-based selection for the left and right posterior parietal cortex. *Nat Neurosci, 9*(6), 740-742.

Mevorach, C., Humphreys, G. W., & Shalev, L. (2009). Reflexive and preparatory selection and suppression of salient information in the right and left posterior parietal cortex. *J Cogn Neurosci, 21*(6), 1204-1214.

Mevorach, C., Shalev, L., Allen, H. A., & Humphreys, G. W. (2009). The left intraparietal sulcus modulates the selection of low salient stimuli. *J Cogn Neurosci, 21*(2), 303-315.

Milner, A. D., & Goodale, M. A. (1995). *The Visual Brain in Action*. Oxford: Oxford University Press.

Milner, A. D., & McIntosh, R. D. (2004). Reaching between obstacles in spatial neglect and visual extinction. *Prog Brain Res, 144*, 213-226.

Milner, A. D., Paulignan, Y., Dijkerman, H. C., Michel, F., & Jeannerod, M. (1999). A paradoxical improvement of misreaching in optic ataxia: new evidence for two separate neural systems for visual localization. *Proc Biol Sci, 266*(1434), 2225-2229.

Milner, A. D., Perrett, D. I., Johnston, R. S., Benson, P. J., Jordan, T. R., Heeley, D. W., et al. (1991). Perception and action in 'visual form agnosia'. *Brain, 114 (Pt 1B)*, 405-428.

Moll, L., & Kuypers, H. G. (1977). Premotor cortical ablations in monkeys: contralateral changes in visually guided reaching behavior. *Science, 198*(4314), 317-319.

Mon-Williams, M., & McIntosh, R. D. (2000). A test between two hypotheses and a possible third way for the control of prehension. *Exp Brain Res, 134*(2), 268-273.

Mon-Williams, M., Tresilian, J. R., Coppard, V. L., & Carson, R. G. (2001). The effect of obstacle position on reach-to-grasp movements. *Exp Brain Res, 137*(3-4), 497-501.

O'Craven, K. M., Downing, P. E., & Kanwisher, N. (1999). fMRI evidence for objects as the units of attentional selection. *Nature, 401*(6753), 584-587.

Patla, A. E., & Goodale, M. A. (1996). Obstacle avoidance during locomotion is unaffected in a patient with visual form agnosia. *Neuroreport, 8*(1), 165-168.

Perenin, M. T., & Vighetto, A. (1988). Optic ataxia: a specific disruption in visuomotor mechanisms. I. Different aspects of the deficit in reaching for objects. *Brain, 111 (Pt 3)*, 643-674.

Pessoa, L., Kastner, S., & Ungerleider, L. G. (2003). Neuroimaging studies of attention: from modulation of sensory processing to top-down control. *J Neurosci, 23*(10), 3990-3998.

Rice, N. J., Edwards, M. G., Schindler, I., Punt, T. D., McIntosh, R. D., Humphreys, G. W., et al. (2008). Delay abolishes the obstacle avoidance deficit in unilateral optic ataxia. *Neuropsychologia, 46*(5), 1549-1557.

Rice, N. J., McIntosh, R. D., Schindler, I., Mon-Williams, M., Demonet, J. F., & Milner, A. D. (2006). Intact automatic avoidance of obstacles in patients with visual form agnosia. *Exp Brain Res, 174*(1), 176-188.

Riddoch, M. J., Chechlacz, M., Mevorach, C., Mavritsaki, E., Allen, H., & Humphreys, G. W. (2010). The neural mechanisms of visual selection: the view from neuropsychology. *Ann N Y Acad Sci, 1191*(1), 156-181.

Rosenbaum, D. A., Meulenbroek, R. G., Vaughan, J., & Jansen, C. (1999). Coordination of reaching and grasping by capitalizing on obstacle avoidance and other constraints. *Exp Brain Res, 128*(1-2), 92-100.

Rossetti, Y., Revol, P., McIntosh, R., Pisella, L., Rode, G., Danckert, J., et al. (2005). Visually guided reaching: bilateral posterior parietal lesions cause a switch from fast visuomotor to slow cognitive control. *Neuropsychologia, 43*(2), 162-177.

Rubia, K., Russell, T., Overmeyer, S., Brammer, M. J., Bullmore, E. T., Sharma, T., et al. (2001). Mapping motor inhibition: conjunctive brain activations across different versions of go/no-go and stop tasks. *Neuroimage, 13*(2), 250-261.

Sabes, P. N., & Jordan, M. I. (1997). Obstacle avoidance and a perturbation sensitivity model for motor planning. *J Neurosci, 17*(18), 7119-7128.

Sabes, P. N., Jordan, M. I., & Wolpert, D. M. (1998). The role of inertial sensitivity in motor planning. *J Neurosci, 18*(15), 5948-5957.

Saling, M., Alberts, J., Stelmach, G. E., & Bloedel, J. R. (1998). Reach-to-grasp movements during obstacle avoidance. *Exp Brain Res, 118*(2), 251-258.

Schiegg, A., Deubel, H., & Schneider, W. X. (2003). Attentional selection during preparation of prehension movements. *Visual Cognition, 10*(4), 409-431.

Schindler, I., Rice, N. J., McIntosh, R. D., Rossetti, Y., Vighetto, A., & Milner, A. D. (2004). Automatic avoidance of obstacles is a dorsal stream function: evidence from optic ataxia. *Nat Neurosci, 7*(7), 779-784.

Schneider, W. X., & Deubel, H. (2002). Selection-for-perception and selection-for-spatial-motor-action are coupled by visual attention: A review of recent findings and new evidence from stimulus-driven saccade control. In B. Hommel & W. Prinz (Eds.), *Attention and Performance XIX* (pp. 609-627). Oxford: Oxford University Press.

Serences, J. T., & Yantis, S. (2007). Spatially selective representations of voluntary and stimulus-driven attentional priority in human occipital, parietal, and frontal cortex. *Cereb Cortex, 17*(2), 284-293.

Serences, J. T., Yantis, S., Culberson, A., & Awh, E. (2004). Preparatory activity in visual cortex indexes distractor suppression during covert spatial orienting. *J Neurophysiol, 92*(6), 3538-3545.

Silver, M. A., Ress, D., & Heeger, D. J. (2007). Neural correlates of sustained spatial attention in human early visual cortex. *J Neurophysiol, 97*(1), 229-237.

Song, J. H., & Nakayama, K. (2006). Role of focal attention on latencies and trajectories of visually guided manual pointing. *J Vis, 6*(9), 982-995.

Song, J. H., & Nakayama, K. (2009). Hidden cognitive states revealed in choice reaching tasks. *Trends Cogn Sci, 13*(8), 360-366.

Striemer, C. L., Chapman, C. S., & Goodale, M. A. (2009). "Real-time" obstacle avoidance in the absence of primary visual cortex. *Proc Natl Acad Sci U S A, 106*(37), 15996-16001.

Sylvester, C. M., Jack, A. I., Corbetta, M., & Shulman, G. L. (2008). Anticipatory suppression of nonattended locations in visual cortex marks target location and predicts perception. *J Neurosci, 28*(26), 6549-6556.

Sylvester, C. M., Shulman, G. L., Jack, A. I., & Corbetta, M. (2007). Asymmetry of anticipatory activity in visual cortex predicts the locus of attention and perception. *J Neurosci, 27*(52), 14424-14433.

Tipper, S. P., Howard, L. A., & Houghton, G. (1998). Action-based mechanisms of attention. *Philos Trans R Soc Lond B Biol Sci, 353*(1373), 1385-1393.

Tipper, S. P., Howard, L. A., & Houghton, G. (2000). Attention and Performance XVIII: Behavioral Consequences of Selection from Neural Population Codes. In S. Monsell & J. Driver (Eds.), *Control of Cognitive Processes*. Cambridge: The MIT Press.

Tipper, S. P., Howard, L. A., & Jackson, S. R. (1997). Selective Reaching to Grasp: Evidence for Distractor Interference Effects *Visual Cognition, 4*(1), 1-38.

Tipper, S. P., Lortie, C., & Baylis, G. C. (1992). Selective reaching: evidence for action-centered attention. *J Exp Psychol Hum Percept Perform, 18*(4), 891-905.

Tipper, S. P., Meegan, D. V., & Howard, L. A. (2002). Action-centered negative priming: Evidence for reactive inhibition. *Visual Cognition, 9*(4), 591-614.

Torres, E., & Andersen, R. (2006). Space-time separation during obstacle-avoidance learning in monkeys. *J Neurophysiol, 96*(5), 2613-2632.

Tresilian, J. R. (1998). Attention in action or obstruction of movement? A kinematic analysis of avoidance behavior in prehension. *Exp Brain Res, 120*(3), 352-368.

Tresilian, J. R. (1999). Selective attention in reaching: when is an object not a distractor? *Trends Cogn Sci, 3*(11), 407-408.

Tresilian, J. R., Mon-Williams, M., Coppard, V. L., & Carson, R. G. (2005). Developmental changes in the response to obstacles during prehension. *J Mot Behav, 37*(2), 103-110.

Trommershauser, J., Landy, M. S., & Maloney, L. T. (2006). Humans rapidly estimate expected gain in movement planning. *Psychol Sci, 17*(11), 981-988.

Trommershauser, J., Maloney, L. T., & Landy, M. S. (2003a). Statistical decision theory and the selection of rapid, goal-directed movements. *J Opt Soc Am A Opt Image Sci Vis, 20*(7), 1419-1433.

Trommershauser, J., Maloney, L. T., & Landy, M. S. (2003b). Statistical decision theory and trade-offs in the control of motor response. *Spat Vis, 16*(3-4), 255-275.

Trommershauser, J., Mattis, J., Maloney, L. T., & Landy, M. S. (2006). Limits to human movement planning with delayed and unpredictable onset of needed information. *Exp Brain Res, 175*(2), 276-284.

Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale & R. J. W. Mansfield (Eds.), *Analysis of Visual Behavior* (pp. 549−586). Cambridge, MA: MIT Press, .

Vaughan, J., Rosenbaum, D. A., & Meulenbroek, R. G. (2001). Planning reaching and grasping movements: the problem of obstacle avoidance. *Motor Control, 5*(2), 116-135.

Weir, P. L., Weeks, D. J., Welsh, T. N., Elliott, D., Chua, R., Roy, E. A., et al. (2003). Influence of terminal action requirements on action-centered distractor effects. *Exp Brain Res, 149*(2), 207-213.

Welsh, T. N., & Elliot, D. (2005). The effects of response priming on the planning and execution of goal-directed movements in the presence of a distracting stimulus. *Acta Psychologica, 119*, 123-142.

Welsh, T. N., & Elliott, D. (2004). Movement trajectories in the presence of a distracting stimulus: evidence for a response activation model of selective reaching. *Q J Exp Psychol A, 57*(6), 1031-1057.

Welsh, T. N., Elliott, D., & Weeks, D. J. (1999). Hand deviations toward distractors. Evidence for response competition. *Exp Brain Res, 127*(2), 207-212.

Welsh, T. N., & Zbinden, M. (2009). Fitts's law in a selective reaching task: the proximity-to-hand effect of action-centered attention revisited. *Motor Control, 13*(1), 100-112.

Chapter 2

2. Seeing All the Obstacles in Your Way: The effect of visual feedback and visual feedback schedule on obstacle avoidance while reaching[1]

2.1. Introduction

Humans are adept at reaching to targets in cluttered environments. This suggests the existence of a sophisticated goal-directed reaching system that can rapidly select targets and plan trajectories toward them while avoiding potential obstacles. Experiments examining reaching and grasping movements in the presence of non-target objects have indeed shown that obstacles, distracting stimuli and other potential goal objects all effect the kinematics of the performed action (e.g. Castiello, 1996; Deubel & Schneider, 2004; Jackson, Jackson, & Rosicky, 1995; Jax & Rosenbaum, 2007; Mon-Williams, Tresilian, Coppard, & Carson, 2001; Tipper, Howard, & Jackson, 1997; Tresilian, 1998; van der Wel, Fleckenstein, Jax, & Rosenbaum, 2007). Those studies specifically quantifying obstacle avoidance behaviour have shown that objects interfering with the transport or grip phase of a movement result in automatic deviations away from the obstacle and a slowing of the reach (Chapman & Goodale, 2008; Mon-Williams et al., 2001; Tresilian, 1998). Our own work (Chapman & Goodale, 2008) exploring this behaviour was motivated by the finding from the patient literature that the dorsal visual stream plays a key role in obstacle avoidance. These patient studies demonstrate both preserved avoidance in patients with preserved dorsal stream function (i.e. neglect (McIntosh, McClements, Dijkerman, Birchall, & Milner, 2004; Milner & McIntosh, 2004), extinction (McIntosh, McClements, Schindler et al., 2004; Milner & McIntosh, 2004) and visual form agnosia (Rice et al., 2006)), and impaired avoidance in patients with damage to the dorsal stream (i.e. optic ataxia (Rice et al., 2008; Schindler et al., 2004)). In

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extending the patient work, we adopted a similar paradigm, a reaching task where participants made reaches to a target strip (i.e. specified in depth but not direction) without visual feedback of the hand. Removing visual feedback at movement onset is an important aspect of the studies with patients as it ensures that one can isolate deficits in movement planning as opposed to deficits in online control. In the real world, however, vision of your hand is rarely occluded at the precise moment you begin to move; nor do you typically perform reaches to a target whose location is not specified. It is possible that denying participants' vision during the reaching movement affected their avoidance behaviour. For example, knowing that they would not be able to see their hand, the obstacle or the goal during the reach, participants may have reacted cautiously and given more room for error in their reach, leading to increased avoidance. To test this possibility, the current study examines obstacle avoidance behaviour during reaches to a specific target location when vision of the hand is available in flight (V) with the same reaches when vision is not available (NV).

However, the possible effects of visual feedback during obstacle avoidance may not be as simple as an effect of allowing or removing vision. Instead, effects could be driven by the *expectation* of having or not having vision during an upcoming reaching. Indeed, when manipulating visual feedback in reach tasks, it has been shown that not only are there differences between V and NV trials (Elliott, Binsted, & Heath, 1999; Elliott, Carson, Goodman, & Chua, 1991; Elliott, Chua, Pollock, & Lyons, 1995; Heath, 2005; Heath, Westwood, & Binsted, 2004), but also that the order of the V and NV trials within an experimental block plays an important role (Chua & Elliott, 1993; Elliott & Allard, 1985; Elliott, Helsen, & Chua, 2001; Heath, Rival, & Neely, 2006; Jakobson & Goodale, 1991; Khan, Elliott, Coull, Chua, & Lyons, 2002; Neely, Tessmer, Binsted, & Heath, 2008; Whitwell & Goodale, 2009; Whitwell, Lambert, & Goodale, 2008; Zelaznik, Hawkins, & Kisselburgh, 1983). It should be noted that the majority of the aforementioned studies manipulated vision by occluding both the target and the limb while two occluded only the limb (Chua & Elliott, 1993; Elliott et al., 1995). One study provided a direct test of the effects of target and limb occlusion separately and together (Heath, 2005), and demonstrated that occlusion of both the limb and target yields the most robust NV versus V differences. In one early study investigating the role of feedback and feedback schedule in a simple reach-to-point task, researchers showed that lateral errors were larger for NV trials than V trials, and importantly, that the difference in error between NV and V trials was larger when trials were blocked as opposed to randomized (Zelaznik et al., 1983). That the blocked schedule, where all the trials of one type of feedback are received consecutively, shows larger differences than a randomized schedule, where the visual feedback on any given trial is randomly determined, has at least two possible explanations. It could be the case that the unpredictability of feedback associated with the randomized schedule caused participants to adopt a different strategy from the one they used in the blocked schedules where feedback was perfectly predictable. In other words, in the blocked trials, they could use their knowledge of what was going to happen next to plan the action on the upcoming trial. Alternatively, it could be the case that the repetitive nature of the blocked trials causes the motor system to simply repeat what it did on the last trial(s) and to use knowledge about the nature of the schedule to predict what will happen next. To test between these alternatives, Zelaznik and colleagues (1983) ran an experiment where the availability of visual feedback alternated from trial to trial. With an alternating schedule, the predictability of the type of feedback is high, just as high as it is in the blocked trials. But in terms of making use of trial to trial consistency, the alternating schedule is no different from the randomized schedule. In fact, given that there are likely to be small runs of consecutive trials with the same feedback type in the random schedule, the alternating schedule has minimal consistency. Therefore, if reaching behaviour with the alternating schedule resembles reaching behaviour with the blocked schedules, and has large NV versus V differences, then this would suggest that participants can use their knowledge about the nature of the schedule to predict what to do on an upcoming trial. However, if the alternating schedule is more like the random schedule with small differences between NV and V, then this would suggest that the motor system controlling reaching in these situations is simply relying on trial history. Under the alternating schedule, Zelaznik et al. found significant differences in errors between NV and V trials. Unfortunately, as the alternating condition was run in a separate experiment in this study, the magnitude of this difference between conditions could not be compared to the blocked or random schedules. Neverthless, the authors concluded that accuracy on V trials is superior to NV trials and that this difference is independent of the type of feedback that was experienced on earlier trials.

Since the Zelaznik et al. study (1983), there have been several studies targeting the differences in reaching and grasping kinematics between blocked and random visual feedback schedules. In reach to grasp studies (Fukui & Inui, 2006; Heath et al., 2006; Jakobson & Goodale, 1991; Whitwell & Goodale, 2009; Whitwell et al., 2008), the difference between V and NV trials in blocked schedules is characterized by a larger opening of the hand and more time spent in the later phase of the movement for NV as compared to V trials, presumably reflecting the need to build in a margin of error when visual feedback is not available. In one grasping study, when trials were presented with a random feedback schedule (Jakobson & Goodale, 1991), the hand now opened wider on both V and NV trials as compared to the blocked-V trials. These results suggest that when performing grasping during a random feedback schedule, the uncertainty causes V trials to be treated like NV trials. More recent studies both support (Heath et al., 2006) and challenge (Fukui & Inui, 2006; Whitwell & Goodale, 2009; Whitwell et al., 2008) this view. Those that challenge the view show that with longer reaches, V trials, even during random schedules, show smaller hand openings (albeit the opening remains larger than the blocked-V trials). This suggests that with longer movements, there is enough time for participants to use visual information, despite its unpredictability (Fukui & Inui, 2006; Whitwell & Goodale, 2009; Whitwell et al., 2008). Other research has supported the original view that in random schedules with high uncertainty, participants adopt a strategy that matches the blocked-NV trials – that is they prepare themselves as though they will not receive, and therefore cannot maximally use, vision (Heath et al., 2006).

Only one of the above grasping studies directly tested the effects of predictability by introducing an alternating feedback schedule (Whitwell et al., 2008). Here, the results from the alternating and random schedules showed identical differences between NV and V trials. This gives strong support for the idea that differences between blocked and random schedules have more to do with the motor system using recent trial history than with the employment of a cognitive strategy based on predictability. Recently, this view has received more support in a grasping study showing that the effect of having vision (i.e. smaller hand openings) accumulates over trials, such that consecutive V trials show progressively smaller hand openings, while consecutive NV trials show progressively larger hand openings (Whitwell & Goodale, 2009).

Although some progress has been made in determining whether the motor system uses conscious prediction or trial history to cope with changes in the availability of visual feedback during grasping, there is almost no work that has examined this question in the case of pointing, particularly in the context of a more complicated reaching task like obstacle avoidance. Since the initial Zelaznik study (1983), pointing on blocked trials with visual feedback (V) has been shown to result in faster reaction times (Khan et al., 2002), increased accuracy (Chua & Elliott, 1993; Elliott & Allard, 1985; Heath, 2005; Heath et al., 2004; Khan et al., 2002), and more time spent during the later phases of movement (i.e. decelerating, or time spent after peak velocity) (Chua & Elliott, 1993; Elliott et al., 1991; Khan et al., 2002) than pointing on blocked trials without visual feedback (NV). In a randomized schedule of V and NV trials, the differences between feedback trials tend to become smaller (Chua & Elliott, 1993; Elliott & Allard, 1985; Khan et al., 2002; Neely et al., 2008; Zelaznik et al., 1983). Reach-to-point studies that have included an alternating feedback schedule (Khan et al., 2002; Zelaznik et al., 1983), which theoretically could have addressed whether the motor system makes use of conscious knowledge or trial history, have not run this schedule in the same experiment alongside blocked and random schedules making direct comparison difficult. In both these studies, however, the alternating schedule still showed a significant difference between the V and NV trials, providing at least some suggestion that pointing movements made with an alternating schedule may be closer to those made with blocked schedules. Despite the ambiguity surrounding the results of the alternating schedule, and the reduction of the NV/V difference when randomized, it is clear that whenever visual feedback is available, it can be used to increase endpoint accuracy – usually resulting in movements with longer deceleration phases (for review see: Elliott et al., 2001). A sensitive technique that reveals the accuracy benefits of V trials is to compare how well positions throughout the movement predict the variability observed in the movement endpoint (Heath, 2005; Heath et al., 2004; Neely et al., 2008); for extensive review of this and other procedures analyzing variability see: (Khan et al., 2006; Messier & Kalaska, 1999). In general, NV trials show higher correlations between mid-reach or late-reach positions and endpoint than the V trials do. This is likely due to the fact that visual feedback can modulate the late reach response, and thus reduce how well the position of an earlier point predicts endpoint position. This correlation analysis was recently used in a reach-to-point study that examined blocked versus random feedback schedules (Neely et al., 2008). This elegant study replicated the finding that hand position at 50% and 75% of movement during blocked-NV trials showed a much higher correlation with endpoint than the 50% and 75% position of blocked-V trials. Importantly, *both* NV and V trials in the random schedule showed the higher correlation between earlier position and endpoint that was characteristic of the blocked-NV trials. This provides strong evidence that in this reach-to-point study, a random schedule led to an offline control strategy whereby all randomly ordered trials were treated like NV trials.

While the primary aim of the current study is to investigate how the availability of vision affects obstacle avoidance behaviour, as the above discussion demonstrates it is equally important to consider what effects the expectation of vision (or not) and recent trial history may have in this experiment. It is possible that a more complicated reaching task involving the encoding and avoidance of potential obstacles will reveal different strategies than have been shown for simpler pointing tasks that have previously investigated the effect of feedback schedule. Thus, in the current experiment, every participant completed both NV (both limb and target occluded) and V trials under the three feedback schedules: blocked, random, and alternating. In addition to the kinematic measures we have previously used to test for the effects of obstacles (Chapman & Goodale, 2008), we included both an endpoint variability analysis and the correlation analysis discussed above in an effort to quantify the feedback and schedule effects in this experiment. We predicted that participants would still show sensitivity to the position of obstacles on V trials and when reaching to a specific target. It is possible, however, that with visual feedback participants would be less conservative executing their movements in the presence of obstacles and as a consequence their deviations away from the obstacles would decrease; this would be manifest as an interaction between obstacle position and the availability of feedback. With respect to visual feedback and visual feedback schedule, previous results from reach-to-point studies suggest that NV trials, regardless of schedule, will result in more endpoint variability, higher correlations between mid-reach positions and endpoint and shorter deceleration phases. In contrast, V trials should show an effect of schedule, with blocked-V trials showing prolonged deceleration and lower correlations between position and endpoint than the random-V trials. In all cases, we would predict that visual feedback will reduce endpoint variability, but perhaps to less of an extent when trials are randomized as compared to blocked. The critical case of alternating V and NV trials remains an open and interesting question and we were not certain what to expect.

2.2. Materials and Methods

2.2.1. Participants

A group of 24 right-handed (determined by self-report) adults (16 male) were included in this study. All participants had normal or corrected-to-normal vision and all participants were naïve to the purpose of the experiment. The present study is part of ongoing research that has been approved by the local ethics committee.

2.2.2. Materials and design

With the exception of the manipulation of vision, all methods and materials were identical to our previous study investigating obstacle avoidance (Chapman & Goodale, 2008). Participants sat in front of a dimly lit 1m x 1m table covered in black fabric with a laterally centered start button 15 cm from the front edge of the table, and a target LED 45 cm away from the start button (see Figure 2.1). Participants wore PLATO liquid crystal display (LCD) goggles (Translucent Technologies, Toronto, Canada), which allowed the manipulation of visual feedback, and had OPTOTRAK (Northern Digital Inc., Waterloo, Canada) infrared markers (IREDs) taped to the tip of their right index finger and the base of their right pinky finger. When recording, the position of each IRED was tracked by two OPTOTRAK cameras at a rate of 100 Hz for 3 s. Marker wires were held in place with elastic wrist and elbow bands to allow for unrestricted arm movement.

Tall rectangular objects (4x4x25 cm, with IREDs in the middle of the top facing surface) were placed on the table in one of 8 configurations (including one with no objects, None) at a depth of 24 cm. There were four different configurations with one object; Left-Out (object inside edge 15 cm to the left of midline, 1-L-Out), Left-In (10 cm to the left of midline 1-L-In), Right-Out (15 cm to the right of midline, 1-R-Out), and Right-In (10 cm to the right of midline, 1-R-In), and three configurations with two objects, Both-In (inside edges 10 cm to either side of midline, 1-B-In), Left-In/Right-Out (Left 10 cm, Right 15 cm away from midline, 2-L-In) and Left-Out/Right-In (Left 15 cm, Right 10 cm away from midline, 2-R-In). A Both-Out configuration has previously been shown to be redundant (Chapman & Goodale, 2008) and was therefore not included in the current study. For details of the arrangements, see Figure 2.1.

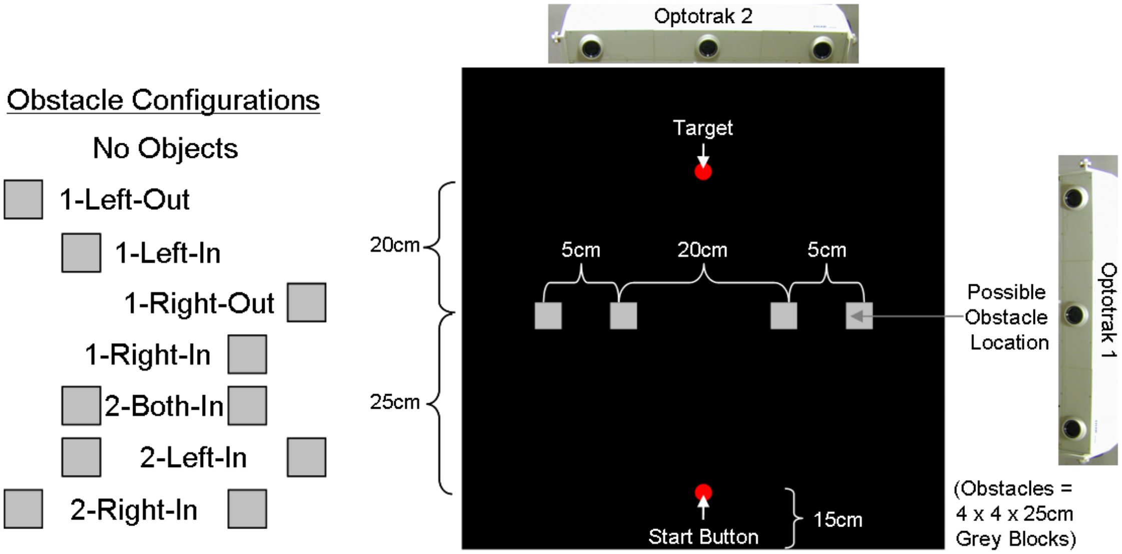

Figure 2.1. Experimental setup and obstacle configurations. Participants made reaches from the start button to the target-LED which were on a 1 m x 1 m black fabric board. When obstacles (4 cm square base, 25 cm tall) were present they appeared in one of eight configurations (shown on left) at a depth of 25 cm. Movements were recorded using two OPTOTRAK cameras (one right, one in front) at 100 Hz.

2.2.3. Procedure

Each trial started with participants placing their right index finger on the start button. The goggles were closed, allowing the experimenter to place the objects in one of the above arrangements without the participant seeing the object positions. The trial was triggered by the experimenter, which caused the goggles to open and started the OPTOTRAK recording for 3 s. The participants were instructed to reach to the target (red LED) quickly and accurately as soon as it became visible (i.e. the goggles opened). They were told to ignore other objects that were present in the array and that there could be one, two, or no objects present on any given trial. If a participant made contact with an object, they were instructed to avoid hitting them on subsequent trials. The release of the start button upon movement initiation caused the goggles to close on trials with no visual feedback (NV). On trials with visual feedback (V), the goggles remained open for the duration of the data collection.

The experiment consisted of 192 trials, 64 each of three visual feedback schedules: blocked, random, and alternating. In the blocked schedule, visual feedback remained constant (i.e. 32 NV trials followed by 32 V trials, with the order of NV and V trials counterbalanced across participants). The randomized schedule consisted of 32 NV and 32 V trials being randomly mixed. The alternating schedule consisted of 32 NV trials alternating with 32 V trials. The order in which participants received the blocked, random, or alternating schedules was counterbalanced. Before starting each block, the experimenter ensured that the participant was aware of what schedule they were about to receive.

Before starting the experiment, participants were given practice trials until they reported being comfortable with the timing (always <10). For the practice trials, participants received the visual feedback schedule they were to encounter first.

2.2.4. Data processing

All analyses were conducted on data from the IRED on the right index finger. Raw 3D data for each trial was filtered using a low-pass Butterworth filter (dual pass, 8 Hz-cutoff, 2^nd order). Instantaneous velocities in each cardinal dimension (x,y,z) were calculated for each time point and the resulting velocity profiles were filtered (low-pass Butterworth filter, dual pass, 12 Hz-cutoff, 2^nd order) and combined to create a vector velocity (i.e. three-dimensional) profile for each trial. Onset of reaches were defined as the first of four consecutive vector velocity readings of greater than 20 mm/s where there was a total acceleration of 20 mm/s^2 across the four points. Reaches were said to terminate with whichever of two conditions was first met: the first of three consecutive displacement readings back toward the start button (i.e. three negative displacements in the y-direction) or the first time the velocity dropped below 20 mm/s.

Missing data from an index finger IRED that was temporarily blocked from the view of the OPTOTRAK cameras due to the positioning of the objects was filled in with data from the pinky IRED. This was accomplished by translating the pinky IRED data to the last known position of the finger IRED, using the pinky IRED data over the missing segment, then stretching (in all three dimensions) the endpoint of the filled sequence to match the position of the finger IRED where it reappeared. When both the index and pinky IREDs were missing, the data were linearly interpolated across the missing region. Linear interpolation was required on <2% of trials, and, where required, was interpolated across an average of less than 16 time points. No trials were rejected due to requiring interpolation.

Trials were rejected for the following reasons: the reach never attained the defined minimum velocity, the reach did not terminate within the recording window, the reach was too short in either duration (<100 ms) or distance (<250 mm in depth), or errors in OPTOTRAK recording (usually due to blocked IREDs) caused velocity spikes of >6000 mm/s. Under these criteria, <1% of the trials were rejected.

All trajectories were translated such that the first reading of the index finger IRED was taken as the origin of the trajectory (i.e. 0,0,0 in 3D Cartesian space, x = horizontal, y = depth, z = vertical) and were normalized to movement time such that they had 100 position measurements, allowing for averaging.

2.2.5. Dependent measures and analysis

Reaction Time (ms): Time from the start of the trial to the first frame defined as movement onset.

Movement Time (ms): Measured as the time between movement onset and the last frame of the reach movement.

Peak Velocity (mm/s): The highest vector velocity obtained during the movement time.

Time to Peak Velocity (ms): The time from the onset of movement until the peak velocity was reached.

Deceleration Time (ms): The time from peak velocity until the end of the movement.

X@100, X@250, X@End (mm): Three measures of lateral deviation (x) were taken, one near the start of the reach (100 mm in depth (y) from start button), one near the middle of the reach (250 mm), and one at the end of the reach (x position of the last frame).

StdX@End and StdY@End (mm): The average standard deviation for each participant's 2D (x,y) endpoints in each condition of interest (see below).

R^2*-25%*, R^2*-50%*, R^2*-75%*: Squared correlations calculated for each participant in each condition of interest (see below) relating the spatial position of the limb in the main movement direction (y) to ultimate movement endpoint in that direction. Separate correlations were calculated between endpoint and points occurring at 25%, 50% and 75% of total movement.

For each participant, each of the temporal and spatial dependent measures (reaction time, movement time, peak velocity, time to peak velocity, deceleration time, x-positions) was calculated on every trial, averaged for each of the 48 conditions and entered into a three-factor Feedback x Schedule x Configuration (2x3x8) repeated-measures (RM) ANOVA. Where significant, an interaction of Feedback and Schedule or Feedback and Configuration was followed up with simple main effects single-factor RM-ANOVAs of

Schedule or Configuration at each level of Feedback. The variability (StdX@End and StdY@End) and correlation (R^2) measures were specifically designed to test the Feedback x Schedule interaction. As such, each participant's average was calculated for the 6 conditions of interest and entered into a two-factor Feedback x Schedule (2x3) RM-ANOVA. Significant interactions for these measures were tested as above. Post-hoc follow-ups to significant main effects and simple main effects compared all possible pairwise comparisons of the relevant factor. All repeated-measures ANOVAs were analyzed using the Greenhouse-Geisser correction for sphericity and taken to be significant at corrected $p < 0.05$. Post-hoc pairwise contrasts used the Bonferroni correction for multiple comparisons with a corrected $p < 0.05$ taken as significant.

2.3. Results

For all dependent measures except two (see below) there were no interactions between Configuration and Feedback or Configuration and Schedule. This indicates that the results of this experiment can be broken into two categories (described in separate sections below), effects due to obstacles and effects due to the presence and schedule of visual feedback. It also demonstrates that our hypothesis regarding the possible use of different obstacle avoidance strategies for V as compared to NV trials was not supported; instead, it appears that participants avoided obstacles similarly when they had vision as when they did not have vision of their hand and the workspace while reaching (see Figure 2.2).

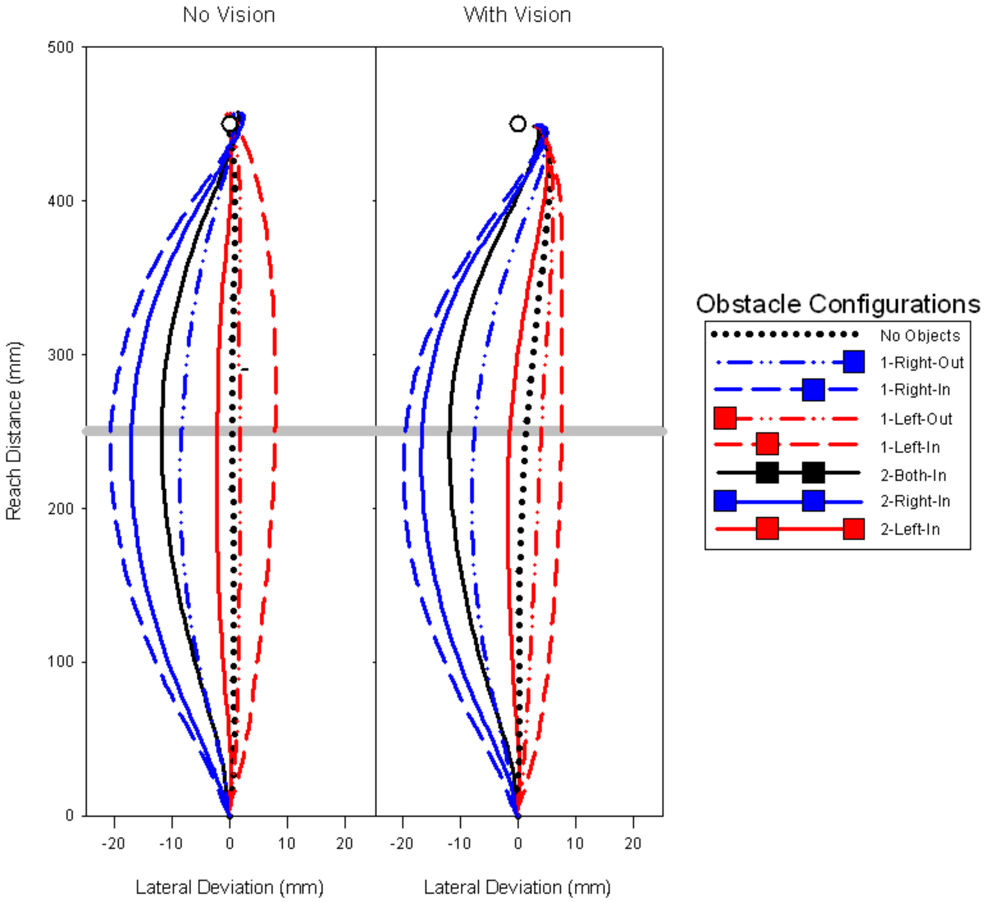

Figure 2.2. Overhead view (x,y) of average reach trajectories made for trials with no vision (NV, left panel) and trials with vision (V, right panel) under all eight obstacle configurations. Thick grey line = object depth, Open circle = target location. Configuration trajectories are coded as follows: Blue = configurations expected to result in left-shifted trajectories (1-R-Out, 1-R-In, 2-R-In), Red = configurations expected to result in right-shifted trajectories (1-L-Out, 1-L-In, 2-L-In), black = symmetrical (2-Both-In) or no object trajectories. Dotted-line = No Objects, Dash-Dot = 1-Object-Out, Dashed = 1-Object-In, Solid = 2-objects. Note the remarkable similarity in trajectories made with and without vision.

2.3.1. Effects due to Obstacles

All temporal and spatial dependent measures showed a significant effect due to object configuration and are summarized in Table 2.1. As predicted from previous work (Chapman & Goodale, 2008), the effects observed due to the positioning of non-target objects between the participant and the reach target demonstrate that the objects were functioning as obstacles, caused interference, and were being avoided. Configurations with objects close to the right (reaching) arm of the participant (2-B-In, 2-R-In, 1-R-In) caused the most interference, yielding longer overall movement times (longer in both the early and late phase of movement) and lower peak velocities. Configurations with objects placed further away on the right (1-R-Out, 2-L-In) caused some interference while configurations with objects only on the left, or no objects (1-L-In, 1-L-Out, None) caused the least interference as characterized by these temporal measures (see Table 2.1). Reaction time effects were largely due to the longest reaction times occurring on trials with no objects, an effect we attribute to the relative novelty of these trials.

Table 2.1 – Dependent measures showing an effect due to obstacle Configuration

Rxn Time (ms)	2 B-In	2 R-In	2-L-In	1 L-In	1 R-In	1 L-Out	1 R-Out	None	*F*
	372.85	373.48	358.26	377.12	384.13	374.53	367.20	393.71	**
	2-L-In < 1-R-In,None;								
Mvmt Time (ms)	2 B-In	2 R-In	2-L-In	1 L-In	1 R-In	1 L-Out	1 R-Out	None	*F*
	669.25	663.00	648.24	638.09	668.19	638.17	647.91	641.23	**
	2-B-In, 2-R-In, 1-R-In > 1-L-In, 1-R-Out; 2-B-In, 1-R-In > 2-L-In, 1-L-In, 1-L-Out, None;								
Time To PV (ms)	2 B-In	2 R-In	2-L-In	1 L-In	1 R-In	1 L-Out	1 R-Out	None	*F*
	267.34	270.57	264.56	255.70	271.97	258.94	264.33	257.85	**
	2-R-In,1-R-In > 1-L-In,1-L-Out,1-R-Out,None; 2-B-In,2-L-In,1-R-Out > 1-L-In; 2-B-In > None;								
Decel Time (ms)	2 B-In	2 R-In	2-L-In	1 L-In	1 R-In	1 L-Out	1 R-Out	None	*F*
	401.91	392.43	383.68	382.39	396.23	379.22	383.58	383.38	**
	2-B-In > 1-L-Out; 1-R-In > 1-R-Out;								
Peak V (mm/s)	2 B-In	2 R-In	2-L-In	1 L-In	1 R-In	1 L-Out	1 R-Out	None	*F*
	1487.75	1498.59	1535.71	1579.85	1505.01	1594.21	1554.99	1587.73	**
	2-B-In,2-R-In,1-R-In < 1-L-In,1-L-Out,1-R-Out,None; 2-B-In < 2-L-In; 2-L-In < 1-L-Out;								
X@100 (mm)	2 B-In	2 R-In	2-L-In	1 L-In	1 R-In	1 L-Out	1 R-Out	None	*F*
	-7.29	-11.26	-1.80	4.38	-14.19	0.76	-6.76	-0.68	**
	1-R-In < 2-R-In < 2-B-In,1-R-Out < 2-L-In,None < 1-L-Out < 1-L-In;								
X@250 (mm)	2 B-In	2 R-In	2-L-In	1 L-In	1 R-In	1 L-Out	1 R-Out	None	*F*
	-12.00	-17.65	-2.26	7.17	-21.33	1.92	-9.16	-0.15	**
	1-R-In < 2-R-In < 2-B-In,1-R-Out < 2-L-In,None < 1-L-Out < 1-L-In;								
X@End NV (mm)	2 B-In	2 R-In	2-L-In	1 L-In	1 R-In	1 L-Out	1 R-Out	None	*F*
	1.22	1.95	-0.88	-0.54	1.60	-1.06	-0.16	-0.74	*
X@End V (mm)	2 B-In	2 R-In	2-L-In	1 L-In	1 R-In	1 L-Out	1 R-Out	None	*F*
	2.59	3.67	3.28	3.42	3.42	3.25	3.30	3.19	NS

The ‘F’ column shows an F-test of the main effect. Where significant, results from pairwise contrasts for each dependent measure are shown below the compared means. * & < or > = $p<0.05$, ** = $p<0.005$. NS = not significant.

Patterns of lateral deviation early (X@100) and mid-reach (X@250) for trials with two objects matched our previous work (Chapman & Goodale, 2008). The trajectories with the 2-R-In objects were shifted the most leftward and the trajectories with the 2-L-In were shifted most rightward. The trajectories with the 2-B-In fell in between (see Table 2.1 and Figure 2.2). The current experiment makes two important additions in quantifying how we react to obstacles. First, when compared to two-object trials, the deviations on one object trials were larger. For example, the 1-R-In trials resulted in leftward deviations that were even larger than those observed on the 2-R-In trials, indicating that the second object in the two-object trials was, not surprisingly, having an effect. This pattern was observed for objects on both sides of space (see Table 2.1 and Figure 2.2). Second, when making reaches to a specific point in space (as opposed to the target strip used in previous work), the lateral deviation at the endpoint (X@End) was largely unaffected by the object configuration. We did observe, however, an interaction between Feedback and Configuration for the X@End measure $F(5.27,94.91) = 3.50$, $p<0.01$. Simple main effect follow-ups revealed that there was no significant effect of configuration on V trials and a small but significant effect of configuration on NV trials. Specifically, it appears that on NV trials there is an overshoot, whereby the finger ended slightly further to the right on trials where the reach was initially pushed to the left (e.g. 2-R-In) than it did on trials where the reach was initially pushed to the right (e.g. 2-L-In). Overshooting the target along the primary axis of movement on NV trials has been shown previously (e.g. Heath et al., 2004), and our results are likely an extension of these findings to the curved trajectories produced when avoiding obstacles.

Table 2.2 – Dependent measures showing an interaction between Feedback and Schedule

Mvmt Time (ms)	Interaction* feedback x schedule				
	Blocked	Random	Alternating	*F*	
No Vision	635.25	672.68	655.51	*	Blk<Rnd
With Vision	654.02	651.67	642.36	NS	-

Decel Time (ms)	Interaction* feedback x schedule				
	Blocked	Random	Alternating	*F*	
No Vision	376.42	403.29	394.91	*	none
With Vision	387.97	383.46	381.26	NS	-

Peak V (mm/s)	Interaction* feedback x schedule				
	Blocked	Random	Alternating	*F*	
No Vision	1607.11	1514.49	1542.81	*	Blk>Rnd
With Vision	1511.65	1528.91	1550.55	NS	-

X@250 (mm)	Interaction* feedback x schedule				
	Blocked	Random	Alternating	*F*	
No Vision	-9.56	-5.27	-6.21	*	Blk<Rnd
With Vision	-6.87	-5.25	-7.08	NS	-

Std X@End (mm)	Interaction* feedback x schedule				
	Blocked	Random	Alternating	*F*	
No Vision	10.55	9.56	8.85	*	none
With Vision	4.79	4.27	4.22	NS	-

The strength of the interaction is indicated in the row with the measure name. F-tests results are shown comparing simple main effect means of each level of Feedback row across the three levels of Schedule. Results from pairwise contrasts are shown next to each significant F-test. * & < or > = $p<0.05$. NS = not significant.

2.3.2. Effects due to Visual Feedback and Schedule

The analysis of the impact of visual feedback and its schedule on the dependent measures in the current experiment affected variables in three different ways. One group of variables showed no significant effect of either factor individually or of an interaction. A second group of variables showed only an effect of visual feedback (see Table 2.3). A final group of variables showed an interaction between the two factors (see Table 2.2). The variables showing no significant Feedback or Schedule effects were two spatial measures (X@100, X@End), reaction time, and time to peak velocity. The fact that reaction time was not modulated by visual feedback or its schedule is a first indication that in our reaching task, the motor strategies employed were different than in previous studies, where reaction time effects were observed due to differences in feedback schedule. The lack of a Feedback or Schedule effect on time to peak velocity is interesting when considered together with the effects of these factors on movement time, deceleration time, and peak velocity measures, which all show a significant interaction between Feedback and Schedule (see Table 2.2 and Figure 2.3). Examining these means reveals that V trials yield a similar velocity profile (variables do not statistically differ), regardless of schedule, while NV trials show a marked difference in velocity profiles across schedules. Specifically, the blocked-NV trials are characterized by higher peak velocities and shorter deceleration times compared to the random-NV trials, with the alternating-NV trials falling somewhere in the middle, but closer to the random-NV trials.

The X@250 and StdX@End variables are the other variables that show an interaction effect, and they follow the same pattern of no difference in schedule across V trials and a difference across NV trials (see Table 2.2). For the X@250 measure, blocked-NV trajectories are, on average, slightly leftward of the random-NV and alternating-NV trajectories (see Table 2.2). The lack of an interaction involving Configuration for this measure indicates that this leftward bias was not the result of participants adopting a different strategy when avoiding obstacles without visual feedback, but rather an accumulated bias that developed across the blocked-NV trials. For the endpoint standard deviation measures, there was, not surprisingly, more variability in endpoint for the NV trials than the V trials, and the endpoint variability did not change across schedules for the V trials. At the same time, the lateral variability across the NV-trials was modulated by schedule such that the blocked-NV trials showed the largest StdX@End with the random and alternating NV trials showing less variability (see Tables 2.2 and 2.3 and Figure 2.4).

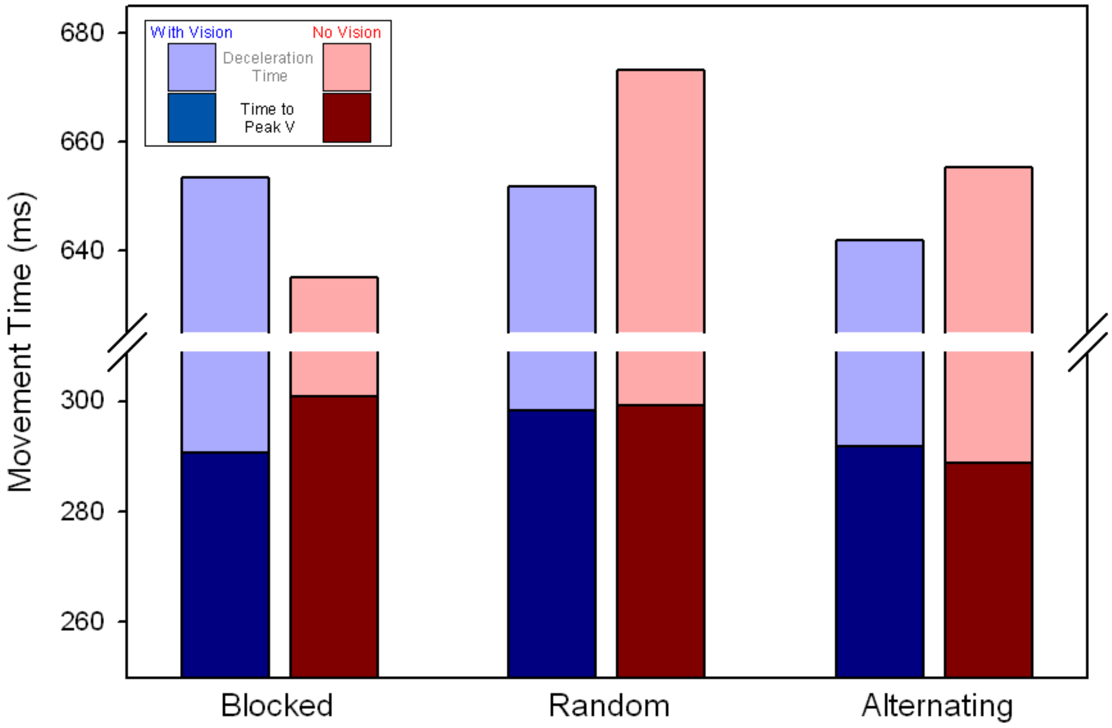

Figure 2.3. The effect of visual feedback (Vision (V) = blue, No Vision (NV) = Red) and schedule (separate sets of bars, blocked, random and alternating) on time to peak velocity (bottom/dark portion of bar) and deceleration time (light/top portion of bar). There are no significant differences on time to peak velocity across all conditions and no difference on deceleration time between the V trials. However, the blocked-NV trials show a significantly shorter deceleration time than the random and alternating-NV trials.

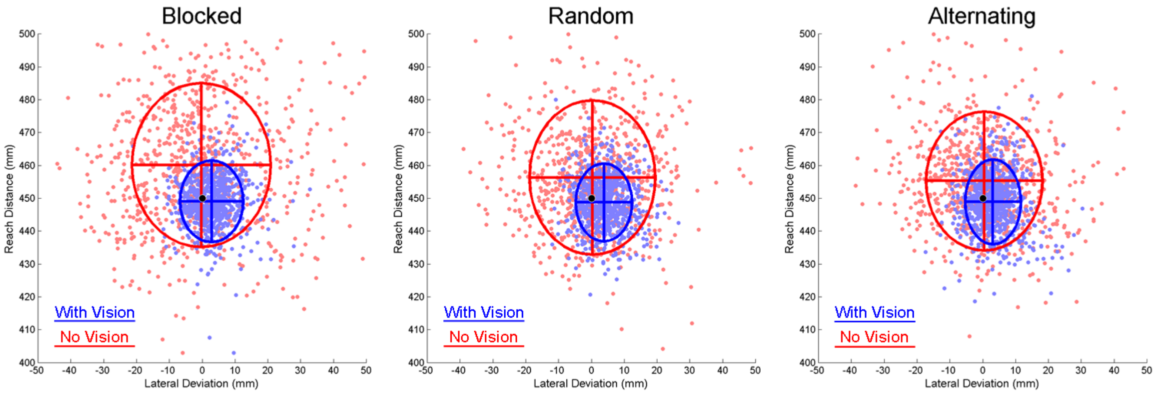

Figure 2.4. Scatter plots of all reach endpoints made with vision (V = Blue) and with no vision (NV = Red) separated into reaches made under the three feedback schedules (blocked, random and alternating). Overlaid are standard deviation ellipses with a width = twice StdX@End and height = twice StdY@End. V trials are more accurate than NV trials and have similar endpoint variability across all schedules. Blocked-NV trials show significantly higher lateral variability than the random and alternating NV trials.

Based on previous work (Neely et al., 2008), we predicted that the correlation measures (R^2) would provide the most sensitive measure of any differences in the effects of Feedback, Schedule, and the interaction between the two. Our results for these measures are shown in Figure 2.5. As predicted, the NV trials show a significantly higher correlation between y-position during the reach and final y-position than the V trials. This is true for correlations between endpoints and points near the beginning (R^2-25%) , endpoints and points in the middle (R^2-50%), and endpoints and points near the end of the reach (R^2-75%)(see Table 2.3). Critically, however, none of the correlation measures was close to showing a significant interaction between Feedback and Schedule (test of interaction: R^2-25%, $F(1.91,34.35) < 1$; R^2-50%, $F(1.98,35.67) < 1$; R^2-75%, $F(1.91,34.34) = 1.09$, $p=0.35$). This represents the clearest evidence that the previously reported use of an off-line control strategy in the face of unreliable visual feedback (Heath et al., 2006; Neely et al., 2008) was not at play in the current experiment.

Table 2.3 – Dependent measures showing an effect due to Feedback only

	NV	V	F
Std Y@End (mm)	11.59	6.19	**
R^2-25%	0.09	0.05	*
R^2-50%	0.19	0.05	**
R^2-75%	0.62	0.18	**

NV = No vision, V = Vision. The ‘F’ column shows an F-test of the main effect. * = p<0.05, ** = p<0.005.

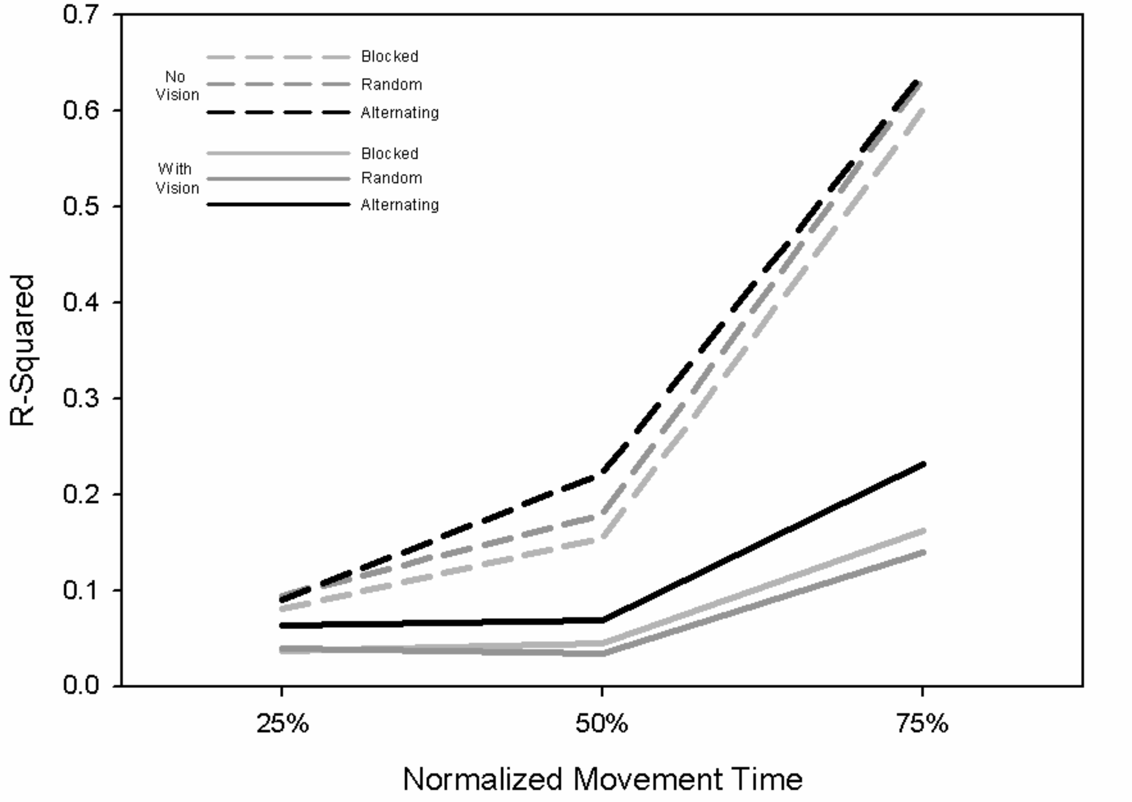

Figure 2.5. The proportion of endpoint variance (R^2) in the depth (y) dimension accounted for by the location of the limb (in the depth (y) dimension) at 25, 50 and 75% of the movement as a function of visual feedback (NV = no vision, dashed lines; V = with vision, solid lines) and schedule (blocked = light grey, random = dark grey, alternating = black). As predicted, NV trials show significantly higher correlations than V trials. However, this is not modulated by schedule, as no interaction effects were found.

2.4. Discussion

This study had two aims: first, to test if obstacle avoidance is different when visual feedback of the hand is available in flight (V) as compared to when it is not (NV) and second, to test the effect of visual feedback schedule (blocked, random or alternating trials) in a more complex reach-to-point task. Avoidance behaviour, as measured by lateral deviations at several points along the reach, was not affected by the availability of visual feedback. In a previous study, we had shown that participants performing reaches without visual feedback were sensitive to the size and position of two objects placed between the start and end of their reach (Chapman & Goodale, 2008). In the current study, we extend those findings and show that this avoidance is the same when participants can see their hand in flight. In addition, we included trials in which only one obstacle appeared and show that the avoidance behaviour is exactly as would be predicted, with single obstacles causing more lateral deviation than comparable two-obstacle configurations. In addition, we found that single obstacles close to the right (reaching) arm of the participants caused the most deviation, replicating the earlier work with two obstacles. Finally, we show that participants can make reaches to a specific point in space (not a strip as was used previously) and remain sensitive to the position of obstacles, while converging on a common endpoint across all configurations.

Previous studies have shown that when participants perform simple rapid reach movements under different feedback schedules, they show large differences between V and NV conditions when trials are blocked and smaller differences when trials are randomized (Chua & Elliott, 1993; Elliott & Allard, 1985; Khan et al., 2002; Neely et al., 2008; Zelaznik et al., 1983). Specifically, blocked-V trials have faster reaction times, less endpoint error, and longer deceleration phases compared to blocked-NV trials. If one considers performance on only the blocked schedules, the observed effects in the current experiment would appear to be entirely consistent with previous work; with performance on blocked-V trials having less endpoint error and a longer deceleration time than performance on blocked-NV trials (see Figures 2.3 and 2.4). But as soon as one includes performance on the non-blocked schedules, the pattern of results does not conform to what one would expect from the results of previous studies. The most striking difference between the current experiment and previous work is the performance on V and NV trials in a randomized schedule. Previous work has shown only small changes in performance on randomized-NV trials relative blocked-NV trials but a dramatic shift in performance on randomized-V trials away from blocked-V performance towards blocked-NV performance (Heath et al., 2006; Jakobson & Goodale, 1991; Khan et al., 2002; Neely et al., 2008). In striking contrast, the current study finds the opposite result: the performance on V trials does not change with schedule while the performance on NV trials does. In fact, all five variables showing a significant interaction between Feedback and Schedule in the current experiment had the identical pattern of results: no difference in performance on V trials across different schedules and marked changes in performance on NV trials. Perhaps the strongest evidence that changes in schedule do not affect performance on V trials comes from the correlation analysis. Here we replicate the well-established result that reaches made on NV trials show a higher correlation between positions throughout the movement and endpoint than reaches made on blocked-V trials (Heath, 2005; Heath et al., 2004; Neely et al., 2008). Critically, however, corresponding correlations on V trials are not different across the schedules: on both random-V and alternating-V trials, correlations remain smaller than those observed on NV trials.

As discussed in the Introduction, if differences in performance on trials with and without visual feedback is due to a conscious control strategy based on knowledge of the upcoming trial type, then one would have expected differences in performance between V and NV trials on the alternating schedule to be similar to the differences observed between blocked V and NV trials. But if the differences in performance between the two kinds of feedback trials are simply a reflection of trial history, then performance on alternating feedback trials should resemble performance on randomized trials. Although no statistically conclusive answer emerged, both the magnitude and direction of V versus NV differences in an alternating schedule were more similar to differences observed with the randomized schedule than with the blocked schedule. This suggests that a motor strategy emerging from trial history was predominantly responsible for behaviour in the alternating schedule. However, given that the alternating schedule has minimal trial consistency and the random schedule will have runs of consecutive trials with the same feedback, the fact that behaviour on the alternating schedule falls between behaviour on the blocked and random schedules suggests some modulation of behaviour based on the knowledge of what was going to happen on an upcoming trial.

What appears to be the driving force behind the results in the current study is that when participants were allowed visual feedback, regardless of its trial-to-trial predictability or the motor system's experience on recent trials, this feedback was exploited to optimize performance. Conversely, when vision was taken away, behaviour was different whether the NV trials occurred consecutively (blocked) or were mixed together (randomized or alternating). When there were consecutive NV trials, there was a significant increase in endpoint variability and peak velocity, a leftward shift of reach trajectories, and a significant decrease in deceleration time. When NV trials were mixed, endpoint variability and peak velocity both decreased while deceleration time increased.

Both the finding of stable performance with vision across schedules and changes in performance on NV trials across schedules are at odds with previous work and require explanation. The stability of the V trials is perhaps not as surprising as it initially appears. As mentioned before, it is well established that regardless of the predictability of the availability of feedback, the visuomotor system uses vision and online control to improve the endpoint accuracy of a reaching movement (for review see: Elliott et al., 2001). This indicates that given enough time on a trial where visual feedback was available (regardless of whether its availability was predictable or not), it can still be used to improve performance. This raises a critical question: In the current study, was there enough time for visual feedback to be used in the same way across all schedules? We believe the answer is yes. Previous studies showing schedule effects in reach-to-point tasks have typically had average reaction times of ~200 ms and movement times of ~400 ms (Khan et al., 2002; Neely et al., 2008). This stands in stark contrast to the current task where reaction times had an average of ~350 ms and movement times an average of ~625 ms. While differences in movement amplitude (45 cm in the current experiment versus 32 cm in Khan et al. 2002 and ~20 cm in Neely et al. 2008) can account for some of the movement time differences, as we report here and have shown previously (Chapman &

Goodale, 2008), obstacle interference results in slower movements. This suggests that in obstacle avoidance tasks of this kind participants might take more time preparing and executing a movement than the speeded movements typically studied in the laboratory. This extra time spent planning the reach prior to movement and the extra time spent allowing for online control may all be an optimization designed to take advantage of vision when it is available. After all, we are an extremely visual species and it makes more sense to default to a strategy where we expect vision to be routinely available. There are few situations in nature where one has vision during the programming phase but not the execution of the movement.

If when performing natural reaches in a more complex environment we are strategically prepared to take full advantage of vision, this could start to explain the changes we observed across schedule for the NV trials. When NV trials are blocked perhaps the repetition of movements made in the absence of online visual control results in an accumulation of error and thus a qualitative shift in the type of reach performed. Instead of a natural reach with a lower peak velocity and longer deceleration time (designed to allow for online control), the reach becomes faster with less deceleration – possibly to get to the endpoint before the representation of the target decays (an argument made previously: Elliott & Allard, 1985; Elliott et al., 1991). Importantly, this atypical reach may be observed only when visual feedback is consistently unavailable. Other recent research has shown the profound effects of repetition on the motor performance (for reviews see: Dixon & Glover, 2004; Rosenbaum et al., 2009; Rosenbaum, Cohen, Jax, Weiss, & van der Wel, 2007). Specifically, Jax and Rosenbaum have shown that the trajectory taken avoiding a virtual obstacle on one trial will influence the trajectory on subsequent trials, even if no obstacle is present (Jax & Rosenbaum, 2007, 2008). In a similar type of experiment, rhythmic tapping movements made in an arc in front of the body showed residual effects from the hand jumping over an obstacle in the subsequent movements where no obstacle was present (van der Wel et al., 2007). Critically, in these experiments, the ‘hand-path priming’ that was observed was shown to accumulate and decay across a set of trials, indicating the existence of at least a short term motor memory. In an extremely relevant study with reach-to-grasp movements, it was shown that the wider hand opening associated with NV trials developed gradually over a sequence of four trials (Whitwell & Goodale, 2009). Similarly, the narrower opening for V trials also developed over time. This line of research clearly demonstrates why it is consecutive trials in the blocked schedule where we see the NV effect in the current experiment. With both the random and alternating schedules participants receive visual feedback approximately every second trial, giving an error signal for use on subsequent trials and resetting and calibrating the visuomotor system. This lack of a long unbroken sequence of NV trials explains why we see a reduction in variability in random-NV and alternating-NV as compared to blocked-NV trials. As was noted earlier, however, there are also sequence differences between the random and alternating schedules. Within the random schedule there are going to be small runs of consecutive trials that by definition are not present in the alternating schedule. Despite this difference, we do not find any effects in our dependent measures that differentiate between the behaviour during random as compared to alternating schedules. We argue, therefore, that on any given trial in a mixed sequence, the visuomotor system is prepared to receive and take advantage of visual feedback. This explains why on the random-NV and alternating-NV trials a prolonged deceleration phase was observed. After all, if the system is prepared to take advantage of visual feedback on a given trial, and then this crucial information is taken away, it is plausible that the reach would slow down and be more conservative – especially in the context of an obstacle avoidance task where the consequence of an error is a potential collision. Although the current study was not designed to systematically investigate the effects of visual feedback repetition, it would be interesting to pursue this avenue of research with this type of natural reaching in complex environments.

To conclude, we show that the avoidance of one or two obstacles when making reaches to a specific point with full vision of the hand is no different than the avoidance behaviour observed when executing reaches with no vision. Moreover, regardless of the predictability or repeated availability of vision, participants perform actions the same way when they have visual feedback. In contrast, when vision is repeatedly unavailable (blocked-NV trials in the current experiment) performance on no vision trials is markedly different from performance in schedules where vision is only periodically unavailable (random-NV and alternating-NV trials). Under the unnatural scenario of a repeated absence of vision during the reach, movements become faster and more variable. But when reaching without visual feedback immediately after a trial when vision was available, participants slow down and show less variability in performance. This finding differs from previous work, and likely reflects different task demands. When participants must avoid obstacles, the planned reach is more complex than a simple reach-to-point movement. In the presence of obstacles, the reaching system needs to encode more than just the target position, and the potential for collision gives reaching errors a tangible consequence. As a result, reaction times and movement times are slower. We believe our findings of consistent reach behaviour across all trials in which vision was available demonstrates that the reach system, when presented with a more natural and complex task like obstacle avoidance, is optimized to take advantage of visual feedback.

2.5. References

Castiello, U. (1996). Grasping a fruit: selection for action. *J Exp Psychol Hum Percept Perform, 22*(3), 582-603.

Chapman, C. S., & Goodale, M. A. (2008). Missing in action: the effect of obstacle position and size on avoidance while reaching. *Exp Brain Res, 191*(1), 83-97.

Chua, R., & Elliott, D. (1993). Visual regulation of manual aiming. *Hum Mov Sci, 12*, 365-401.

Deubel, H., & Schneider, W. X. (2004). Attentional selection in sequential manual movements, movements around an obstacle, and in grasping. In G. W. Humphreys & M. J. Riddoch (Eds.), *Attention in action : advances from cognitive neuroscience* (pp. 69-91). Hove, East Sussex: Psychology Press.

Dixon, P., & Glover, S. (2004). Action and Memory. In B. H. Ross (Ed.), *The psychology of learning and motiviation* (Vol. 45, pp. 143-172).

Elliott, D., & Allard, F. (1985). The utilization of visual feedback information during rapid pointing movements. *Q J Exp Psychol A, 37*(3), 407-425.

Elliott, D., Binsted, G., & Heath, M. (1999). The control of goal-directed limb movements: Correcting errors in trajectory. *Hum Mov Sci, 18*(121-136), 121.

Elliott, D., Carson, R. G., Goodman, D., & Chua, R. (1991). Discrete vs. continuous visual control of manual aiming. *Hum Mov Sci, 10*, 393-418.

Elliott, D., Chua, R., Pollock, B. J., & Lyons, J. (1995). Optimizing the use of vision in manual aiming: the role of practice. *Q J Exp Psychol A, 48*(1), 72-83.

Elliott, D., Helsen, W. F., & Chua, R. (2001). A century later: Woodworth's (1899) two-component model of goal-directed aiming. *Psychol Bull, 127*(3), 342-357.

Fukui, T., & Inui, T. (2006). The effect of viewing the moving limb and target object during the early phase of movement on the online control of grasping. *Hum Mov Sci, 25*, 349-371.

Heath, M. (2005). Role of limb and target vision in the online control of memory-guided reaches. *Motor Control, 9*(3), 281-311.

Heath, M., Rival, C., & Neely, K. (2006). Visual feedback schedules influence visuomotor resistance to the Muller-Lyer figures. *Exp Brain Res, 168*(3), 348-356.

Heath, M., Westwood, D. A., & Binsted, G. (2004). The control of memory-guided reaching movements in peripersonal space. *Motor Control, 8*(1), 76-106.

Jackson, S. R., Jackson, G. M., & Rosicky, J. (1995). Are non-relevant objects represented in working memory? The effect of non-target objects on reach and grasp kinematics. *Exp Brain Res, 102*(3), 519-530.

Jakobson, L. S., & Goodale, M. A. (1991). Factors affecting higher-order movement planning: a kinematic analysis of human prehension. *Exp Brain Res, 86*(1), 199-208.

Jax, S. A., & Rosenbaum, D. A. (2007). Hand path priming in manual obstacle avoidance: evidence that the dorsal stream does not only control visually guided actions in real time. *J Exp Psychol Hum Percept Perform, 33*(2), 425-441.

Jax, S. A., & Rosenbaum, D. A. (2008). Hand path priming in manual obstacle avoidance: Rapid decay of dorsal stream information. *Neuropsychologia*.

Khan, M. A., Elliott, D., Coull, J., Chua, R., & Lyons, J. (2002). Optimal control strategies under different feedback schedules: kinematic evidence. *J Mot Behav, 34*(1), 45-57.

Khan, M. A., Franks, I. M., Elliott, D., Lawrence, G. P., Chua, R., Bernier, P. M., et al. (2006). Inferring online and offline processing of visual feedback in target-directed movements from kinematic data. *Neurosci Biobehav Rev, 30*(8), 1106-1121.

McIntosh, R. D., McClements, K. I., Dijkerman, H. C., Birchall, D., & Milner, A. D. (2004). Preserved obstacle avoidance during reaching in patients with left visual neglect. *Neuropsychologia, 42*(8), 1107-1117.

McIntosh, R. D., McClements, K. I., Schindler, I., Cassidy, T. P., Birchall, D., & Milner, A. D. (2004). Avoidance of obstacles in the absence of visual awareness. *Proc Biol Sci, 271*(1534), 15-20.

Messier, J., & Kalaska, J. F. (1999). Comparison of variability of initial kinematics and endpoints of reaching movements. *Exp Brain Res, 125*(2), 139-152.

Milner, A. D., & McIntosh, R. D. (2004). Reaching between obstacles in spatial neglect and visual extinction. *Prog Brain Res, 144*, 213-226.

Mon-Williams, M., Tresilian, J. R., Coppard, V. L., & Carson, R. G. (2001). The effect of obstacle position on reach-to-grasp movements. *Exp Brain Res, 137*(3-4), 497-501.

Neely, K. A., Tessmer, A., Binsted, G., & Heath, M. (2008). Goal-directed reaching: movement strategies influence the weighting of allocentric and egocentric visual cues. *Exp Brain Res, 186*(3), 375-384.

Rice, N. J., Edwards, M. G., Schindler, I., Punt, T. D., McIntosh, R. D., Humphreys, G. W., et al. (2008). Delay abolishes the obstacle avoidance deficit in unilateral optic ataxia. *Neuropsychologia, 46*(5), 1549-1557.

Rice, N. J., McIntosh, R. D., Schindler, I., Mon-Williams, M., Demonet, J. F., & Milner, A. D. (2006). Intact automatic avoidance of obstacles in patients with visual form agnosia. *Exp Brain Res, 174*(1), 176-188.

Rosenbaum, D. A., Cohen, R. G., Dawson, A. M., Jax, S. A., Meulenbroek, R. G., van der Wel, R., et al. (2009). The posture-based motion planning framework: new findings related to object manipulation, moving around obstacles, moving in three spatial dimensions, and haptic tracking. *Adv Exp Med Biol, 629*, 485-497.

Rosenbaum, D. A., Cohen, R. G., Jax, S. A., Weiss, D. J., & van der Wel, R. (2007). The problem of serial order in behavior: Lashley's legacy. *Hum Mov Sci, 26*(4), 525-554.

Schindler, I., Rice, N. J., McIntosh, R. D., Rossetti, Y., Vighetto, A., & Milner, A. D. (2004). Automatic avoidance of obstacles is a dorsal stream function: evidence from optic ataxia. *Nat Neurosci, 7*(7), 779-784.

Tipper, S. P., Howard, L. A., & Jackson, S. R. (1997). Selective Reaching to Grasp: Evidence for Distractor Interference Effects *Visual Cognition, 4*(1), 1-38.

Tresilian, J. R. (1998). Attention in action or obstruction of movement? A kinematic analysis of avoidance behavior in prehension. *Exp Brain Res, 120*(3), 352-368.

van der Wel, R. P., Fleckenstein, R. M., Jax, S. A., & Rosenbaum, D. A. (2007). Hand path priming in manual obstacle avoidance: evidence for abstract spatiotemporal forms in human motor control. *J Exp Psychol Hum Percept Perform, 33*(5), 1117-1126.

Whitwell, R. L., & Goodale, M. A. (2009). Updating the programming of a precision grip is a function of recent history of available feedback. *Exp Brain Res*.

Whitwell, R. L., Lambert, L. M., & Goodale, M. A. (2008). Grasping future events: explicit knowledge of the availability of visual feedback fails to reliably influence prehension. *Exp Brain Res, 188*(4), 603-611.

Zelaznik, H. Z., Hawkins, B., & Kisselburgh, L. (1983). Rapid visual feedback processing in single-aiming movements. *J Mot Behav, 15*(3), 217-236.

Chapter 3

3. Obstacle avoidance during online corrections[2]

3.1. Introduction

Reaching for an object in the real world is different from reaching movements studied in the typical laboratory experiment in two important respects. First, the position of targets and other objects in the real world often change in a dynamic fashion and second, the workspace in the real world is often cluttered with many different objects. Although the effects of changes in target position and the effects of obstacles have been investigated separately in the laboratory, there have been few studies looking at them together (Aivar, Brenner, & Smeets, 2008; Liu & Todorov, 2007) and none where a real object becomes an obstacle while the hand is in flight. The goal of the current experiment, therefore, was to combine these two aspects of real-world reaching and examine how responses to changes in target position would be affected by a physical obstacle whose level of interference was contingent on the direction of the corrected movement.

Research that has studied the effects of sudden changes in the environment on reaching movements has examined at least two different types of environmental perturbations – changing the target position and changing the ‘visual context’ (by suddenly introducing other objects or visual stimuli into the workspace, see Gomi, 2008 for succinct review). In both cases, if the change occurs while the hand is in flight, it will often induce an automatic response (known as an online correction) toward the new target position (e.g. Brenner & Smeets, 1997; Day & Lyon, 2000; Soechting & Lacquaniti, 1983) or with respect to the change in the visual context (Brenner & Smeets, 1997; Gomi, Abekawa, & Nishida, 2006; Proteau & Masson, 1997; Saijo, Murakami, Nishida, & Gomi, 2005; Whitney, Westwood, & Goodale, 2003) – even if the changes occur without awareness (Goodale, Pelisson, & Prablanc, 1986; Pelisson, Prablanc, Goodale, & Jeannerod, 1986; Prablanc & Martin, 1992). Several elegant studies have shown that the visual

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information required to respond to changes in target position flows through the dorsal visual stream - from early visual areas to the posterior parietal cortex, which has reciprocal connections with premotor areas (Desmurget et al., 1999; Desmurget & Grafton, 2000; Desmurget et al., 2001; Grea et al., 2002; Pisella et al., 2000). Specifically, studies of patients with optic ataxia (whose dorsal stream is damaged) show that these individuals do not respond normally to a perturbation in target position (Pisella et al., 2000). Similarly, disrupting dorsal-stream processing by applying transcranial magnetic stimulation (TMS) at the precise moment a reach is initiated and target position is perturbed selectively impairs the ability to correct the movement towards the new target location (Desmurget et al., 1999). It remains open to debate as to whether online corrections in response to changes in visual context are mediated by the same automatically engaged dorsal-stream processes that control responses to changes in target position. While one prominent theory (Glover, 2004) argues that only visuomotor processes involved in planning a movement should have access to contextual information, other research (Aivar et al., 2008; Brenner & Smeets, 1997; Cameron, Franks, Enns, & Chua, 2007; Coello & Magne, 2000; Gomi et al., 2006; Saijo et al., 2005; Whitney et al., 2003) has demonstrated that online corrections can be influenced by visual context. Indeed, simply by adding contextual features while the hand is in flight, endpoint accuracy improves (Coello & Magne, 2000). Similarly, motion of background elements presented around the target while the hand is moving induces trajectory deviation in the direction of motion, although it is unclear whether the change in trajectory is due to a perceived shift in target position (Brenner & Smeets, 1997; Whitney et al., 2003) or to a reflexive response to retinal motion (Gomi et al., 2006; Saijo et al., 2005). In two recent studies, the effect of suddenly shifting the position of discrete non-target objects (rather than background texture) demonstrated that changes in the position of non-targets can affect reaches with a latency and magnitude that is similar to responses induced by changes in the target position (Aivar et al., 2008; Cameron et al., 2007). One aim of the current study was to contribute to the debate about the effects of visual context by specifically testing how the presence of a non-target object (which can be construed as contextual information) can affect adjustments to reaching movements that are made when the position of the target is suddenly perturbed.

When reaching for an object in the presence of other non-target objects, the other objects can have a profound impact on the performed action. If the non-target objects are treated like potential targets (Chapman et al., 2010) or share critical features with the target (Chang & Abrams, 2004; Howard & Tipper, 1997; Keulen, Adam, Fischer, Kuipers, & Jolles, 2003; Sailer, Eggert, Ditterich, & Straube, 2002; Song & Nakayama, 2006; Tipper, Lortie, & Baylis, 1992; Tipper, Meegan, & Howard, 2002; Welsh & Elliott, 2004) they can act as competing or distracting stimuli and cause large deviations in the path of the hand. Depending on the timing, the task, and the location of non-target objects, these deviations can be made either toward the distracting stimuli or away from them. If the non-target objects act as obstacles that physically restrict the path of the hand, then they are always avoided (Chapman & Goodale, 2008, 2010; Mon-Williams, Tresilian, Coppard, & Carson, 2001; Tresilian, 1998, 1999) with the hand moving away from them and following a path that reduces the likelihood of collision (Hamilton & Wolpert, 2002; Liu & Todorov, 2007; Sabes & Jordan, 1997; Sabes, Jordan, & Wolpert, 1998). Again, work with optic ataxic patients strongly suggests that the dorsal visual stream controls the observed automatic avoidance of obstacles (Schindler et al., 2004), although our own recent work with a patient with damage to primary visual cortex (Striemer, Chapman, & Goodale, 2009) suggests that information about the location of the obstacle can reach dorsal-stream areas via pathways outside of the geniculostriate pathway.

Even though the dorsal stream has been implicated in both online corrections and obstacle avoidance, it remains an open question as to whether or not it is capable of performing both these functions simultaneously. One recent study in our laboratory (Chapman & Goodale, 2010) suggests that the avoidance of obstacles may be relatively unaffected by online control. In this study, we manipulated whether or not vision of the hand and environment was available while reaching. Although removing vision of the hand has been found to significantly reduce the degree to which on-line adjustments are made to the reach trajectory (Elliott, Binsted, & Heath, 1999; Elliott, Carson, Goodman, & Chua, 1991; Elliott, Helsen, & Chua, 2001; Heath, 2005; Heath, Westwood, & Binsted, 2004; Reichenbach, Thielscher, Peer, Bulthoff, & Bresciani, 2009; Sarlegna et al., 2003), removing vision of both the hand and the obstacles during movement execution did not affect the participants' ability to avoid the obstacles. In other words, providing vision during movement execution did not change the obstacle avoidance behaviour – a result that suggests that, in our previous experiment (Chapman & Goodale, 2010), the encoding of the obstacle and the planned reach trajectory were not updated in flight. It is possible, however, that in our previous study the task did not require the motor plan to be altered during the action, and hence, we did not observe any online alterations. To properly test whether or not the representation and effect of an obstacle can be updated during a reach movement, the current study introduced a target perturbation which dynamically altered the degree to which an obstacle interfered with the reach.

One recent study has examined the effects of perturbing the location of either the target or one or two virtual obstacles (placed between the start and target positions) during a rapid pointing movement with a stylus on a touchpad (Aivar et al., 2008). While this study was primarily interested in examining the response latency differences between target and obstacle changes, it elegantly demonstrated that changes in visual context occurring during rapid reach movements can alter trajectories, with participants showing a slightly shorter latency when responding to target changes as compared to obstacle changes. It is unclear, however, how well these results translate to a more natural reach setting involving real obstacles where the consequences of collision are literally tangible. In fact, in the Aivar et al. study (2008), the average incidence of 'collision' (where the hand passed through the virtual obstacle) was close to 40% in some perturbation conditions. In our experience testing the avoidance of real obstacles, participants rarely (<1%) touch an obstacle (even when instructed to ignore it) and are quite alarmed when they do collide with it (Chapman & Goodale, 2008, 2010). As Aivar et al. (2008) suggest, the initial reach deviation they observe in response to the obstacle perturbation probably represents a response to moving visual context (i.e. a moving background e.g. Whitney et al., 2003) and may not be related to an avoidance strategy (though a later second correction in some participants might). To build on their finding, the current study examined natural reach responses to a perturbation in target position in the presence of a three-dimensional object to examine real obstacle avoidance during online corrections.

The overall goal of the current study, therefore, was to investigate what the effect of obstacles would be when they specifically interfered with a corrected movement. This necessitated that the effects of the obstacle be isolated to the portion of the reach occurring after the target was perturbed. That is, if an obstacle was shown to affect a reach prior to the online correction, then any avoidance we observed during the online correction would not be guaranteed to reflect an updated obstacle representation, but rather could merely reflect the correction of an already deviated reach (e.g. see Liu & Todorov, 2007 where they take advantage of planned deviations around obstacles in order to observe online corrections in longer duration movements). To overcome this problem, we capitalized on our earlier observation that obstacles placed at a depth beyond a target no longer affect reach trajectories (Chapman & Goodale, 2008). Participants therefore made reaches to an initial target position in the presence of a single obstacle whose position varied but, critically, remained behind the initial target. When the position of the target was rapidly changed (at reach onset on one third of trials), it was moved both laterally (left or right) and further in depth. Therefore, an obstacle which had been beyond the initial position of the target could now be located between the hand and the new position of the target. We predicted that reaches would be affected by obstacles only when the target jumped to the side of space where the obstacle was positioned; for example, a reach correcting for a rightward jump of a target would be unaffected by an obstacle on the left.

3.2. Methods

3.2.1. Participants

A group of 21 right-handed (determined by self-report) adults (4 male, mean age 21.9 years, range 18 to 51) were included in this study. All participants had normal or corrected-to-normal vision and all participants were naïve to the purpose of the experiment. The present study is part of ongoing research that has been approved by the local ethics committee.

3.2.2. Materials and Design

Participants sat in front of a dimly lit 1 m x 1 m table covered in black fabric with a laterally centered start button located 15 cm from the front edge of the table. Participants wore PLATO LCD goggles (Translucent Technologies, Toronto, Canada) to control visual feedback and had OPTOTRAK (Northern Digital Inc., Waterloo, Canada) infrared markers (IREDs) taped to the tip and the base of their right index finger. During recording, the position of each IRED was tracked by two OPTOTRAK cameras at a rate of 100 Hz for 3 s. Marker wires were held in place with elastic wrist and elbow bands to allow for unrestricted arm movement.

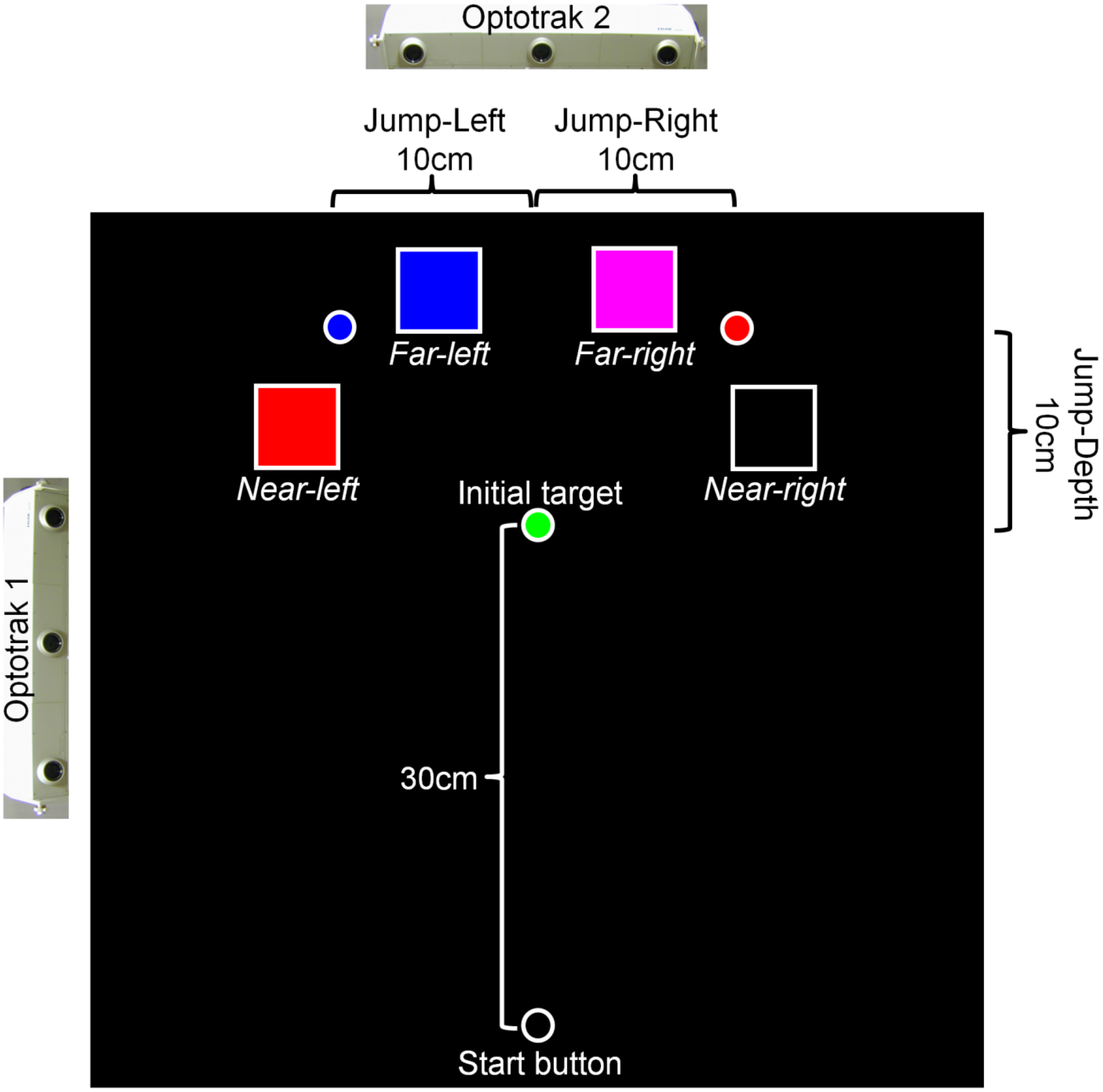

Figure 3.1. Experimental setup with target and object positions. Participants made reaches from the start button to the Initial Target (green circle) which were on a 1 m x 1 m black fabric board. On 1/3 of trials, the target jumped in depth and to the Left (blue circle) or Right (red circle). When an object was present it appeared in one of four positions (indicated by coloured squares, size and position to scale). Movements were recorded using two OPTOTRAK cameras (one left, one in front) at 100 Hz.

Tall rectangular objects (4x4x25 cm, with IREDs in the middle of the top facing surface), were placed in four different positions (2 depths x 2 sides of space): near-right (the centre of the inside edge of the object was 10 cm right of the midline and 35 cm in depth from the start button), far-right (the centre of the front edge of the object was 5 cm right of the midline, 40 cm from start button), near-left (the centre of the inside edge of the object was 5 cm left of midline, 35 cm from start button) and far-left (the centre of the front edge of the object was 10 cm left of midline, 40 cm from start button) [see Figure 3.1]. A fifth condition was included in which no objects were placed on the table.

3.2.3. Procedure

Each trial started with participants placing their right index finger on the start button. The goggles were closed, allowing the experimenter to place the objects without the participant seeing. The trial was triggered by the experimenter, causing the goggles to open and the OPTOTRAK to start recording. Participants were instructed to reach to the target (red LED placed 30 cm directly in front of the start position) quickly and accurately as soon as it became visible (i.e. when the goggles opened). They were told to ignore any objects that were on the table and that there could be one or no objects present on any given trial. On most trials (160/240), the target position remained unchanged. On some trials (80/240), however, the target would ‘jump’ to a new location when the participants released the start button. Of the 80 target jump trials, 40 were jumps to the left (10 cm to the left and 10 cm further in depth) and 40 were jumps to the right (10 cm to the right and 10 cm further in depth) [see Figure 3.1]. The 40 jump-left and 40 jump-right trials were evenly split across the five obstacle conditions, such that there were 8 repetitions of each obstacle condition and jump direction. All trials were completely randomized. Prior to the experiment participants were given 24 practice trials where no objects were present. On 16 of the practice trials, the target did not jump; on 4 trials, there was a rightward jump; and on 4 trials there was a leftward jump.

3.2.4. Data Processing

All analyses were conducted on data from the IRED on the tip of the right index finger. Raw 3D data for each trial was filtered using a low-pass Butterworth filter (dual pass, 10

Hz-cutoff, 2nd order). Instantaneous velocities in each cardinal dimension (x,y,z) were calculated for each time point and the resulting velocity profiles were filtered (low-pass Butterworth filter, dual pass, 12 Hz-cutoff, 2nd order) and combined to create a vector velocity (i.e. three-dimensional) profile for each trial. Onset of reaches were defined as the first of four consecutive vector velocity readings of greater than 20 mm/s where there was a total acceleration of 20 mm/s^2 across the four points. Reaches were said to terminate when whichever of two conditions was first met: the first of three consecutive displacement readings back toward the start button (i.e. three negative displacements in the y-direction) or the first time the velocity dropped below 20 mm/s.

Missing data from a fingertip IRED that was temporarily blocked from the view of the OPTOTRAK cameras due to the positioning of the objects was filled in with data from the finger-base IRED. This was accomplished by translating the base IRED data to the last known position of the tip IRED, using the base IRED data over the missing segment, then stretching (in all three dimensions) the endpoint of the filled sequence to match the position of the tip IRED when it reappeared. When both IREDs were missing, the data were interpolated using the inpaint_nans function (available online at: http://www.mathworks.com/matlabcentral/fileexchange/4551) in Matlab. Interpolation was required on only 5 trials across an average of less than 3 time points.

Trials were rejected for the following reasons: The reach was too short in either duration (<100 ms) or distance (<150 mm in depth), the obstacle was misplaced by the experimenter, or a collision with an object was detected (object moved by more than 5 cm). Under these criteria, <1% of the trials were rejected (for complete analysis of removed trials, see section 3.3.3). All trajectories were translated such that the first reading of the index finger IRED was taken as the origin of the trajectory (i.e. 0,0,0 in 3D Cartesian space, x = horizontal, y = depth, z = vertical). Trials were then spatially normalized using functional data analysis techniques (Ramsay & Silverman, 2005) whereby B-splines were fit to each dimension of the raw data. This allowed us to extract the lateral (x) values from 200 points equally spaced across the reach distance (y) (for details, see Chapman et al., 2010).

3.3. Results

We analyzed data from experimental trials only. To identify reaches to an incorrect target position (i.e. not reacting to a target jump), we performed a cluster analysis of each participant's reach endpoints (in the x and y dimension) when they reached toward each of the three target positions (collapsed across all object positions) and removed any reaches with endpoints further than 5 cm from the mean of their largest cluster. Every participant's largest cluster of points was within 5 cm of the actual target position and less than 2% of trials were removed for having an incorrect endpoint. To account for trials where participants performed two discrete movements (rather than one continuous online correction) we also removed trials where there was a reacceleration in the y-dimension that exceeded 20% of the peak y-velocity. While some reacceleration was expected (given that targets jumped 10 cm in depth) we wanted to isolate true online corrective behaviour; less than 2% of trials were removed for exceeding the reacceleration criterion (for complete analysis of removed trials, see section 3.3.3). After trial removal, any participant with fewer than 4 repetitions of any condition (jump-type x obstacle-position) was excluded from analysis. Three participants were removed with the application of this criterion, leaving n=18 for all statistical analysis.

3.3.1. Spatial trajectories

For each participant the spatially normalized reach trajectories were averaged across each of the 15 experimental conditions (3 jump-types x 5 object-positions). We then conducted a set of planned repeated-measures functional-ANOVAs (implemented in Matlab 7, using custom code adapted from: http://www.psych.mcgill.ca/misc/fda/) to separately examine the effects of obstacles when participants reached to the initial target position and the effects of obstacles when they made a correction to a jumped-target. The functional-ANOVA compared the lateral (x) deviation at different reach distances (y) across the different conditions. This statistically sensitive technique, which extends a traditional univariate ANOVA to all points in a curve, allows a quantification of not only if, but also where and with what magnitude, the trajectories differed (Ramsay & Silverman, 2005, see Chapman et al., 2010 for recent use and details of this technique). Because we used a repeated-measures design in the functional-ANOVAs, we applied a

Greenhouse-Geisser correction for correlations across conditions at each time point. The obvious advantage of using functional versus discrete measures of movements is that a more complete description of the evolution of differences is available. However, this necessitates that each trajectory be fit mathematically, and, as a relatively new analysis technique, statistical conventions (i.e. appropriate alpha levels) have yet to be agreed upon. For this reason, we present the functional output corresponding to the range ($p < 0.1$ to $p < 0.00001$) of statistical significance across the movement (see significance bars and legends in Figures 3.2 and 3.3) to allow for a complete depiction of the pattern of differences.

3.3.1.1. Reaches to initial target position

Since it was important to establish the baseline effects of the objects, we compared reaches made to the initial target position with objects in each position. The results of the repeated-measures functional-ANOVA are shown with the grey significance bar in Figure 3.2. The position of the grey colouring corresponds to the locations along the reach distance (y) where the trajectories differed in the lateral (x) dimension, with the intensity of the colour corresponding to the magnitude of the statistical difference. As can be seen, the objects had a significant effect on lateral deviation throughout the reach. To investigate this effect, we conducted functional pair-wise comparisons (implemented as two-level repeated measures functional-ANOVAs) between all pairs of trajectories (see inset, Figure 3.2). This analysis revealed that the differences in trajectories due to objects were entirely driven by the objects in the ‘near’ positions. That is, when an object is in the near-right position (black trace, Figure 3.2) the average trajectory was significantly shifted to the left and when the object was in the near-left position (red trace) the trajectory was shifted to the right. These two trajectories were significantly different from all the other trajectories, and no other trajectories significantly differed from one another. It should be noted that while there were clearly significant differences due to the presence of obstacles, these effects are very small (x-axis magnified 8 times in Figure 3.2) with the largest difference from baseline spanning less than 5 mm. This subtle yet significant deviation speaks to the remarkable sensitivity of the visuomotor system when avoiding potential obstacles. However, it does indicate that the two ‘near’ object positions interfered with the reach even during unperturbed reaches, and thus may result in different reach behaviour when online corrections are required.

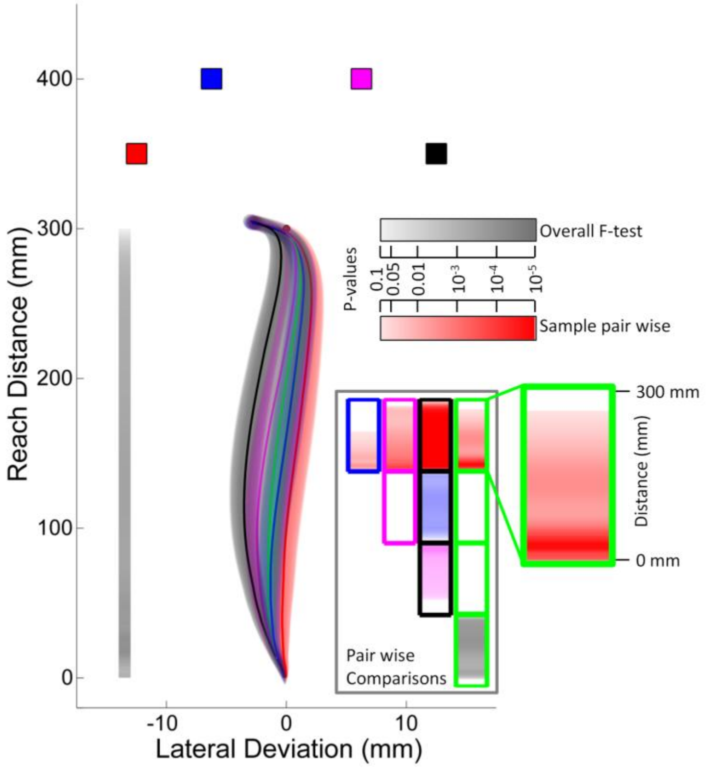

Figure 3.2. Overhead view (x,y) of average (average of 18 participants' individual average) reach trajectories to the initial target (small red circle) with objects in each position (position and size not to scale). Trajectory traces are colour coded to match the object positions (green = no objects, note: x-axis magnified 8x). Shaded area around trajectory traces represents average standard error across 18 participants. Grey significance bar to the left gives a measure of where there were statistical differences (magnitude of difference is proportional to intensity of grey – see P-Value legend, note P-values are Greenhouse-Geisser corrected) between trajectories in the lateral dimension. Inset: Functional pair-wise comparisons between all possible pairs of trajectories arranged as a matrix. Each row (colour inside of box) and column (border of box) corresponds to a different object position with the intersection being the comparison between those two trajectories. Within each intersection box, the position of the coloured area corresponds to where along the reach distance (y) the trajectories differed in the lateral (x) dimension with the intensity of the colour corresponding to the magnitude of the statistical difference (see P-value legend and exploded box to side, where the (red) Near-Left trajectory is being compared to the (green) No-Object trajectory).

3.3.1.2. Reaches to jumped target positions

For clarity, we separately analyzed reaches on jump-target trials with objects to the left of midline (near-left and far-left, Figure 3.3a) and reaches made on jump-target trials with objects to the right of midline (near-right and far-right, Figure 3.3b). Within each of these sets of trajectories (objects-left and objects-right) we conducted three functional-ANOVAs: one comparing jump-left versus jump-right trials (results indicated with green significance bars), and the second and third comparing the effect of the objects on the jump-left and jump-right trials respectively (results indicated with the grey significance bars on the left and right of plots).

For both the objects-left and the objects-right, the difference between jump-left and jump-right trials begins to be (and thereafter remains) significant ($p < 0.05$) approximately 17 cm (or 43%) into the y-movement (see green significance bars, Figure 3.3). This is markedly different from how the reaches on no-jump trials were affected by the objects.

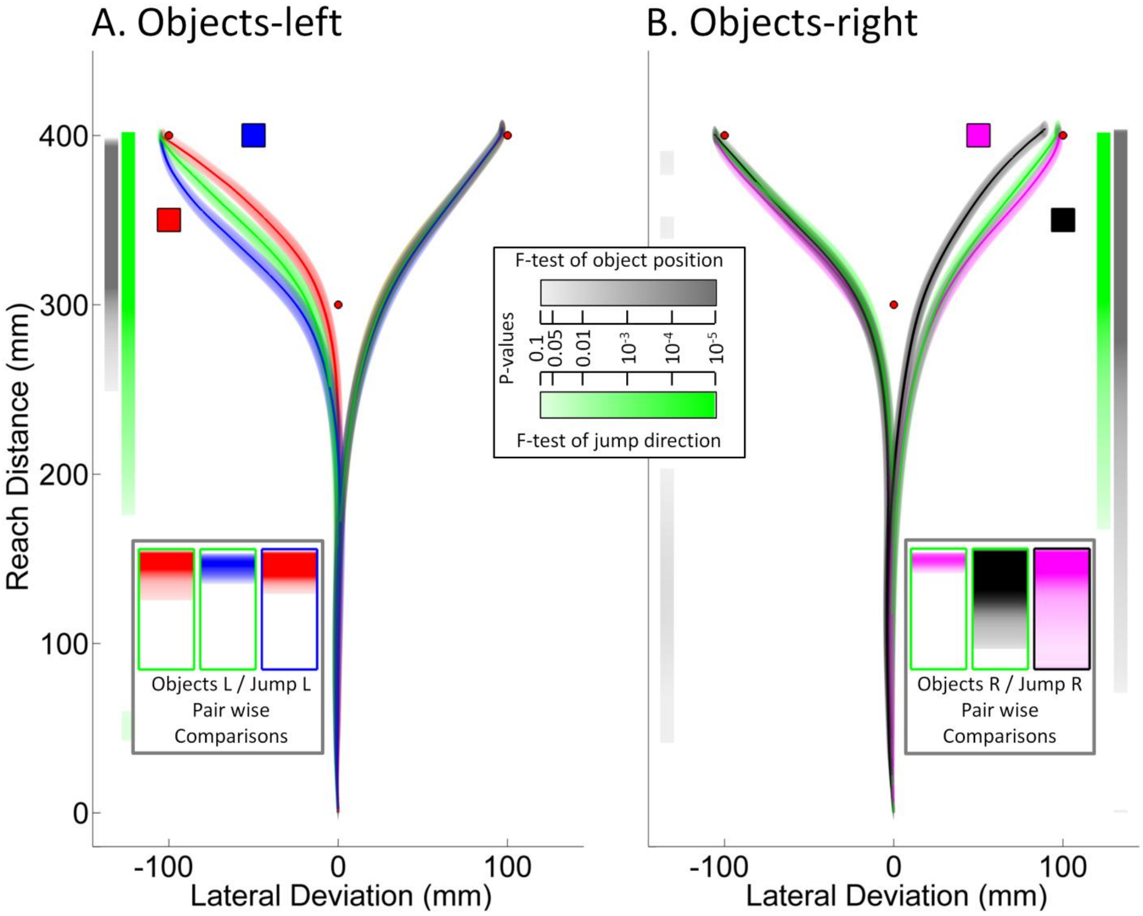

Figure 3.3. Overhead view (x,y) of average reach trajectories to the jumped target positions with objects on the Left (A) or Right (B). Trajectory traces are colour coded to match the object positions (green = no objects, object size not to scale). Shaded area around trajectory traces represents average standard error across 18 participants. The grey significance bars denote where there was an effect due to obstacles for a given jump direction and the green significance bars denote where the jump-left and jump-right trials were significantly different (magnitude of lateral deviation difference is proportional to intensity of colour – see P-Value legend – note its location does not obscure any part of the significance bar in (B). Insets: Functional pair wise comparisons between trajectories for target jumps left and obstacles-left (A) and target jumps right and obstacles-right (B). Configuration of pair wise comparison boxes is identical to Figure 3.2.

On object-left trials (Figure 3.3a), the effect due to objects emerges much later in the reach (25 cm or 63% of y-movement, grey significance bar to the left, Figure 3.3a) *but only* on trials where the target jumped to the left. That is, when the target jumped to the right there was no difference between either of the object conditions or the baseline (no object, green-trace) trials. When we investigated the effect of left-objects on left-jump trials further, the pair-wise functional comparisons (see inset Figure 3.3a) confirmed what is visually apparent – the left-near (red-trace) reaches were driven further in depth and to the right, while the left far (blue-trace) reaches were driven closer in depth and to the left relative to the baseline (no-object, green-trace) reaches.

The pattern observed on the object-right trials (Figure 3.3b) is similar, though it is somewhat obscured by the interference that was observed when participants reached to the initial target position (described above). That is, reaches with objects in the near-right location (black-traces) were initially shifted slightly left, leading to significant differences in trajectories early in the movement (grey significance bars to the left and right, Figure 3.3b). Importantly, however, these differences were observed for both jump-left and jump-right trials. Critically, only on the jump-right trials did the effects due to objects persist (and become more significant) late in the reach. The pair-wise functional comparisons (inset Figure 3.3b) confirmed this finding, with only the near-right trace being significantly different from the baseline (no-object, green trace) trials early in the movement. The pair-wise comparisons also revealed how the objects affected the reaches during the online correction. Similar to the left-object trials, on the right-object trials the near-right location (black-trace) drove the hand further in depth and to the left, while the far-right location (pink trace) drove the hand closer in depth and to the right.

Overall, once the initial interference effects were accounted for, there were two major findings from the analysis of the reach trajectories on jump-target trials. First, the deviation due to the hand reacting to the jumped target occurred earlier (in space) than the effects due to objects. Second, these object effects, which occurred exclusively during the online correction, showed a clear pattern of obstacle avoidance, consistently moving the hand away from the object position.

3.3.2. Temporal profiles

Of course, it is not possible to characterize the effect of obstacles by analyzing only the spatial component of the reach. What appear to be automatic and fluid spatial deviations away from objects that interfere with corrected movements could actually come at the expense of significant velocity reductions. To examine the temporal component of the reaches we analyzed three dependent measures determined from the vector (3D) velocity: peak-velocity, time to peak velocity and percent time to peak velocity. To complement the velocity analysis, we also examined reaction time and movement time. Above, we described a spatial definition of where trajectories on target-jump trials became significantly different from no-jump trials, but here we wanted to provide a rigorous temporal definition of correction latency for reactions to jumps in both directions. To calculate this, we performed 2 two-level (jump-left vs. no-jump and jump-right vs. no-jump) MANOVAs (with three dependent variables, one each for x, y and z velocities) at each time point (defined by frames) for each participant. The correction latencies were defined as the first time point where these MANOVAs became ($p<0.05$) and remained significant for the longest number of consecutive frames.

For each participant, each of the non-latency measures was entered into a two-factor jump-type x object-position (3x5) repeated-measures (RM) ANOVA and the latency measure was entered into a two-factor jump-direction x object-position (2x5) RM-ANOVA (all RM-ANOVAs Greenhouse-Geisser corrected, significant at $p<0.05$). Means and results for these tests are shown in Table 3.1. The average vector velocity and lateral velocity (where the greatest differences due to jumped targets were expected) traces for no-object trials, as well as the left and right correction latencies are shown in Figure 3.4a. The vector and lateral velocity traces for trials with objects are shown in Figure 3.4b. The results naturally fell into two categories – effects due to jump direction and effects due to object position.

Table 3.1 – The means and statistical results for the temporal dependant measures.

Reaction time (ms)

	No-Obj	Near-L	Far-L	Far-R	Near-R	F	
	351.79	331.65	331.59	335.26	333.92	**	No-Obj > Rest

Movement time (ms) Interaction** Jump-type x Object-position

	No-Obj	Near-L	Far-L	Far-R	Near-R	F	
No-jump	471.44	468.93	470.03	471.97	468.33	ns	
Jump-L	695.78	719.98	714.65	692.96	696.49	*	Near-L > No-Obj, Far-R, Near-R
Jump-R	625.91	615.85	608.59	635.85	759.27	**	Near-R > Rest; Far-R > Near-L

Peak velocity (mm/s) Interaction* Jump-type x Object-position

	No-Obj	Near-L	Far-L	Far-R	Near-R	F	
No jump	1334.78	1325.37	1323.28	1326.80	1322.42	ns	
Jump-L	1319.81	1320.90	1307.08	1319.77	1332.48	ns	
Jump-R	1402.48	1389.38	1400.22	1392.95	1344.26	*	none

Time to peak velocity (ms) Interaction* Jump-type x Object-position

	No-Obj	Near-L	Far-L	Far-R	Near-R	F	
No jump	223.70	221.90	222.74	223.48	223.07	ns	
Jump-L	217.56	228.11	229.94	223.53	226.94	ns	
Jump-R	250.66	250.72	256.52	250.63	231.67	*	Near-R < Near-L, Far-L

Percent time to peak vel (%) Interaction** Jump-type x Object-position

	No-Obj	Near-L	Far-L	Far-R	Near-R	F	
No jump	47.44	47.17	47.44	47.39	47.50	ns	
Jump-L	31.44	31.72	32.33	32.39	32.72	ns	
Jump-R	40.72	41.28	42.50	39.89	31.11	**	Near-R < Rest; Far-R < Near-L

Correction latency (ms)

	No-Obj	Near-L	Far-L	Far-R	Near-R	F
Jump-L	299.44	317.78	309.44	310.55	313.89	ns
Jump-R	268.89	266.67	269.44	278.89	286.11	ns

Where significant, the strength of an interaction is indicated in the row with the measure name. The ‘F’ column shows the results of an F-test of the main effect (or simple main effect) of the means in a given row (Greehouse-Geisser corrected). Results from pair wise contrasts (Bonferroni corrected) are shown next to each significant F-test. * & < or > = $p<0.05$, ** = $p<0.005$. ns = not significant.

3.3.2.1. Effects due to jump direction

Overall reaches requiring corrections to the left were much slower than reaches requiring corrections to the right (independent of object position). This resulted in reaches with longer movement times, lower peak velocities and more time spent decelerating (earlier peak velocities) for jump-left as compared to jump-right trials. Given these velocity differences, it is not surprising that we also observed longer correction latencies for reaches correcting left than for reaches correcting right (see Table 3.1 and Figure 3.4a, correct-left versus correct-right differences are also reflected in our analysis of error trials, see section 3.3.3). This finding replicates the result that is obtained when right-handed participants make online corrections to the left and right with their right hand (Carnahan, 1998) and is consistent with biomechanical factors like limb inertia (Gordon, Ghilardi, Cooper, & Ghez, 1994).

3.3.2.2. Effects due to object position

Of more interest to the current study were the effects of the non-target objects on trials when the target jumped at reach onset. Since we predicted that objects to the left and right of midline would have different effects depending on the direction of the target jump, we were specifically interested in investigating interactions between jump-type (or jump-direction) and object-position. As such, any variable with a significant interaction between these factors was further investigated by running a single factor RM-ANOVA of the five obstacle positions for each of the three jump-types (see Table 3.1).

It should be noted that reaction time showed a significant effect only for object position. This was driven by slower responses when no object was present, a finding which replicates our previous work (Chapman & Goodale, 2010). Aside from reaction time, all other non-latency measures showed a significant interaction between jump-type and object-position. The results from movement time follow from the trajectory results. Reaches that deviated from the no-object trajectories showed longer movements. That is, there was no significant effect of object position on movement time when making reaches to the initial target position but a significant effect of object position on both jump-left and jump-right trials. For both left and right jumps, the movement times were longer when objects were on the side of the final target position (i.e. left objects for left jumps) and longest for the objects in the near positions.

From only movement times, however, it is difficult to tell if these longer duration movements are the result of a larger distance travelled by the hand or a decrease in velocity. When examining the interaction between target-position and object-position for the velocity variables (peak velocity, time to peak velocity and percent time to peak velocity) it appears that only for jump-right trials does the position of the object actually cause a significant slowing of the reach. Specifically, there was no effect of object-position when the target remained in the initial position or when the target jumped to the left, but for jump-right trials, all velocity variables showed an object-position effect. From pair-wise comparisons (Bonferroni corrected, $p<0.05$), the significant object effect on jump-right velocities was shown to be caused almost entirely by a significant slowing of the reach (lower peak velocity and longer deceleration phase) only when the object was in the near-right location. While no specific velocity measure showed an effect of obstacle position on jump-left trials, it should be noted that there was evidence of temporal interference caused by the near-left location, as suggested by the velocity profiles (Figure 3.4b) where the jump-left trials with objects in the near-left position (red dashed trace) show departures from the no-object trials (green shaded region) especially in the lateral velocity profile.

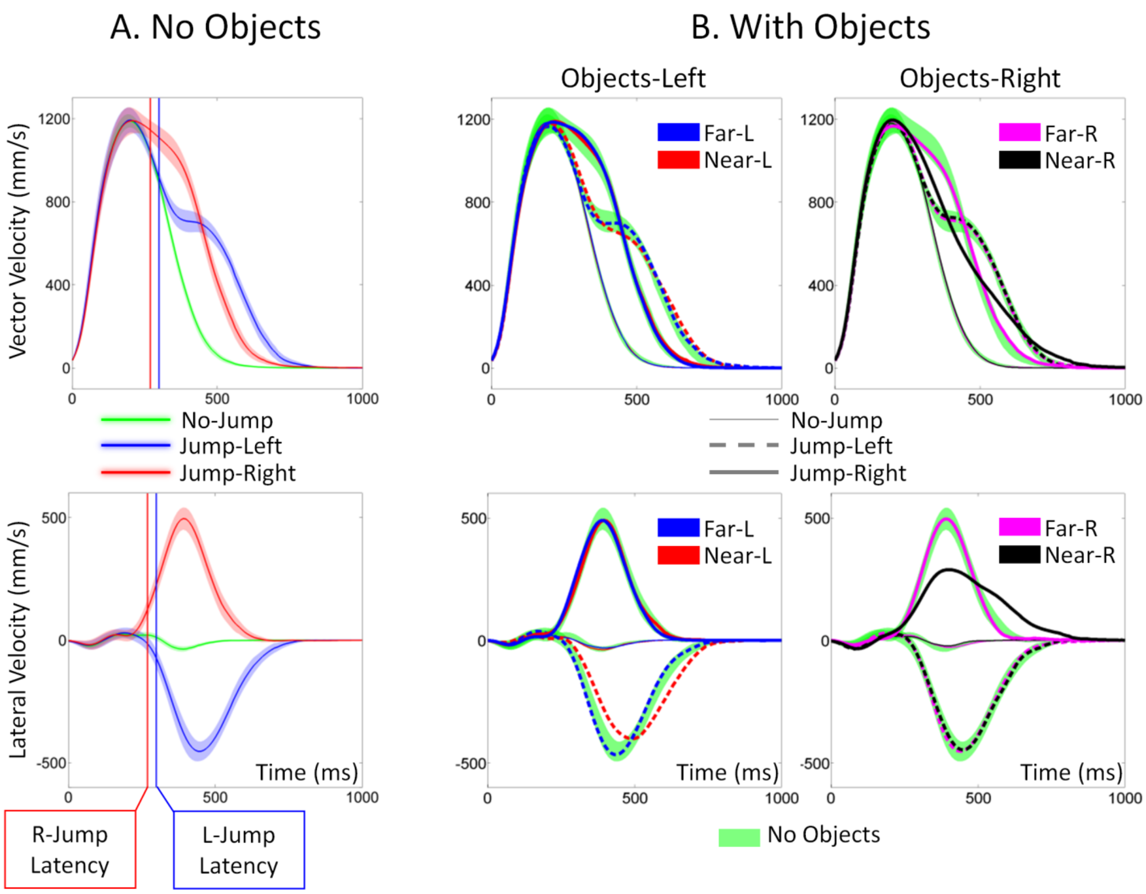

Figure 3.4. Average vector velocity (top) and lateral velocity (bottom) traces for trials with (A) No objects and (B) Objects. (A) Trace colour denotes jump direction: green = no jump, blue = jump left, red = jump right. Shaded area around trajectory traces represents average standard error across 18 participants. Vertical lines denote the correction latency for jumps to the right (red) and left (blue). (B) Trace colour denotes the position of the object: blue = Far-Left, red = Near-Left, magenta = Far-Right, black = Near-Right. The style of the line denotes the jump direction: thin = No-Jump, dashed = Jump-Left, thick = Jump-Right. The green shaded region corresponds to the shaded regions in A) (No Objects) and serves as a baseline.

From the observed effects, it is clear that objects that become obstacles during an online correction can interfere with the movement spatially and temporally. However, it is critical to know if this interference occurs before or after the correction is initiated. To test this, we looked at the effect of object position on the correction latencies. If the position of the object had an effect on correction latencies, then it could be argued that the observed obstacle interference occurred prior to the initiation of the online correction. Importantly, the correction latencies showed neither a significant interaction between object-position and jump-direction, nor a significant main effect of object position for either the jump-left or jump-right trials. This suggests that the observed obstacle interference occurs only *after* the correction has been initiated.

Taken together, the results from analyzing the temporal profiles of the reach suggest that the fluid avoidance of obstacle during online corrections seen in the spatial trajectories can occur without any significant alteration in the velocity of the reach. However, if the risk for collision during a correction was high (which is certainly the case for the near-right position, which accounted for all 10 collisions detected across all participants, see section 3.3.3) we saw that the spatial avoidance was accompanied by significant velocity reductions. This effect can be seen in Figure 3.4b. Here, for reaches with objects on the left, only reaches corrected left and with an object in the near-left position (dashed red trace) showed some evidence of temporal interference. This effect was much stronger for reaches with objects on the right, where reaches corrected right with an object in the near-right position (thick black trace) showed large velocity reductions.

3.3.3. Supplemental Error Analysis

Some trials were rejected prior to extracting the reach trajectory from the recorded data. Here we elaborate on the exact number of trials that were rejected for each of the following reasons: (1) The reach was too short in either duration (<100ms, 3 total trials) or distance (<150mm in depth, 6 total trials), (2) the obstacle was misplaced by the experimenter (18 total trials), (3) or a collision with an object was detected (object moved by more than 5 cm, 13 total trials).

The most interesting of these rejected trials are the collisions. Of the 13 collisions detected, 10 occurred on trials where a target jumped (these 10 collisions were spread across 8 subjects, meaning that 10 subjects had no collisions on jump trials). The three that occurred on the non-jump trials were likely the result of the table being shifted (thus causing the obstacle to topple) or the experimenter moving the obstacle prior to the completion of data recording (thus the object would appear to move during the trial).

Interestingly, all 10 of the collision trials occurred when the target jumped to the right and the obstacle was in the Near-Right position. This confirms that in this configuration the chance for collision was highest, thereby lending credence to our interpretation of the velocity slowing observed on these trials being related to the potential for collision. It is possible (though highly unlikely given that less than 50% of our subjects (8/18) had collisions on less than 25% (2/8) of trials in this configuration) that by excluding these trials we may have biased our results and exaggerated the avoidance effect. To rule out this possibility, we show in Figure 3.5 the trajectory traces (thin black lines) from each of the 10 collision trials overlaid on the relevant average trajectories from Figure 3.3b. It is clear from this figure that on only one collision trial was the trajectory significantly closer to the object than on the trials when it was successfully avoided. The remaining nine collision trials are all pushed away from the obstacle position, relative to the baseline trials (green) and the majority of them (7/9) are actually further from baseline than the plotted average. Overall, this indicates that even if had we included these 10 trials, the average would – if anything – be shifted even further from baseline. It also indicates that it may not have been the hand but the forearm that was colliding with the obstacles (in fact from anecdotal observation it was almost always the forearm that struck the obstacle). Finally, we would also argue that on trials when the obstacle was successfully avoided in this configuration, the margin for error was quite small – again strengthening our claim that for corrections to the right with an object in the near right location special care is required (as reflected in our velocity analysis).

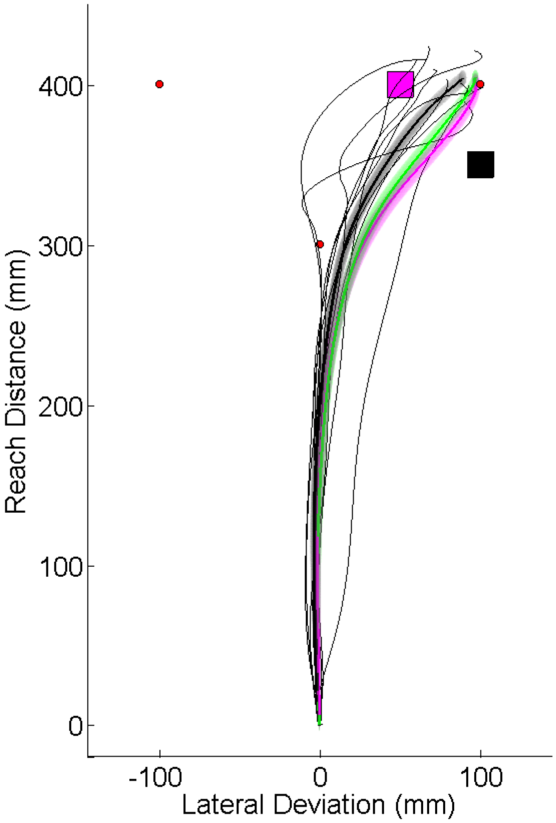

Figure 3.5. Collision trajectories (thin black traces) from Jump-right, obstacle Near-Right trials overlaid on average trajectory traces taken from Figure 3.3b. Only one collision trial seems to follow a path significantly different than the non-collision trials from the same configuration (thick black trace with average standard error).

A second set of trials was removed after reach extraction for having an incorrect endpoint (61 total trials, see Table 3.2). Again, it could be the case that by removing only these trials, we were removing some set of data that biased our results to show a larger avoidance effect (there does appear to be some bias toward removing trials that jumped left with obstacles on the left, see Table 3.2). To argue against this possibility we show a scatter plot of the endpoints of trials rejected due to this criterion (see Figure 3.6). On only one trial did a participant incorrectly point to a jumped target location when in fact the target did not jump (green dot). By comparison, the vast majority (42/61) of these trials were rejected because participants failed to correct to the jumped target location, instead completing a movement toward to the initial target position (red and blue dots within the green circle). Of the remaining trials (18/61), 3 incorrectly ended to the right when the target jumped left (blue dots in the red circle) while 15/61 appear to be the result of partially corrected movements, mostly ending beyond the initial target and between the two jump locations. Of trials that were rejected for an incorrect endpoint, 39/61 were on trials when the target jumped left (blue dots) and 21/61 were on trials when the target jumped right (red dots). This pattern confirms that participants had a slightly harder time correcting to leftward jumps. More importantly, this analysis of endpoint errors shows that these rejected trials were due to problems in correction and had no specific relevance to the reported avoidance effect.

Table 3.2 – Tally of rejected trials.

	Jump-Left					Jump-Right				
	No	Near-L	Far-L	Far-R	Near-R	No	Near-L	Far-L	Far-R	Near-R
Endpt	12	9	13	5	0	8	1	3	6	3
Accel	9	7	15	5	6	5	2	0	6	1

Rejected trials broken across reason for rejection (Endpoint, row 1, see Figure 3.6; Acceleration, row 2, Figure 3.7), Jump-direction and Obstacle Position. More trials were rejected that Jumped-Left, corresponding to the greater difficulty correcting in this direction. There appears to be some bias for rejecting trials that jumped left, specifically when obstacles were on the left – justifying further analysis of behaviour on these error trials to confirm we did not selectively bias our data to show an avoidance effect. Note one trial rejected due to endpoint came from a No-Jump trial and is not represented in this table (but see green dot in Figure 3.6)

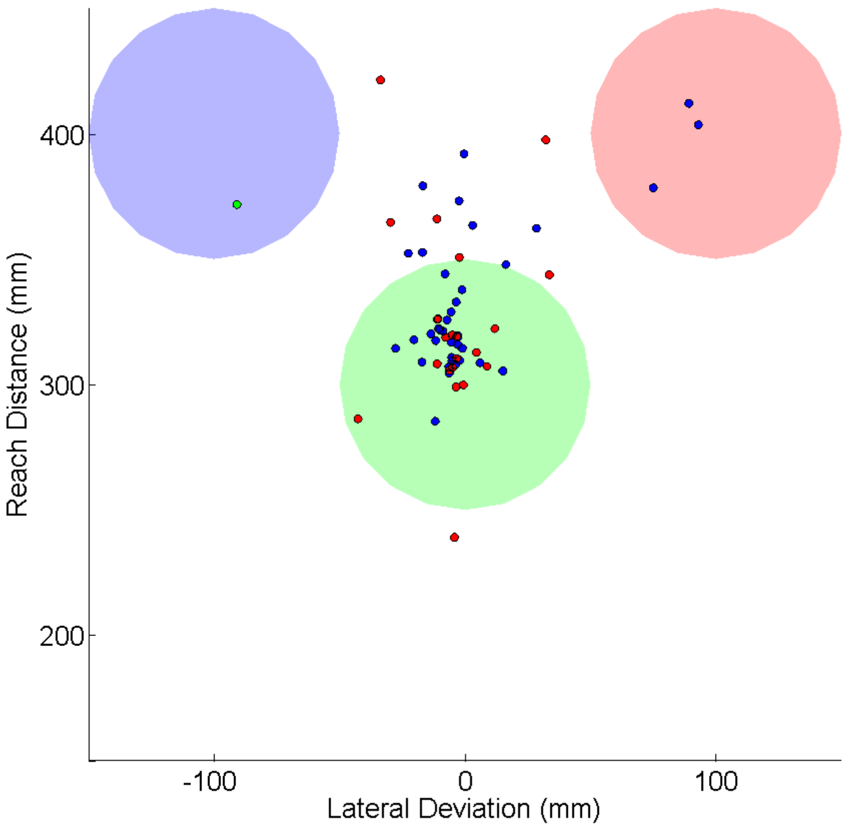

Figure 3.6. Analysis of endpoints of trials removed for having an incorrect endpoint. Green dot = no-jump trial, Blue-dots = jump-left trial, Red-dots = jump-right trial. Large green, blue and red circles indicate the approximate size and location of the cluster regions defined as correct for each of the initial, jump-left and jump-right trials respectively (note actual cluster location determined for each individual - see main text). The majority of rejected trials were ones that terminated at the initial target when a correction was required.

A final set of trials was removed after reach extraction for having re-accelerations suggesting a non-continuous correction toward a jumped target (56 total trials, Table 3.2). Of these, the majority (42/56) were on jump-left trials compared to only 14/56 on jump-right trials. This again confirms that correcting to the right occurred more automatically in the current study. Again, it is possible that the subset of trials that were removed could have biased our data (this again appears as if it may be true since more trials that jumped left with obstacles on the left were removed, see Table 3.2). To clarify this issue we plot the average trajectories on the rejected trials in cases where an obstacle needed to be avoided. The most important thing to note about these trajectories is that they all come much closer to (indeed in most cases cross) the initial target position. This confirms that these trials represent cases where participants likely completed the reach to the initial target before making a second movement toward the jumped location. As such, we had good reason to reject these trials as not being representative of true online corrections. It is also clear, however, that even during these double movements the position of the obstacle still influenced the latter half of the movement. This is specifically true on the left where the obstacles induced a clear pattern of avoidance. On the right, the pattern of avoidance is slight, but these trajectories represent the average of only 6 trials (magenta) and a single trial (black) so it is difficult to draw conclusions from this specific pattern.

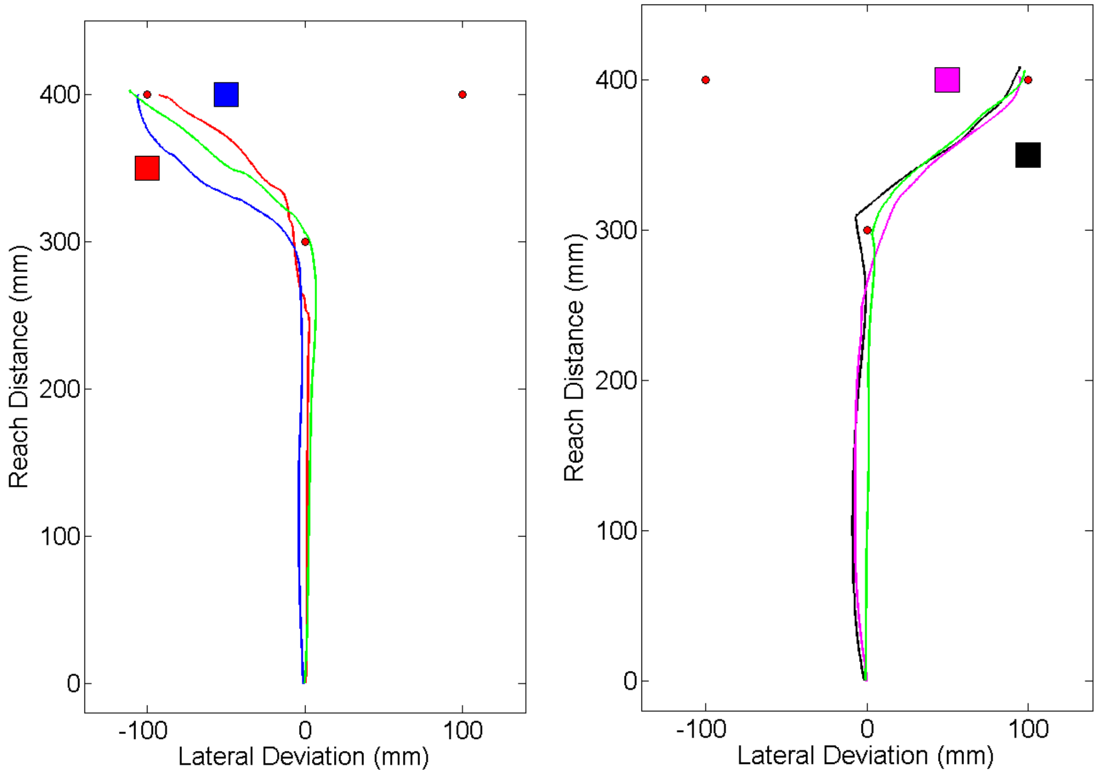

Figure 3.7. Trajectories of trials removed for having significant re-accelerations during online corrections. Left panel – Jump-left trials with objects on the left. Right panel – Jump-right trials with objects on the right. Green lines = no-object trials, Red line = Object Near-Left, Blue line = Object Far-Left, Magneta = Object Far-Right, Black = Object Near Right. Note all trajectories come close to crossing the initial target position, suggesting two separate movements. Despite this, obstacle avoidance effects persist, especially for Jump-Left trials (left-panel).

3.4. Discussion

The primary aim of the current study was to test whether or not participants could avoid an obstacle that became an impediment to a reach only after the initial reach target changed position during the movement. The results from the analysis of the spatial trajectories (Figure 3.3) clearly demonstrate that obstacle avoidance while correcting a reach toward a new jumped-target is possible. Critically, avoidance was observed only when the new target position caused an object to become an obstacle (i.e. when the new position was on the same side of space as the object) and not when the target jumped away from the object. The results from the analysis of the velocity profiles of these reaches (Figure 3.4) demonstrated that in some cases, this spatial avoidance was accompanied by a significant slowing of the reach (when objects were between the hand and the new target, especially on the right) and in others, the spatial avoidance occurred without a significant alteration in the speed of the movement (when objects were at the same depth as the new target).

The design of the current study allowed us some insight into two questions currently being debated in the field of visuomotor control. First, by isolating the obstacle avoidance to the corrected portion of the reach, we were able to provide evidence that the visual context (i.e. objects other than the participant's hand and the target) can affect a reach during online corrections. To make this claim, it was necessary to show that the avoidance effects occurred after the correction to the jumped target. We confirmed this using both a spatial definition of when the correction occurred (reactions to jumped targets occurred closer in depth than avoidance effects, see Figure 3.3) and a temporal definition of when the correction occurred (correction latencies were unaffected by obstacle position, see Table 3.1). The finding that a non-target object has an effect on reaching that is restricted to the automatically corrected portion of the reach is consistent with two recent studies showing that position changes of items other than the target that occurred while the hand was in flight caused deviations in the trajectory of the reach. In one case, the non-target object was the target of an upcoming movement (Cameron et al., 2007) and in the other, the non-target objects were virtual obstacles (Aivar et al., 2008).

The response to perturbations of virtual obstacles observed by Aivar et al. (2008) leads to the second question we were able to investigate: whether or not reacting to real objects during the online correction of a real reach would be different than that observed for corrections in the presence of virtual obstacles during a rapid stylus-pointing task. By varying both the side of space the objects were on and the depth at which they were placed, we were able to show that objects with a higher risk for collision altered not only the spatial trajectories but also significantly slowed the reach. This was especially evident on trials with objects placed in the near-right position when targets jumped to the right (thick black line, Figure 3.4b). The noticeable slowing of reaches on these near-right / jump-right trials may have been caused by the near-right obstacle position being occluded by the moving arm. We do not favour this explanation for two reasons. First, the objects were 25 cm tall and at least some part of the object was always visible regardless of the position of the arm. Second, in previous work (Chapman & Goodale, 2008), short objects which could have been completely occluded by the moving arm resulted in less interference, opposite to the current result for the near-right / jump-right trials. Indeed, we believe the significant slowing noted on these trials was a result of the biomechanics and physical arrangement of the hand and arm which meant the direct path to the new target position was blocked by the near-right object (the difficulty of this configuration was confirmed in an analysis of the collision trials, see section 3.3.3 and Figure 3.5). We also observed some slowing on trials with an object in the near-left position where targets jumped left (dashed red trace, Figure 3.4), but no slowing when objects were in the far positions, or when they were on the side opposite the target jump. This almost parametric slowing is entirely consistent with the degree to which the object was actually an obstacle to the corrected movement. While there are other methodological differences between the current study and the work conducted by Aivar and colleagues (2008), we believe that this novel finding of reach slowing in accord with obstacle interference demonstrates that the real-world consequences of collision with a three-dimensional object results in different reaches from those performed in a virtual context.

It is possible that the different effects we observed between near and far objects on corrected movements had to do with the interference we saw for near objects on non-jump trials (see Figure 3.2). That is, it could be that the slow-down we observed later in the reach for corrected movements toward near objects was actually a consequence of the original deviations induced in the early trajectory by objects in these positions. We do not support this interpretation for two reasons: first the deviation induced by the near objects on non-jump trials was very small (less than 5 mm for both the near-left and near-right object) and occurred only in the lateral dimension, while deviations that occurred during avoidance were much larger (more than 10 mm) and occurred laterally and in depth. Second, the onset of the correction was independent of the position of the objects (see Table 3.1). Specifically, for both the jump-right and jump-left trials, the difference between the correction latency for the near and far locations of objects on the same side of the jump was less than 5 ms. It appears then, that the visuomotor system automatically avoids obstacles in a sensible fashion – providing a margin of error around all objects near the hand path, but slowing the reach only for corrected movements where obstacles truly impede the movement. This extra time likely allows for more deliberate control of an action where the chance of an undesirable collision is high.

Given this study and previous findings, what can be concluded about the representation and encoding of obstacles during movement planning and execution? First, we believe that non-target objects in the reach environment are encoded and accessed similarly to target objects – that is a representation is available during both planning and execution. Until now, there was plenty of evidence showing that obstacles encoded during movement planning affected the subsequent reach movement (Chapman & Goodale, 2008, 2010; Mon-Williams et al., 2001; Tresilian, 1998, 1999). It remained inconclusive, however, whether or not this obstacle representation could be accessed in flight causing the reach (and/or the obstacle representation) to be updated online. Here we show that, like the position of a target, the position of an obstacle can be dynamically accessed and can influence corrected movements. Although we were successful in isolating the obstacle effects to the corrected portion of the reach, we are unable to state conclusively that the observed avoidance during a corrected movement was the result of planned obstacle representations being integrated into the trajectory rather than the result of a new obstacle representation being created in-flight. This issue is ultimately related to whether online correction mechanisms – which use feedback to reduce the error between the original and corrected movement goals – include a feed-forward/predictive signal in the error estimate or whether the error signal arises from purely sensory mechanisms (for discussion of this point see Desmurget & Grafton, 2000). Given the inherent delays in sensory feedback, however, some sort of feed-forward mechanism seems necessary. Recent behavioural and modeling studies confirm the role of prediction in successful online correction (e.g. Danion & Sarlegna, 2007; Gritsenko, Yakovenko, & Kalaska, 2009). One particularly relevant finding is that online corrections to a new target position made while a person was holding a mass in a pinched-grip showed that the grip force adjustments required to accelerate the mass toward a corrected target position preceded the actual in-flight trajectory adjustment (Danion & Sarlegna, 2007). That the grip adjustment can lead the trajectory shift suggests that the consequences of the corrected movement were predicted and compensated for before the trajectory was altered. In the context of the current study, it therefore suggests that the consequences of the corrected movement and the subsequent deviation around the obstacle are predicted and rely on planned obstacle representations. It also suggests that one should be able to see obstacle influences prior to the correction if the expectation is that a corrected movement will be interfered with. That is, if one designed an experiment where the expectation of a target jump was high (much greater than the 1/3 used here) and the direction of the corrected movement was predictable (the target always jumped in one direction) then even the initial movement should be affected by an obstacle that interfered only with the corrected movement. In this case, it would make sense for predictive mechanisms to anticipate the obstacles potential interference and adopt an initial reach that made the upcoming correction easier to perform.

The second conclusion regarding obstacle representations that we infer from the current study is that non-target objects are encoded and accessed by the dorsal visual stream. Since dorsal stream structures have been implicated in both the avoidance of obstacles during non-corrected movements (Schindler et al., 2004) and in performing online corrections toward jumped-targets (Desmurget et al., 1999; Pisella et al., 2000) it follows logically that a task combining both would recruit similar neural pathways. To support this idea, studies recording from cells in the monkey dorsal visual stream have shown populations of neurons that encode multiple potential reach targets (Cisek & Kalaska, 2002, 2005). Given our findings demonstrating sensitivity to obstacles during corrected movements, we believe that the encoding of multiple objects extends to both target and non-target objects. Moreover, recent neuroimaging work in humans (Gallivan, Cavina-Pratesi, & Culham, 2009) has shown that objects within reachable space were preferentially encoded (relative to objects beyond reach) when participants were passively viewing the workspace. While these objects were sometimes the targets of action, on trials in which no action was performed, there was still evidence of encoding in the superior parietal cortex, a critical structure for visuomotor processing in the dorsal stream.

This notion of reachable space provides an elegant way of summarizing our results. When performing reaches to the initial target position where no jump occurred (the majority of trials) the evidence for obstacle encoding was minimal (near objects) or non-existent (far objects). However, on trials where the target did jump and an object impeded the corrected movement, we observed automatic avoidance sensitive to the risks of collision. This suggests that the potential obstacles were encoded on every trial and that reachable space is defined not just by the part of our environment we are most likely to act in but includes everything within reach of our acting hand. This conclusion resonates with a recent review (Baldauf & Deubel, 2010) which argues that visuomotor planning (or ‘visual preparation’) automatically results in the dynamic deployment of attention across all of reachable space. This attentional landscape allows for multiple relevant locations in the workspace to be processed in parallel. Following from this idea, in the current experiment potential targets and potential obstacles must have been encoded simultaneously in order to produce the reported effects on reach behaviour. Presumably there are limits on both the number of objects that can be represented in parallel as well as the spatial extent over which the concurrent representation of objects can occur (explaining why objects well out of reach have no effect on movements). Exactly what defines reachable space, the objects in it and how it must be dynamically modulated both by our movements through the environment and by our goals remains an open and interesting question.

3.5. Conclusion

Rather than consider only the encoding of the hand and target, it should be acknowledged that the entire reach environment must be represented in order for humans to successfully act in the real world. It is obvious that obstacles in the environment necessarily affect our movements; after all the consequences of colliding with a particularly dangerous obstacle are likely more dire than the consequences of missing a target. Here we provide evidence that obstacle encoding shares one critical feature with target encoding in that movements were automatically deviated in reaction to changes in both target and obstacle information that occurred while the hand was in flight.

3.6. References

Aivar, M. P., Brenner, E., & Smeets, J. B. (2008). Avoiding moving obstacles. *Exp Brain Res, 190*(3), 251-264.

Baldauf, D., & Deubel, H. (2010). Attentional landscapes in reaching and grasping. *Vision Res, 50*(11), 999-1013.

Brenner, E., & Smeets, J. B. (1997). Fast Responses of the Human Hand to Changes in Target Position. *J Mot Behav, 29*(4), 297-310.

Cameron, B. D., Franks, I. M., Enns, J. T., & Chua, R. (2007). Dual-target interference for the 'automatic pilot' in the dorsal stream. *Exp Brain Res, 181*(2), 297-305.

Carnahan, H. (1998). Manual asymmetries in response to rapid target movement. *Brain Cogn, 37*(2), 237-253.

Chang, S. W., & Abrams, R. A. (2004). Hand movements deviate toward distracters in the absence of response competition. *J Gen Psychol, 131*(4), 328-344.

Chapman, C. S., Gallivan, J. P., Wood, D. K., Milne, J. L., Culham, J. C., & Goodale, M. A. (2010). Reaching for the unknown: Multiple target encoding and real-time decision-making in a rapid reach task. *Cognition, 116*(2), 168-176.

Chapman, C. S., & Goodale, M. A. (2008). Missing in action: the effect of obstacle position and size on avoidance while reaching. *Exp Brain Res, 191*(1), 83-97.

Chapman, C. S., & Goodale, M. A. (2010). Seeing all the obstacles in your way: the effect of visual feedback and visual feedback schedule on obstacle avoidance while reaching. *Exp Brain Res, 202*(2), 363-375.

Cisek, P., & Kalaska, J. F. (2002). Simultaneous encoding of multiple potential reach directions in dorsal premotor cortex. *J Neurophysiol, 87*(2), 1149-1154.

Cisek, P., & Kalaska, J. F. (2005). Neural correlates of reaching decisions in dorsal premotor cortex: specification of multiple direction choices and final selection of action. *Neuron, 45*(5), 801-814.

Coello, Y., & Magne, P. (2000). Determination of target distance in a structured environment: Selection of visual information for action. *European Journal of Cognitive Psychology, 12*(4), 489-519.

Danion, F., & Sarlegna, F. R. (2007). Can the human brain predict the consequences of arm movement corrections when transporting an object? Hints from grip force adjustments. *J Neurosci, 27*(47), 12839-12843.

Day, B. L., & Lyon, I. N. (2000). Voluntary modification of automatic arm movements evoked by motion of a visual target. *Exp Brain Res, 130*(2), 159-168.

Desmurget, M., Epstein, C. M., Turner, R. S., Prablanc, C., Alexander, G. E., & Grafton, S. T. (1999). Role of the posterior parietal cortex in updating reaching movements to a visual target. *Nat Neurosci, 2*(6), 563-567.

Desmurget, M., & Grafton, S. (2000). Forward modeling allows feedback control for fast reaching movements. *Trends Cogn Sci, 4*(11), 423-431.

Desmurget, M., Grea, H., Grethe, J. S., Prablanc, C., Alexander, G. E., & Grafton, S. T. (2001). Functional anatomy of nonvisual feedback loops during reaching: a positron emission tomography study. *J Neurosci, 21*(8), 2919-2928.

Elliott, D., Binsted, G., & Heath, M. (1999). The control of goal-directed limb movements: Correcting errors in trajectory. *Hum Mov Sci, 18*(121-136), 121.

Elliott, D., Carson, R. G., Goodman, D., & Chua, R. (1991). Discrete vs. continuous visual control of manual aiming. *Hum Mov Sci, 10*, 393-418.

Elliott, D., Helsen, W. F., & Chua, R. (2001). A century later: Woodworth's (1899) two-component model of goal-directed aiming. *Psychol Bull, 127*(3), 342-357.

Gallivan, J. P., Cavina-Pratesi, C., & Culham, J. C. (2009). Is that within reach? fMRI reveals that the human superior parieto-occipital cortex encodes objects reachable by the hand. *J Neurosci, 29*(14), 4381-4391.

Glover, S. (2004). Separate visual representations in the planning and control of action. *Behav Brain Sci, 27*(1), 3-24; discussion 24-78.

Gomi, H. (2008). Implicit online corrections of reaching movements. *Curr Opin Neurobiol, 18*(6), 558-564.

Gomi, H., Abekawa, N., & Nishida, S. (2006). Spatiotemporal tuning of rapid interactions between visual-motion analysis and reaching movement. *J Neurosci, 26*(20), 5301-5308.

Goodale, M. A., Pelisson, D., & Prablanc, C. (1986). Large adjustments in visually guided reaching do not depend on vision of the hand or perception of target displacement. *Nature, 320*(6064), 748-750.

Gordon, J., Ghilardi, M. F., Cooper, S. E., & Ghez, C. (1994). Accuracy of planar reaching movements. II. Systematic extent errors resulting from inertial anisotropy. *Exp Brain Res, 99*(1), 112-130.

Grea, H., Pisella, L., Rossetti, Y., Desmurget, M., Tilikete, C., Grafton, S., et al. (2002). A lesion of the posterior parietal cortex disrupts on-line adjustments during aiming movements. *Neuropsychologia, 40*(13), 2471-2480.

Gritsenko, V., Yakovenko, S., & Kalaska, J. F. (2009). Integration of predictive feedforward and sensory feedback signals for online control of visually guided movement. *J Neurophysiol, 102*(2), 914-930.

Hamilton, A. F., & Wolpert, D. M. (2002). Controlling the statistics of action: obstacle avoidance. *J Neurophysiol, 87*(5), 2434-2440.

Heath, M. (2005). Role of limb and target vision in the online control of memory-guided reaches. *Motor Control, 9*(3), 281-311.

Heath, M., Westwood, D. A., & Binsted, G. (2004). The control of memory-guided reaching movements in peripersonal space. *Motor Control, 8*(1), 76-106.

Howard, L. A., & Tipper, S. P. (1997). Hand deviations away from visual cues: indirect evidence for inhibition. *Exp Brain Res, 113*(1), 144-152.

Keulen, R. F., Adam, J. J., Fischer, M. H., Kuipers, H., & Jolles, J. (2003). Distractor interference in selective reaching: dissociating distance and grouping effects. *J Mot Behav, 35*(2), 119-126.

Liu, D., & Todorov, E. (2007). Evidence for the flexible sensorimotor strategies predicted by optimal feedback control. *J Neurosci, 27*(35), 9354-9368.

Mon-Williams, M., Tresilian, J. R., Coppard, V. L., & Carson, R. G. (2001). The effect of obstacle position on reach-to-grasp movements. *Exp Brain Res, 137*(3-4), 497-501.

Pelisson, D., Prablanc, C., Goodale, M. A., & Jeannerod, M. (1986). Visual control of reaching movements without vision of the limb. II. Evidence of fast unconscious processes correcting the trajectory of the hand to the final position of a double-step stimulus. *Exp Brain Res, 62*(2), 303-311.

Pisella, L., Grea, H., Tilikete, C., Vighetto, A., Desmurget, M., Rode, G., et al. (2000). An 'automatic pilot' for the hand in human posterior parietal cortex: toward reinterpreting optic ataxia. *Nat Neurosci, 3*(7), 729-736.

Prablanc, C., & Martin, O. (1992). Automatic control during hand reaching at undetected two-dimensional target displacements. *J Neurophysiol, 67*(2), 455-469.

Proteau, L., & Masson, G. (1997). Visual perception modifies goal-directed movement control: supporting evidence from a visual perturbation paradigm. *Q J Exp Psychol A, 50*(4), 726-741.

Ramsay, J. O., & Silverman, B. W. (2005). *Functional Data Analysis* (2nd ed.). New York: Springer.

Reichenbach, A., Thielscher, A., Peer, A., Bulthoff, H. H., & Bresciani, J. P. (2009). Seeing the hand while reaching speeds up on-line responses to a sudden change in target position. *J Physiol, 587*(Pt 19), 4605-4616.

Sabes, P. N., & Jordan, M. I. (1997). Obstacle avoidance and a perturbation sensitivity model for motor planning. *J Neurosci, 17*(18), 7119-7128.

Sabes, P. N., Jordan, M. I., & Wolpert, D. M. (1998). The role of inertial sensitivity in motor planning. *J Neurosci, 18*(15), 5948-5957.

Saijo, N., Murakami, I., Nishida, S., & Gomi, H. (2005). Large-field visual motion directly induces an involuntary rapid manual following response. *J Neurosci, 25*(20), 4941-4951.

Sailer, U., Eggert, T., Ditterich, J., & Straube, A. (2002). Global effect of a nearby distractor on targeting eye and hand movements. *J Exp Psychol Hum Percept Perform, 28*(6), 1432-1446.

Sarlegna, F., Blouin, J., Bresciani, J. P., Bourdin, C., Vercher, J. L., & Gauthier, G. M. (2003). Target and hand position information in the online control of goal-directed arm movements. *Exp Brain Res, 151*(4), 524-535.

Schindler, I., Rice, N. J., McIntosh, R. D., Rossetti, Y., Vighetto, A., & Milner, A. D. (2004). Automatic avoidance of obstacles is a dorsal stream function: evidence from optic ataxia. *Nat Neurosci, 7*(7), 779-784.

Soechting, J. F., & Lacquaniti, F. (1983). Modification of trajectory of a pointing movement in response to a change in target location. *J Neurophysiol, 49*(2), 548-564.

Song, J. H., & Nakayama, K. (2006). Role of focal attention on latencies and trajectories of visually guided manual pointing. *J Vis, 6*(9), 982-995.

Striemer, C. L., Chapman, C. S., & Goodale, M. A. (2009). "Real-time" obstacle avoidance in the absence of primary visual cortex. *Proc Natl Acad Sci U S A, 106*(37), 15996-16001.

Tipper, S. P., Lortie, C., & Baylis, G. C. (1992). Selective reaching: evidence for action-centered attention. *J Exp Psychol Hum Percept Perform, 18*(4), 891-905.

Tipper, S. P., Meegan, D. V., & Howard, L. A. (2002). Action-centered negative priming: Evidence for reactive inhibition. *Visual Cognition, 9*(4), 591-614.

Tresilian, J. R. (1998). Attention in action or obstruction of movement? A kinematic analysis of avoidance behavior in prehension. *Exp Brain Res, 120*(3), 352-368.

Tresilian, J. R. (1999). Selective attention in reaching: when is an object not a distractor? *Trends Cogn Sci, 3*(11), 407-408.

Welsh, T. N., & Elliott, D. (2004). Movement trajectories in the presence of a distracting stimulus: evidence for a response activation model of selective reaching. *Q J Exp Psychol A, 57*(6), 1031-1057.

Whitney, D., Westwood, D. A., & Goodale, M. A. (2003). The influence of visual motion on fast reaching movements to a stationary object. *Nature, 423*(6942), 869-873.

Chapter 4

4. Mental Blocks: fMRI reveals top-down modulation of early visual cortex when obstacles interfere with grasp planning[3]

4.1. Introduction

Even after the visuomotor system has solved the difficult problem of selecting a specific target from the many that occupy our cluttered environment, non-target objects can function as obstacles that significantly alter the trajectory of the movement (Chapman & Goodale, 2008, 2010a, 2010b; Mon-Williams, Tresilian, Coppard, & Carson, 2001; Tresilian, 1998, 1999). This suggests the brain must flexibly encode objects to both attract and repel movements depending on whether the object is a potential target or a potential obstacle. Studies of patients with damage to the dorsal visual stream (Goodale & Milner, 1992) have implicated the posterior parietal cortex as being critical for obstacle encoding (Milner & McIntosh, 2004; Rice et al., 2008; Rice et al., 2006; Schindler et al., 2004). Specifically, optic ataxic patients with damage to dorsal stream structures show significantly less deviation away from obstacles than normal participants (Schindler et al., 2004). Using functional magnetic resonance imaging (fMRI), we sought to identify what brain areas encode obstacles in normal individuals.

Studying real actions in the MRI environment is difficult due to the spatial constraints and the artifacts introduced by hand motion (Culham, 2006). To overcome these difficulties we adapted an obstacle task that interferes with grasping movements (which are easier to perform with less space, Tresilian, 1998, see Figure 1.9) for use in a slow event-related planning paradigm designed to isolate the visuomotor planning response (where artifacts do not occur). FMRI paradigms using delay periods have isolated planning responses in eye-movement tasks (Curtis, Cole, Rao, & D'Esposito, 2005; Curtis

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& Connolly, 2008; Curtis & D'Esposito, 2006; Curtis, Rao, & D'Esposito, 2004; Ikkai & Curtis, 2008) and have demonstrated preparatory activity in attentional cueing paradigms (Bressler, Tang, Sylvester, Shulman, & Corbetta, 2008; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; Serences, Yantis, Culberson, & Awh, 2004; Sylvester, Jack, Corbetta, & Shulman, 2008). Importantly, separating instructions with delay periods has also been used to isolate movement planning responses in reaching tasks (Beurze, de Lange, Toni, & Medendorp, 2007, 2009).

Interestingly, tasks requiring attentional direction recruit a network of brain areas that are similar to those active in movement planning. Specifically, a dorsal parietal-frontal network has been shown to control the locus of attention (Beck & Kastner, 2009; Corbetta, Patel, & Shulman, 2008; Corbetta & Shulman, 2002; Kastner & Ungerleider, 2000; Riddoch et al., 2010; Serences & Yantis, 2007), with the intraparietal sulcus (IPS) playing a central role. This IPS activity aligns with parietal areas of activation when participants perform actions (Andersen & Buneo, 2002; Andersen & Cui, 2009; Astafiev et al., 2003; Beurze et al., 2007, 2009; Culham, Cavina-Pratesi, & Singhal, 2006; Culham & Valyear, 2006; Curtis & Connolly, 2008) as well as with the lesion sites of patients in the obstacle studies described above (e.g. Milner & McIntosh, 2004; Schindler et al., 2004). Recent studies using fMRI (Mevorach, Shalev, Allen, & Humphreys, 2009), transcranial magnetic stimulation (TMS, Mevorach, Humphreys, & Shalev, 2006b, 2009; Silvanto, Muggleton, Lavie, & Walsh, 2009), and both techniques together (Mevorach, Hodsoll, Allen, Shalev, & Humphreys, 2010; Ruff et al., 2008) have shown that the IPS exerts top-down control over early visual areas. One particularly relevant study demonstrated that applying TMS over the left IPS interfered with participants’ ability to ignore salient information and reduced distractor suppression in early visual areas (Mevorach et al., 2010).

These previous studies, however, have relied on response-irrelevant spatial cues (i.e. arrows or verbal instructions to attend to one side of space or stimulus feature) to indicate which parts of a display are to be attended and which are to be ignored. Although this type of cueing is sufficient to produce IPS activation and the corresponding modulation of visual cortex (enhancement of attended locations and suppression of unattended locations), it is far removed from real-world settings where the demands of attention are directly linked to our interactions with the environment. That is, in real-world tasks – such as reaching for objects in cluttered environments – our goal-directed actions dictate which objects should be selected as targets and which should be ignored as non-targets. Furthermore, when non-targets are physical objects that could impede a desired movement, they require avoidance, which some researchers have argued may be implemented by inhibiting activity at obstacle locations (Howard & Tipper, 1997; Tipper, Howard, & Jackson, 1997; Welsh & Elliott, 2004). With this in mind, we were specifically interested in what would happen to the coding of non-target objects in visual cortex when those objects were potential obstacles as a consequence of their position with respect to the path of a planned movement. Thus, rather than relying on an arbitrary instruction to indicate whether or not a non-target object should be ignored (or avoided), we used an action task in which the requirements of the movement naturally determined how a non-target object should be treated. In this real-world scenario where non-target objects must be avoided in order to successfully complete the required response, we predicted that coding of those objects in visual cortex would be suppressed, similar to what happens with irrelevant stimuli or unattended visual locations in more cognitive tasks. In addition, given the previous patient literature, the overlap in attention and action networks, and the shared visual properties of distractors and obstacles, we predicted that the IPS would play a critical role in obstacle encoding, perhaps providing a source for the signals that modulate the activity associated with non-target objects in early visual cortex.

4.2. Materials and Methods

4.2.1. Participants

Fifteen (8 males, mean age 26.2) right-handed (determined by questionnaire, Oldfield, 1971) participants were scanned using blood-oxygenation-level-dependent functional magnetic resonance imaging (BOLD fMRI, Kwong et al., 1992; Ogawa et al., 1992). Informed consent was obtained in accordance with procedures approved by the University of Western Ontario’s (London, Ontario, Canada) Health Sciences Research Ethics Board. All participants were naive with respect to the experimental hypothesis and were only informed of the required experimental tasks.

4.2.2. Setup and Apparatus

Participants directly viewed (head was stabilized by foam and tilted ~30°,) and grasped a centrally located target object (10 cm tall square (4 cm sides) white wooden block) placed on an angled black platform that straddled the participants' hips (see Figure 4.1 and Figure 4.2a). Two obstacles (10 cm tall 3.5 cm diameter white wooden cylinders) were controlled by the experimenter via handles that extended outside the bore of the scanner. The obstacles were invisible beneath the platform when lowered, but were visible and directly to the left of or behind the target object (3.5 cm away from facing surface) when raised (see Figure 4.1 and Figure 4.2c). The exact placement of the platform was adjusted to match each participant's arm length such that the required grasp movements were comfortable. A small green fixation light-emitting-diode (LED; too dim to illuminate the scene) and bright yellow illuminator LED were attached to flexible plastic stalks (Loc-Line, Lockwood Products, Lake Oswego, OR) and placed immediately above the target object (fixation) and in front of the platform (illuminator).

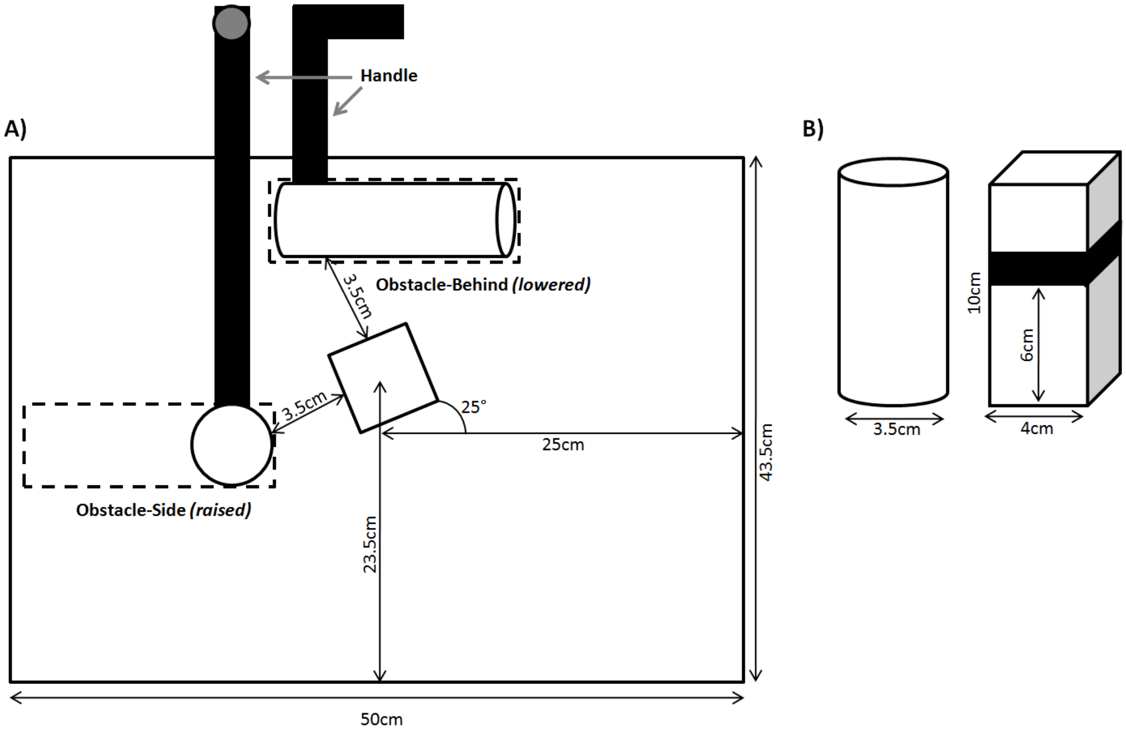


Figure 4.1: (A) Schematic (not to scale) top-down view of platform (see Figure 4.2). Square target object (which was set into a slight recess in the platform) was rotated slightly (20°) to allow for comfortable grasps. Note, the depth of the fixation LED was at the center of the target object. When raised (as for Obstacle-Side in figure), the closest edge of an obstacle was 3.5 cm directly perpendicular from the facing side of the square target object. Each obstacle was controlled by turning a long (1 m) plastic handle that extended outside the bore of the magnet. When lowered (as for Obstacle-Behind in figure) the entire obstacle was lowered into a slot (dashed box) below the surface of the platform and was not visible. (B) Target object and obstacle object are shown schematically to provide dimensions.

4.2.3. Procedure

Participants were required to grasp the target object using one of two wrist postures (Thumb-Front or Thumb-Side) and obstacles could be in one of three configurations (not present, to the side or behind the target object), leading to 6 total conditions in a 2x3 design (see Figure 4.2c). All grasps used only the index finger and thumb placed on opposing surfaces of the target object. A strip of black tape was placed on the target object to indicate the required height of the thumb and index finger placement, ensuring that all grasps were positioned at the same height on the object (see Figure 4.1). A 'Thumb-Front' grasp required the wrist to be flexed with the thumb on the front and index finger on the back of the object while a 'Thumb-Side' grasp required the wrist to be extended and the thumb on the left and the index finger on the right of the object (see Figure 4.2c). Thus, it was only the required wrist posture together with the particular position of the obstacle which determined whether or not the placement of the index finger or thumb would be interfered with (Tresilian, 1998).

To isolate the visuomotor planning response from the visual and motor execution responses, we used a slow event-related planning paradigm consisting of three distinct phases: 'Preview', 'Plan' and 'Execute' (see Figure 4.2b). We adapted this paradigm from previous work with eye-movements and working memory that have successfully parsed delay activity from the transient responses to the onset of visual input and movement execution (Curtis et al., 2005; Curtis & D'Esposito, 2003; Curtis et al., 2004). Each trial was preceded by a period where participants were in complete darkness except for the fixation LED upon which they maintained their gaze. The trial began with the illumination of the workspace. For the Preview phase, participants were told to fixate the middle of the black strip on the target object. After 11 s of the Preview phase, a 1 s auditory cue was given that instructed either "Thumb-Front" or "Thumb-Side" and marked the onset of the Plan phase. Throughout the Plan phase participants were instructed to maintain fixation of the black strip on the target object. Although participants knew the object to be grasped during the Preview phase, only in the Plan phase did they have all the information necessary to prepare the upcoming movement. After 11 s of the Plan phase, a 1 s auditory "Go" cue instructed participants to immediately execute the instructed action, initiating the Execute phase where the subject performed the instructed hand movement (approximately 2-3 s). Two seconds after the end of the Go cue, the illuminator was extinguished. Once the illuminator was extinguished, participants returned their gaze to the fixation point. Fourteen seconds of darkness/fixation then allowed the BOLD response to return to baseline prior to the next trial. Small LEDs were positioned underneath the platform and directed towards the experimenter (not visible to the participant) to cue them about the upcoming obstacle position without the participant's knowledge. Regardless of the obstacle change between two trials, the experimenter always turned both obstacle handles to equate any somatosensory stimulation that occurred from this event. The six trial types were pseudo-randomly intermixed twice within each run (twelve 40 s trials per run) so that each trial type was preceded and followed equally often by every other trial type across the entire experiment. Participants completed eight experimental runs. During the anatomical scan and prior to entering the scanner, a brief practice session was conducted (equivalent to the length of one experimental functional run) in order to familiarize participants with the paradigm, especially the delay timing which required performing the cued action only at the "Go" cue.

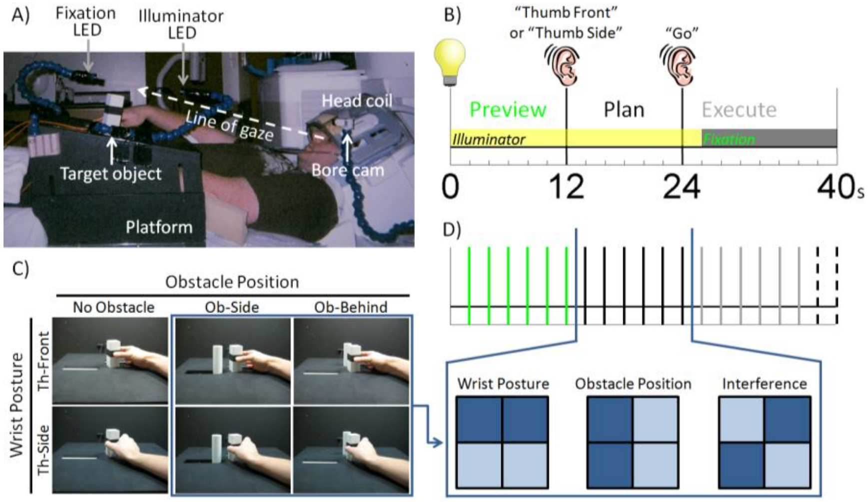


Figure 4.2: Experimental setup, timing, conditions and contrasts. (A) Participant setup from side view. Participants' heads were tilted to allow direct viewing of the target object. (B) Timing of one event related planning trial. Trials were preceded by a period of darkness with participants maintaining fixation and started with the 'Preview' phase commencing with the illumination of the bore (0 s, fixation extinguished, illuminator remains on). Auditory cue for wrist posture (@12 s) signaled the start of the "Plan" phase. A second auditory "Go" cue (@24 s) signaled the start of the "Execute" phase and cued participants to perform the grasp. The illuminator was extinguished and replaced by fixation 2 s after the "Go" cue, followed by 14 s of darkness/fixation before the start of the next trial. (C) The experimental conditions shown from participant's point of view in the 2 (Wrist Posture) x 3 (Obstacle Position) design. Participants grasped a square target object at a set height (black strip) using one of two wrist postures (Thumb-front or Thumb-side) with no obstacle present, an obstacle beside the target object or an obstacle behind the target object. Border around the right-most 4 boxes indicates the 2x2 design used for analysis (see D). (D) A deconvolution design was used to analyze the data with a spike predictor at each volume (20x2s volumes for each trial). The first 6 volumes comprised the "Preview" phase (green spikes), the 7-12 volumes the "Plan" phase (black spikes), the 13-18 volumes the "Execute" phase (grey spikes) and the final two volumes (dashed spikes) were used as baseline. A 2x2x6 (time) RFX-ANOVA (see C) tested for effects of Wrist Posture, Obstacle Position and Interference, as well as changes of each effect over time, in the Plan phase.

4.2.4. Acquisition and preprocessing of fMRI data

Scanning was performed on a 3 Tesla Siemens MAGNETOM Tim Trio MRI scanner. Functional MRI volumes were collected using an optimized T2*-weighted echoplanar imaging (EPI) (TR = 2000 ms, TE = 30, 3.3 mm isotropic voxels, field of view = 211 x 211 mm, matrix size = 64 x 64, flip angle = 78°). Anatomical MRI volumes were collected with an ADNI T1-weighted MPRAGE sequence (TR = 2300 ms, TE = 2.98 ms, field of view and matrix size = 192 x 240 x 256, flip angle = 9°, 1 mm isotropic voxels). We used a combination of parallel imaging coils to achieve a good signal:noise ratio and to enable the subject to view the workspace directly (without mirrors) without occlusion. Beneath the head, we tilted (by ~20-30°) the bottom half (6 elements) of the system's standard 12-channel head coil; above the forehead (but not occluding vision), we suspended a 4-channel flex coil (see figure 4.2a). Physiologic fluctuations were compensated for every segment of every slice using a point-based navigator correction scheme collected at the beginning of every spiral read-out. Each volume was comprised of 38 contiguous oblique slices acquired at a 30° caudal tilt with respect to the anterior commissure to posterior commissure line (Damasio, 1995), providing near whole brain coverage. Following slice scan-time correction, 3D motion correction (with intersession alignment to the volume closest in time to the anatomical scan; trilinear-sync interpolation), high-pass temporal filtering (3 cycles/run) and functional-to-anatomical co-registration, functional and anatomical images were transformed into Talairach space (Talairach & Tournoux, 1988). Functional data were spatially smoothed using a Gaussian kernel of 6 mm (full-width at half-maximum).

An MR-compatible infrared-sensitive camera (MRC Systems GmbH, bore cam, see figure 4.2a) was optimally positioned to record the participant's movements during functional runs. Any trials with early initiation errors or errors in wrist posture (6 trials across all subjects) were modeled as predictors of no interest and were excluded from statistical contrasts. For each participant, functional data from each session were screened for motion and/or magnet artifacts with cine-loop animation. No extreme motion (> 1 mm) was detected for any run of any participant.

4.2.5. Data Analysis

4.2.5.1. Analysis motivation

We were both theoretically and practically motivated to restrict our analysis to brain activations prior to movement execution. Theoretically, the previous neuropsychological work which forced participants to perform actions without vision following a brief visual preview of the workspace (e.g. Schindler et al., 2004), specifically implied that a deficit in motor *planning* was at the root of impaired obstacle avoidance. Practically, motion artifacts motivated us to restrict our analysis only to periods in which no movement was required (see section 4.5.1 for further discussion of this point). Modeling neural activity changes during the delay phases (Preview and Plan), however, raises important analytical considerations. Traditional single event GLM designs (e.g. a convolved spike predictor at the start of the Preview or Plan phase) prove to be a poor model for capturing activity that is sustained (or even increasing) near the end of the expected hemodynamic response (Curtis & D'Esposito, 2003). To account for this limitation, previous researchers using delay paradigms have elected to separately model several within trial events (for example the stimulus onset, the delay activity, and the response, Curtis et al., 2005; Curtis & Connolly, 2008; Curtis & D'Esposito, 2003, 2006; Curtis et al., 2004; Ikkai & Curtis, 2008). A variety of techniques following this general logic have been employed. In most studies, the transient events are modeled as single events (spike predictors) convolved with a given hemodynamic response function (HRF). What differs is the modeling of the delay response. In some, the delay is also modeled as an HRF-convolved single event (Yoon, Curtis, & D'Esposito, 2006), while in others it takes the form of an HRF convolved with a sustained boxcar (or zero degree polynomial, Curtis & D'Esposito, 2006; Curtis et al., 2004). Most recently, this research group has used a shifted (4 s) linear combination of a non-convolved boxcar and line (first order polynomial) to capture delay activity (Curtis & Connolly, 2008; Ikkai & Curtis, 2008; Srimal & Curtis, 2008). Finally, in one study, these researchers elected to model the activity with non-convolved spike predictors at every time point (a deconvolution design, Curtis et al., 2005). A problem with any of the above delay models using a convolved boxcar or non-convolved but shifted boxcar and line when applied to the current data is that, depending on the shape of the HRF or the amount of the shift, the delay activity may not have reached baseline before the onset of the Execute phase. Given the above comments and evidence for motion artifacts during the early Execute phase, these time points with problematic activation would therefore be attributed in part to the Plan delay activity response. The previously mentioned research has examined eye movement responses, and was therefore relatively unaffected by motion artifacts.

4.2.5.2. Analysis overview

Given the problems associated with modeling delay activity in the context of a task with motion artifacts, we adopted a full deconvolution design (spike predictors at each volume) to eliminate any motion artifact contamination. One potential limitation of the deconvolution design is that it loses the characteristic shape associated with a typical hemodynamic response predictor. That is, while a typical convolved predictor accounts for variations in time based on the shape of the underlying HRF, the single deconvolution predictors lacks this temporal sensitivity. To account for these changes across time, we therefore include time as a factor in our analyses of the Preview and Plan phase activity (see section 4.2.5.4). Given that most previous studies of obstacle avoidance (Chapman & Goodale, 2008, 2010b; Mon-Williams et al., 2001; Tresilian, 1998) have not introduced a delay between the visual presentation of the workspace and the cue to execute, we did not know at what point in the Plan phase the encoding of obstacles would occur. Although the hemodynamic response function peaks approximately 4-6 s after the event, the rise can begin immediately. If the neural activity is transient, the BOLD response then falls; however, planning may very well be a sustained process, in which case the activation could remain high for the duration of the planning phase. Thus the initial and final predictors in any phase may still carry a signal, albeit a smaller one than the peak, and we evaluated the full period.

As a result, all data were analyzed using a group voxelwise random effects (RFX) analysis of a deconvolution design. Our design was an adaptation of the previous delay paradigm studies that separately modeled several within-trial events to properly measure delay period activity (Curtis et al., 2005; Curtis & D'Esposito, 2003; Curtis et al., 2004). Single spike predictors were inserted at every volume of a trial, similar to previous work

(Curtis et al., 2005). The 20 predictors were subdivided with the first six being classified as ‘Preview’, the next six (7-12) as ‘Plan’, the next six (13-18) as ‘Execute’ and the final two (19-20) as baseline (see figure 4.2d). Data were processed using a percent signal change transformation. All analyses were performed using Brain Voyager (BV) QX (version 2.08, Maastricht, The Netherlands).

4.2.5.3. Isolating a Plan network

Given our theoretical motivation to explore movement planning, our first objective was to characterize the network of brain areas involved in the planning of a grasp movement. We reasoned that areas involved in movement planning should show heightened responses once grasp instruction has been given (Plan phase) as compared to a simple visual response when subjects did not know which movement would be performed (Preview phase). This logic is an extension of recent studies that examined planning responses to temporally spaced instructions about target location and effector in fMRI movement tasks (Beurze et al., 2007, 2009). These researchers argued that brain areas responsible for integrating target location and effector information would show activation to the first of the two instructions (the order of instructions was randomized) and a *higher* activation when the second instruction was given – suggesting that the second response was higher because of the role of those areas role in integrating the two motor-relevant signals.

For this analysis, we had no a priori reason to select some subset of spike predictors (i.e. those in the middle portion of each phase) as being more or less indicative of Preview and Plan phase activity. Therefore, to identify a Plan network, we looked across the whole brain for voxels where the average response to the six Plan predictors was higher than the average for the six Preview predictors (we also examined areas with a Preview > Baseline response, see section 4.5.2 and Figure 4.7). We used a minimum statistical threshold of $p<0.001$ and analyzed only clusters of voxels larger than 324 mm^3 (minimum cluster size estimated by Monte Carlo simulations of $p<0.05$, implemented in the cluster threshold plug-in for BVQX). The resulting statistical map of all positively active voxels (see Figure 4.3) was then used as a mask for further analysis. From the Plan > Preview map, we extracted foci of activity within a 10 mm cube centered on a peak voxel, provided that they were more than 10 mm apart (see Figure 4.3).

4.2.5.4. Obstacle effects in the Preview and Plan phases

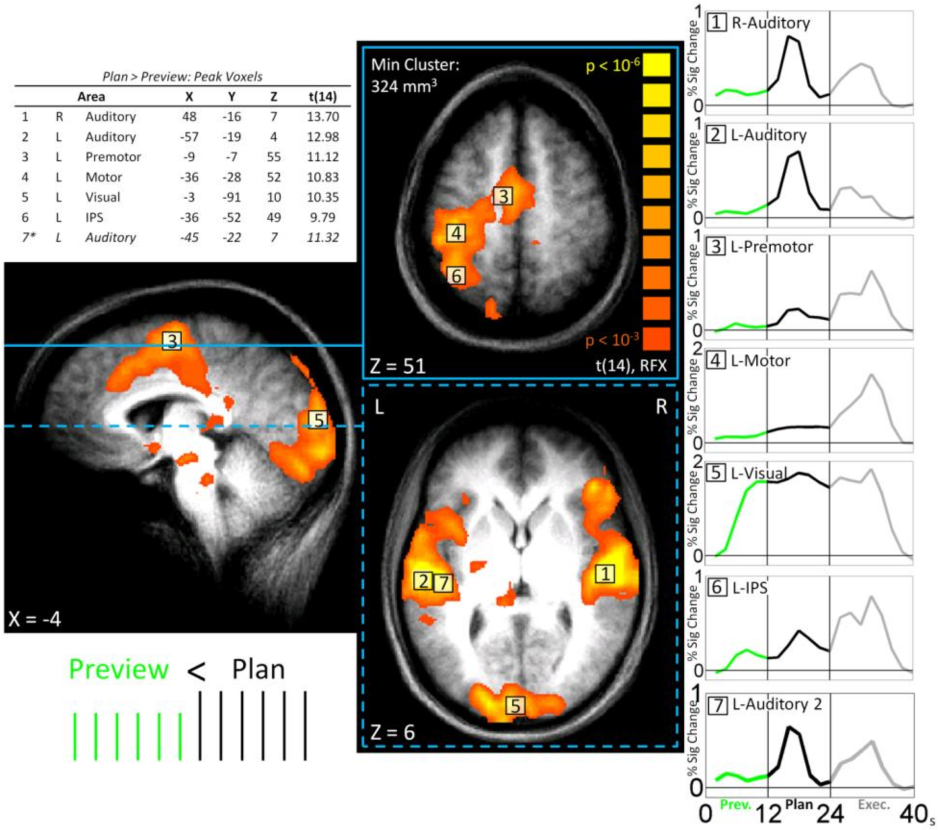
Within the Plan network (see preceding section), we wanted to isolate brain areas that were modulated by our conditions of interest. For the Plan phase, we analyzed the subset of our trials that formed a 2x2 (Wrist-posture x Obstacle-Position) design (see figure 4.2c and 4.2d). Of course, as described above, it was important to remain sensitive to the temporal evolution of the hemodynamic response, and thus time was included as a factor, resulting in a 2x2x6 (6 time points in the Plan phase) RFX ANOVA applied to all voxels within the Plan network. This analysis allows us to look for three ‘main effects’ of interest: 1) main effect of Wrist-Posture (collapsed across Obstacle-Position and Time), 2) main effect of Obstacle-Position (collapsed across Wrist-Posture and Time), 3) an interaction between Wrist-Posture and Obstacle-Position which, critically, is a ‘main effect’ of Obstacle-Interference. That is, there are two cases where the alignment of the grasping digits is not interfered with by the position of the obstacle (Thumb-front / Obstacle-Side, and Thumb-Side / Obstacle-Behind) and two cases where the alignment of the digits is interfered with by the obstacle (Thumb-front / Obstacle-Behind and, Thumb-side / Obstacle-Side). Importantly, any area showing activation related to this interaction would be independent from the effects of obstacle position or wrist posture alone, suggesting a higher-level obstacle encoding specific to movement interference, a factor unique and important in a task requiring the planning of real actions. Including Time as a factor meant we could also examine how each of these three effects interacted temporally. That is, not only could we ask the question of whether a brain area was preferentially activated for a given effect, but also were there any areas where the magnitude of these effects differentially varied across time. We report all areas that showed any of these three effects or any of the three effects that interacted with Time. The main effect of Time was not analyzed since all areas within the Plan network were selected because they were active, and would necessarily have shown this effect.

The analysis for the Preview phase was identical, save for the fact that no information about Wrist-Posture is known during this phase. As a result, the RFX ANOVA applied to the Preview phase reduced to a 2x6 (Obstacle-Position x Time) design, applied to all voxels with the Plan network. We report activity from all voxels active for a main effect of Obstacle-Position or interaction of this effect across time, considered significant at $p < 0.001$ with a minimum cluster size of 108 mm^3 (determined by Monte Carlo simulation of $p<0.01$, BVQX cluster threshold plug-in).

4.3. Results

4.3.1. Plan > Preview network and mask

In addition to bilateral temporal lobe activation consistent with a response to an auditory cue, we identified a plan network encompassing a large swath of cortex contralateral to the moving hand (left-hemisphere) extending from early visual areas in the occipital lobe (where activity is bilateral) dorsally along the left intraparietal sulcus (IPS) and into both left motor and medial frontal areas including premotor cortex (see figure 4.3). This network matches well with the results of previous work that has isolated the planning response of right hand movements (Beurze et al., 2007, 2009). Our analysis of the peak voxels of activation (separated by > 10 mm) within this network reveal at least 6 distinct foci of activity (in descending order of activity): Right and left auditory cortex (accounting for the three highest peak voxels, see Figure 4.3), left premotor cortex, left motor cortex, left visual cortex and left IPS. All active voxels were included as part of the mask used for our further analysis.



Plan > Preview: Peak Voxels

	Area		X	Y	Z	t(14)
1	R	Auditory	48	-16	7	13.70
2	L	Auditory	-57	-19	4	12.98
3	L	Premotor	-9	-7	55	11.12
4	L	Motor	-36	-28	52	10.83
5	L	Visual	-3	-91	10	10.35
6	L	IPS	-36	-52	49	9.79
*7**	*L*	*Auditory*	*-45*	*-22*	*7*	*11.32*

Figure 4.3: Regions active during grasp-planning. A group voxelwise analysis identified areas that were more active ($p<0.001$, minimum cluster size 324 mm^3) during the "Plan" phase (average of volumes 7-12) than the "Preview" phase (average of volumes 1-6). The resulting statistical map is presented on an average anatomical MRI of all 15 participants in standardized space and was used as a mask for the remaining analysis. Peak voxels were obtained that were more than 1cm apart (see table top left). All active voxels within a 1 cm^3 box centered on each peak voxel were selected and the resulting % BOLD signal change throughout the trial for these areas is shown on the right (note scale differences for [4] and [5]). Data is shown from the six most active hotspots (numbers corresponding to descending significance). Differences between plan and preview emerging in the time courses are necessarily true given the contrast performed and are shown to illustrate qualitative differences between areas involved in grasp planning. **Note a 7th area (3rd most active voxel, see table) was found in L-Auditory cortex just beyond 1cm from the other peak voxel – as their activity was almost identical, we treated them as one area for ordering the hotspots.*

For a qualitative characterization of the differences between these six areas within the Plan > Preview network, we plot the average percent signal change from all active voxels within a 1 cm cube centered on the peak voxel (see right side, Figure 4.3) averaged across the 15 subjects. Given the contrast used to define this network of areas, it is not surprising that Plan activity was higher than the Preview activity in each plot. Despite this, striking variation in the time courses is evident across areas. While auditory cortex shows the characteristic hemodynamic response (e.g. Sylvester et al., 2008 who also used an auditory cue in a delay paradigm) known to accompany a transient auditory event elicited by an instruction (in the Plan and less so during the Execute phase) the activity in the other areas is more complex. The L-Premotor, L-Visual and L-IPS ([3], [5] and [6] in Figure 4.3 respectively) show a definitive rise and fall of activation across the plan phase but the L-Motor ([4] in Figure 4.3) remains relatively flat, instead showing a gradual ramping up of activity prior to movement. More importantly, both the L-Visual and L-IPS areas show activity above baseline during the preview phase (see Figure 4.7). These latter areas, which show both a distinct visual and planning response, are ideal candidates to perform the necessary visuomotor integration (Beurze et al., 2007, 2009) to encode obstacles – after all, interference is defined by the interaction between the purely visual properties of the scene and the planned action, and only taken together can these two features combine to determine the level a given object interferes with an upcoming movement.

4.3.2. Wrist-Posture

There were no areas showing any effects of Wrist-Posture or any showing interactions between Wrist-Posture and Time in the Plan phase. This suggests that the encoding of wrist posture, which, unlike obstacle position and interference does not rely on any visual property of the workspace, is likely occurring during the movement itself. Due to the motion artifacts and somatosensory confounds introduced into the data during movement execution (which may significantly differ with wrist posture) we elected to focus our analysis on neural activity that occurred during the Preview and Plan phases.

4.3.3. Preview Phase

4.3.3.1. Right Visual Cortex

One area in right visual cortex showed a significant interaction between Obstacle-Position and Time during the Preview phase (see Figure 4.4 and Table 4.1). No areas showed a main effect of Obstacle-Position and no other areas showed the Obstacle-Position x Time interaction. To characterize this interaction, comparisons across obstacle positions were conducted at each time point (significant ($p<0.05$) comparisons indicated with an asterisk in the time course plot in Figure 4.4). This analysis revealed that activity on Obstacle-Side trials ramped up more quickly, and reached higher sustained levels than activity on Obstacle-Behind trials. This resulted in smaller differences due to Obstacle-Position at the early time points and larger differences at later time points. The higher activity for the Obstacle-Side trials is intuitive, given that participants were fixating the centrally located target object and the Obstacle-Side position would have a much larger left visual field presence, activating right occipital cortex.

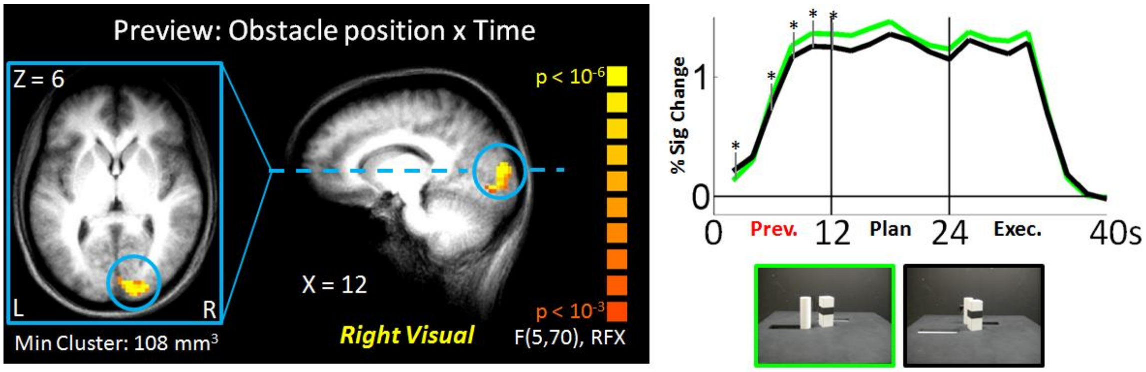


Figure 4.4: Right Visual area showing significant Obstacle-Position x Time interaction (p<0.001, minimum cluster 108 mm^{3}) during the Preview phase. The resulting statistical map is presented on an average anatomical MRI of all 15 participants in standardized space. The % BOLD signal change throughout the trial is shown to the right (Green line = Ob-side, Black line = Ob-behind). The plotted differences emerging in the Preview phase are necessarily true by virtue of the contrast being shown and the full time course is shown for illustrative purposes of activity across the entire trial. Asterisk (*) above Preview time points in the time course plot denotes significant differences in post-hoc comparisons (p < 0.05).

4.3.4. Plan Phase

4.3.4.1. Right Visual Cortex

Two clusters of voxels within the right visual cortex area that was defined during the Preview phase (see Figure 4.4 and green outline in Figure 4.5) also showed significant effects from the 2x2x6 (Wrist-Posture x Obstacle-Position x Time) RFX ANOVA during the Plan phase (see Figure 4.5 and Table 4.1). The first, dorsal to the calcarine sulcus (Figure 4.5a) showed a main effect of Obstacle-Position, responding more strongly on Obstacle-Side trials (green trace in time course and green outline in bar plots, Figure 4.5a) than on Obstacle-Behind trials (black trace and outline in Figure 4.5a). The second, ventral to the calcarine sulcus (Figure 4.5b) showed an effect of Interference (that is, an interaction between Wrist-Posture and Obstacle-Position), with lower activity on trials where the position of the obstacle interfered with the planned movement (red trace in time course, red fill in bar plots, Figure 4.5b) than on trials when the position of the obstacle did not interfere with the movement (blue trace and fill in Figure 4.5b). These effects were confirmed by extracting the average beta value across the six Plan predictors for both areas for each of the 15 subjects and running a traditional 2x2 (Wrist-Posture x Obstacle-Position) repeated-measures (RM) ANOVA. As this is identical to the contrast performed to identify the regions, the main effect of Obstacle-Position for the first area ($F(1,14) = 69.36$, $p < 10^{-6}$) and Interference interaction for the second area ($F(1,14) = 28.21$, $p < 10^{-4}$) were of course significant. More interestingly, this examination of beta values revealed that in addition to the Obstacle-Position main effect which defined the first area, this cluster of voxels also showed a significant effect of interference ($F(1,14) = 8.96$, $p < 0.01$). Moreover, the second area, defined by the Interference interaction, also showed a main effect of obstacle position ($F(1,14) = 16.81$, $p < 0.001$). Post-hoc comparisons (four total, comparing beta values between Obstacle-Positions within each Wrist-Posture, then between Wrist-Postures within each Obstacle-Position, significant ($p<0.05$) comparisons denoted by asterisks in bar plots of Figure 4.5) showed that for both areas, betas for the thumb-front wrist-posture (broken fill) were larger when planning a movement with an obstacle behind (green border) than an obstacle to the side (black border) of the object (first area, $p < 10^{-5}$; second area, $p < 10^{-4}$). This is consistent with both the Obstacle-Position and the Interference effect. Importantly, for both areas, within the obstacle-behind trials (the Obstacle-Position with the lower activity) betas for trials when planning a thumb-side wrist posture (solid fills) were larger than betas when planning a thumb-front Wrist-Posture (first area, $p < 0.05$; second area, $p < 0.01$). Additionally, within obstacle-side trials, the reverse pattern was visible (though significant only in the second area) with larger betas when planning a thumb-front than thumb-side Wrist-Posture (first area, $p = 0.146$; second area $p < 0.01$). Given that the Obstacle-Position and Interference effects would counteract each other for the obstacle-side/thumb-side (high beta for Obstacle-Position, low beta due to Interference) and obstacle-behind/thumb-side (low beta for Obstacle-Position, high beta due to lack of Interference) it is not surprising that no significant differences in either area were found between Obstacle-Positions within the thumb-side Wrist-Posture.

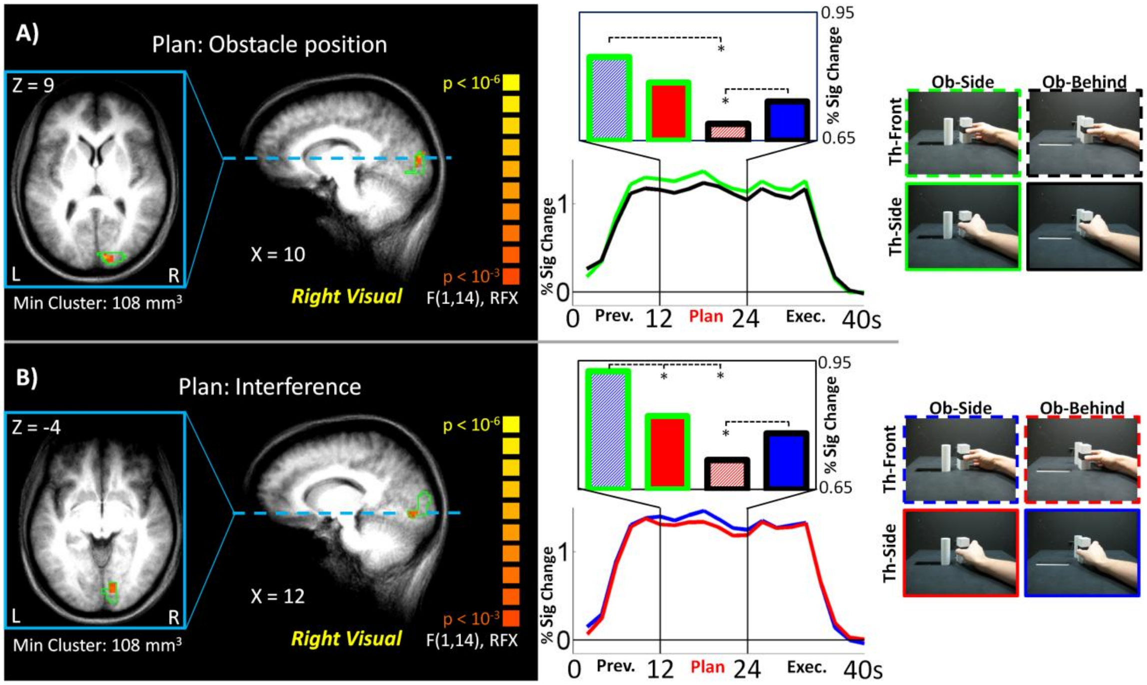


Figure 4.5: (A) Right Visual area showing significant Obstacle-Position effect ($p<0.001$, minimum cluster 108 mm^3) during the Plan phase. (B) Right Visual area showing significant Interference effect ($p<0.001$, minimum cluster 108 mm^3) during the Plan phase. The resulting statistical maps are presented on an average anatomical MRI of all 15 participants in standardized space. The green outline on anatomical images corresponds to the Right Visual area indentified during the Preview phase (see Figure 4.4).The % BOLD signal change throughout the trial is shown to the right of each area (A: Green line = Ob-side, Black line = Ob-behind; B: Red line = Interfere, Blue line = No-Interfere). The plotted differences emerging in the Plan phase are necessarily true by virtue of the contrast being shown and the full time course is shown for illustrative purposes of activity across the entire trial. Above each time course is a bar-plot depicting the significant effect where bar border colour denotes Obstacle-Position (Green = Ob-side, Black = Ob-behind), bar fill colour denotes Interference (Red = Interfere, Blue = No-Interfere) and bar fill type denotes Wrist-Posture (Solid = Th-Side, broken = Th-Front). Asterisk (*) above bar plots denotes significant differences in post-hoc comparisons ($p < 0.05$).

Overall, this pattern of results suggests that the encoding of objects in right-visual cortex is suppressed on trials where the object interferes with the planned movement. This interference effect is embedded within a more general activation preference for the obstacle-side trials where the obstacle falls to the left of fixation. This general interpretation was confirmed by extracting the betas from predictors during the Plan phase for the entire right visual cortex area identified as coding obstacle position in the Preview phase (see Figure 4.4). Within this larger area, there was still a strong obstacle-position effect ($F(1,14) = 34.02$, $p < 10^{-4}$) and, importantly, a significant interference effect ($F(1,14) = 7.69$, $p < 0.05$). Moreover, the same comparisons as described above revealed that within each obstacle position, the interference condition was lower than the no-interfere condition (obstacle-side, $p<0.05$, obstacle-behind, $p<0.05$). Comparisons within wrist postures also followed the same pattern as above with a significant difference between obstacle positions within the thumb-front trials ($p < 10^{-4}$), and no difference between obstacle positions on thumb-side trials.

4.3.4.2. Left Posterior IPS

One area in the left posterior parietal cortex showed a significant Interference x Time interaction (Obstacle-Position x Wrist-Posture x Time) during the Plan phase (see Figure 4.6 and Table 4.1). Located near the posterior end of the left IPS (Left-pIPS, contralateral to the acting hand), this area thus showed an interference effect that changed across the Plan phase. To characterize this interaction, we again extracted the beta values from each participant for each Obstacle-Position x Wrist-Posture combination – this time for each of the six time points since this was an effect that changed across time. We then ran a 2x2x6 RM-ANOVA on the extracted betas, necessarily showing the expected 3-way interaction (Interference x Time, $F(5,70) = 6.17$, $p < 10^{-4}$). To unpack this interaction, we ran two separate RM-ANOVAs examining the interference difference (Interfere – No-Interfere) for each wrist posture across the six time points. The resulting interference differences across time are shown for both the thumb-front (dashed purple line) and thumb-side (solid purple line) wrist postures (Figure 4.6, line plot above time course). For both wrist postures, this RM-ANOVA showed that the interference difference was significantly changing across time (Thumb-Front, $F(5,70) = 2.73$, $p<0.05$;

Thumb-Side, F(5,70) = 4.21, $p<0.005$). To understand exactly how this difference was evolving, we examined the slope of the line (linear trend) that fit the interference difference collapsed across Wrist-Postures. The resulting mean slope was significantly greater than 0 (mean = 0.0217, $p < 0.05$, shown as the thick black line in top plot, Figure 4.6. The thin grey lines are the slopes for the linear fit to each individual subjects' data, and the thicker dashed purple and solid purple lines are the mean slopes for each wrist posture separately). This positive slope indicated that activation on trials when movements were planned where the wrist posture and obstacle position resulted in interference increased across the Plan phase relative to activation on trials when movements were planned where the obstacle position did not interfere with the required wrist posture.

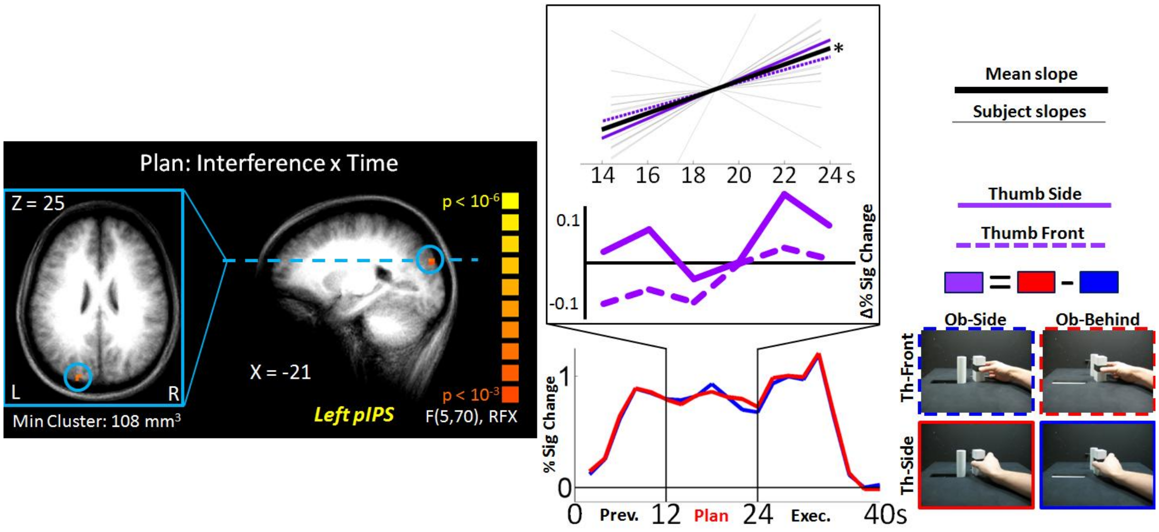


Figure 4.6: Left Posterior IPS area showing significant Interference x Time interaction ($p<0.001$, minimum cluster 108 mm^3) during the Plan phase. The resulting statistical map is presented on an average anatomical MRI of all 15 participants in standardized space. The % BOLD signal change throughout the trial is shown below and to the right (Red line = Interfere, Blue line = No-Interfere). The plotted differences emerging in the Plan phase are necessarily true by virtue of the contrast being shown and the full time course is shown for illustrative purposes of activity across the entire trial. Above the time course is a line-plot depicting how the difference between Interfere and No-Interfere trials (purple lines) develops across the Plan phase (Solid line = Th-Side, Broken line = Th-Front). Above the line-plot is a plot of the grand mean slope (thick black line) of the linear fit to the difference plot (collapsed across Wrist-Posture). Each subject's mean slope is shown with the thin grey lines. Also shown is the mean slope for each Wrist-Posture (Solid line = Th-Side, Broken line = Th-Front). Asterisk (*) next to grand mean slope indicates it was significantly positive ($p < 0.05$).

4.3.4.3. Other Activated Areas

Two other areas within the Plan network showed a significant main effect of Obstacle-Position during the Plan phase (see Table 4.1). Both a cluster of voxels in the medial frontal gyrus (MFG, slightly lateralized to the right) and a cluster of voxels in left visual cortex showed higher activity for Obstacle-Side as compared to Obstacle-Behind trials. Extracted betas from both areas necessarily showed a significant effect of obstacle position (MFG $F(1,14) = 27.83$, $p<0.001$; left-visual $F(1,14) = 31.45$, $p<10^{-4}$). The same comparisons described above revealed that for the MFG, across both wrist postures, the obstacle-side betas were larger than the obstacle-behind beta (thumb-front, $p<0.05$; thumb-side $p<0.001$). The results were similar for the left visual area, though only the thumb-front comparison reached significance (thumb-front, $p<0.005$; thumb-side, $p=0.121$). Importantly, neither of these areas showed any sign of an Interference effect (premotor, $F(1,14) < 1$, $p>0.50$; left-visual, $F(1,14) < 1$, $p>0.66$).

Table 4.1 – Peak voxel Talaraich coordinates of all active areas

Area	**Time**	**Effect**	**Cluster**	**Peak Voxel**				
				X	Y	Z	d.f.	F
R Visual	Prev	Ob-Position x Time	3861 mm^3	18	-88	10	(5,70)	16.13
R Visual	Plan	Ob-Position	648 mm^3	9	-88	10	(1,14)	46.32
R Visual	Plan	Interference	270 mm^3	18	-70	-17	(1,14)	26.57
L pIPS	Plan	Interference x Time	135 mm^3	-21	-85	25	(5,70)	5.85
MFG	Plan	Ob-Position	135 mm^3	3	-10	67	(1,14)	26.67
L Visual	Plan	Ob-Position	135 mm^3	-21	-91	-2	(1,14)	27.42

All areas within the Plan network (see section 4.3.1) showing significant effects from an RFX ANOVA applied to the Preview (2x6, Obstacle-Position x Time) and Plan (2x2x6 Obstacle-Position x Wrist-Posture x Time) phases. For each area, the experimental phase, significant effect, cluster size and Talairach coordinates and F-statistic (with degrees of freedom) of the peak voxel is shown.

4.4. Discussion

4.4.1. Summary

We adapted a reach-to-grasp obstacle paradigm (Tresilian, 1998) for use in an fMRI experiment to examine the encoding of obstacles in normal individuals. We employed a slow event-related planning paradigm that allowed us to isolate brain areas that were preferentially involved with visuomotor planning (Plan) as compared to the visual presentation of the workspace (Preview, see Figure 4.3). Within this planning network, we first identified a region of right visual cortex that had higher activity during the Preview phase (steeper BOLD response, group voxelwise design) on trials with an obstacle to the side of the target object than on trials with an obstacle behind the target object (see Figure 4.4). We then applied a 2x2x6 Wrist-Posture x Obstacle-Position x Time RFX ANOVA to the Plan phase predictors to examine how neural activity varied as a function of whether or not the position of an obstacle interfered with the planned placement of the fingers during an upcoming grasping movement. Importantly, this design allowed us to test for the effects of obstacle Interference (Obstacle-Position x Wrist-Posture interaction) independently from the effects of Obstacle-Position and Wrist-Posture. Moreover, the inclusion of time as a factor enabled us to remain sensitive to temporal variations of these effects across the Plan phase.

As we were specifically interested to see how the visual cortical encoding of obstacle objects changed once the motor requirements of the task were known, we had a special interest in any Plan phase activity that fell within right visual cortex area which had shown obstacle position sensitivity during the Preview phase. Indeed, we found that two clusters of activation from within the same right visual cortex region defined during Preview (see Figure 4.4) were shown to have effects from the RFX analysis of the Plan phase (see Figure 4.5). One of the areas was extracted as showing a main effect of Obstacle-Position (the same effect that defined the larger region during the Preview phase) and a second area was extracted as showing an Interference interaction. On closer examination, activity from both smaller areas and from the entire Preview-defined right visual cortex region all showed both an Obstacle-Position main effect and an Interference effect. Importantly, the Interference effect showed that on trials where the obstacle interfered with an upcoming movement activity was reduced relative to trials when the obstacle did not interfere. We believe this provides strong evidence that the motor implications of objects can result in alterations of their cortical representation. In this case, an obstacle that required avoidance resulted in a suppressed visual signal.

We also found that one area in the left posterior IPS showed significantly increasing activity across the Plan phase on those trials in which the obstacles interfered with the grasp compared to trials with no interference (see Figure 4.6). This is consistent with the suggestion from work with neurological patients that the dorsal visual stream plays a critical role in the avoidance of obstacles (Milner & McIntosh, 2004; Rice et al., 2008; Rice et al., 2006; Schindler et al., 2004). It should be noted that these neuropsychological experiments investigated the effects of obstacles that interfered with reach-to-point movements. It remains an open and interesting theoretical question as to whether or not avoidance during pointing relies on the same neural mechanisms as those reported here for reaching-to-grasp actions.

Finally, we found two additional areas within the plan network which showed a small obstacle position effect – one in the medial frontal gyrus and one in left visual cortex (for Talairach coordinates of all areas, see Table 4.1). In both cases, trials with an obstacle to the side of the target object resulted in higher activity than trials with an obstacle behind the target object.

4.4.2. The role of Right-Visual Cortex and the Left-pIPS

Given that the obstacle-side placement of the non-target object was further to the left of the fixated target object than the obstacle-behind placement, the observed contralateral right visual cortex preference for this configuration was predictable. However, the resulting modulation of the right visual cortex activity during the Plan phase, where the only additional information was a motor instruction, is a novel and important finding. Specifically, on trials in which the non-target object could potentially interfere with the planned movement, activity in the right visual cortex was suppressed relative to trials in which the non-target object did not interfere with the planned movement. As an interaction, this effect was independent of the main effect of obstacle position, and statistical analysis revealed that activity was reduced on interference trials for the obstacle in both positions.

The modulation of visual cortex has been reported previously in work that looked exclusively at spatial attention. These studies showed that visual cortical activity when a target is present (Gazzaley, Cooney, McEvoy, Knight, & D'Esposito, 2005; Mevorach et al., 2010; Ruff et al., 2008) and preparatory activity in anticipation of a target (Bressler et al., 2008; Kastner et al., 1999; Serences et al., 2004; Sylvester et al., 2008) are modulated by attentional cues. Most often, activity at retinotopic locations coinciding with the focus of attention is higher, while activity at other areas is reduced (Beck & Kastner, 2009; Kastner & Ungerleider, 2000, 2001; Pessoa, Kastner, & Ungerleider, 2003; Smith, Singh, & Greenlee, 2000). This modulation is thought to sharpen the encoding of objects at the attended location (Fischer & Whitney, 2009) while at the same time reducing the suppressive effects of distractors at other locations (Kastner, De Weerd, Desimone, & Ungerleider, 1998). Our study, however, is the first to show that the suppression of the neural encoding of an object can be tied to its role as an obstacle to movement. Whether obstacle avoidance requires that obstacle representations be suppressed has remained a point of debate (Castiello, 1999; Tresilian, 1999) and here we provide evidence that suppression is indeed occurring at obstacle locations, but only when participants plan a movement that is (potentially) interfered with by the obstacle.

That we find increasing activity in the left-pIPS that is concurrent with the visual cortex modulation is also in line with previous work on the allocation of attention. In this work, the modulation of activity in the visual cortex by the IPS and other frontal-parietal areas (e.g. frontal eye-fields) is a common finding from research into directed spatial attention (Beck & Kastner, 2009; Corbetta et al., 2008; Corbetta & Shulman, 2002; Desimone & Duncan, 1995; Pessoa et al., 2003; Serences & Yantis, 2007). In fact, several recent studies have reported visual cortex modulation (and IPS involvement) that is tied specifically to the suppression of salient, but irrelevant, visual distractors (Mevorach et al., 2010; Mevorach, Humphreys, & Shalev, 2006a; Mevorach et al., 2006b; Mevorach, Humphreys et al., 2009; Mevorach, Shalev et al., 2009). Although the distracting information in these studies was not a physical obstacle that had to be avoided, obstacles do represent a class of objects that require that they be ignored – at least as potential targets for the ensuing movement. In one particularly relevant study, Mevorach and colleagues (Mevorach et al., 2010) had participants perform a global/local task using compound letter stimuli (e.g., a large letter 'H' comprised of smaller letter 'D's). By varying stimuli parameters, these investigators were able to make either the local or the global elements the more salient dimension. In cases where participants were required to respond to the less salient dimension, the left IPS was shown to be active and activity in early visual cortex was suppressed. Their interpretation was that the left IPS was specifically involved in providing the top-down signals needed to ignore the highly salient distractors. These authors demonstrated a causal link between activity in IPS and these visual areas by combining fMRI with repetitive TMS, disrupting the function of the left IPS and showing more activity (i.e. a reduction in suppression) in the early visual areas. Given these results, we believe the observed left pIPS activity in the current experiment is linked to the top-down control of attention which modulates activity in early visual cortex.

We do not claim that the results of the current study can speak directly to the question of a causal role for the IPS in modulating visual cortex. In fact, if anything, the observed right visual cortex modulation due to obstacle interference appears to develop more quickly than the increase in left pIPS activity. We raise two considerations regarding this apparent temporal discontinuity. First, the hemodynamic response is notoriously sluggish, meaning that the temporal resolution of any fMRI effect is relatively poor. Therefore, trying to draw conclusions about relative timing in this study should be approached with caution. Second, and more importantly, the hemodynamic response to suppression is relatively unknown. It could be the case that the visual cortex suppression might appear earlier because the BOLD response in visual cortex was already high, and reducing activity in an already active area may occur relatively quickly. Because the response in the IPS to the interference represents the generation of a new signal (and not the reduction of an already active one), the hemodynamic response in this region might be expected to lag behind the one in visual cortex, and thus appear later in the time course. Therefore, instead of trying to make claims about causality from the current experiment (which was not designed to test for these effects), we have based our interpretation of the results (namely that the reported concurrent left pIPS and right visual cortex modulations based on obstacle interference represent a top down effect) on the significant amount of previous work showing the direction of modulation is from the IPS to visual cortex (Mevorach et al., 2010; Mevorach et al., 2006b; Mevorach, Humphreys et al., 2009; Mevorach, Shalev et al., 2009; Ruff et al., 2008; Silvanto et al., 2009).

4.4.3. The role of MFG and Left-Visual cortex

In addition to the region in right visual cortex, one region in the medial frontal gyrus (MFG, closest to the premotor area defined in Figure 4.3) and one in left visual cortex responded more during the Plan phase on trials when an obstacle was to the side of the target object relative to trials when an obstacle was behind the target object. While more medial than traditionally defined premotor areas, the reported MFG activity is near areas that have been implicated in visually guided action planning (e.g. Chouinard & Paus, 2006). In contrast, the left visual cortex activity, in the absence of any visual objects on the right side of space, appears somewhat puzzling. In offering our speculation of what this activity might represent, it is important to consider two key ways in which the left visual cortex activity differs from the right visual cortex activity described earlier. First, the left visual activity showed an Obstacle-Position preference only during the Plan phase. This is unlike the right visual activity where the obstacle encoding was established during the Preview phase. Second, the left visual activity showed no indication that the Object-Position preference was modulated by obstacle interference. This is in stark contrast to the right visual cortex region where the entire swath of cortical tissue identified during the Preview phase (Figure 4.4) showed evidence of an Interference effect. Moreover, this suggests that whatever role this activity plays in visuomotor planning it must be equivalent across trials for a given object position. Finally, we believe an explanation of the left visual activity that also offers an explanation for the concurrent MFG activity is ideal.

With these considerations in mind, we would argue that the MFG and left visual activity we report corresponds to visuomotor target selection processes. Furthermore, we support a view of visuomotor selection within a more general framework of competitive object / action-plan representations (Baldauf & Deubel, 2010; Beck & Kastner, 2009; Cisek, 2007; Cisek & Kalaska, 2010; Desimone & Duncan, 1995) and the view that selection processes are mirrored by inhibitory processes (Houghton & Tipper, 1994). That is, if objects compete in parallel for limited resources, the selection of one object necessarily comes at the expense of inhibiting other objects within the visual workspace. In addition, capacity limits mean that selection and inhibition effects can extend throughout the visual field, even in the absence of objects (similar to the anticipatory attentional effects described earlier, Bressler et al., 2008; Kastner et al., 1999; Serences et al., 2004; Sylvester et al., 2008). The role of medial frontal cortex (particularly dorsal premotor cortex) in response-related target selection has been clearly established in both monkeys (e.g. Cisek & Kalaska, 2005) and humans (for review see Chouinard & Paus, 2006). The fact that the activation appears only during the Plan phase lends support to the proposal that the observed activity in the MFG and the left visual field is intrinsically linked to action planning. Moreover, since target selection demands remain stable across the experiment, this would explain why the observed effects were not modulated by interference.

This interpretation still leaves the confusion as to why a visuomotor target-selection response would result in differential activity based on the position of the obstacle. We believe that the reason this occurs is due to the automatic inhibition of non-target objects. According to one model of selection/inhibition (Houghton & Tipper, 1994), objects that match an internal template of a target (in this experiment, a feature of the target could be ‘rectangular’) are automatically enhanced, while those that do not match the target (in this case the mismatching feature could be ‘circular’) are inhibited. If, as we argue above, the repercussions of object selection and inhibition extend to all parts of the visual field, then the automatic inhibition of an object in the obstacle-side position (which is more lateral than the relatively central obstacle-behind position) may result in a relative boost in signal to the field opposite the inhibited object. In this case, that would mean we would see an increase in the left visual cortex during only reach planning, which is what we observe. Additionally, the likely overlap between the visual encoding of the target object and an object in the obstacle-behind position means that enhancement of the target-related activity in these cases may be somewhat obscured by the counteractive inhibition of the obstacle. This could mean that target selection on obstacle-side trials proceeds more easily with greater net enhancement, resulting in the increased MFG activation on these trials. This of course raises the question of why we did not detect the inhibition in the right visual field, and only saw the corresponding boost in the left visual field. We believe this is a result of the strong bottom-up visual signal driving the obstacle encoding in right visual cortex – only in the absence of a visual object (as in the left visual field) can we see these subtle target selection effects (note the magnitude of obstacle position effects in left visual cortex are approximately half of those in right visual cortex).

We acknowledge that this interpretation is highly speculative, and that it requires that the process of target selection (and corresponding non-target inhibition) occur independently from the suppression due to interference that we noted earlier. However, it does have the advantage that it explains why this activity would manifest only during the Plan phase and why the interference effect would be absent from these areas and that it fits with a previously demonstrated role of the medial frontal cortex.

4.4.4. A Unified Perspective of Posterior Parietal Activity

The major finding from the current experiment is that the visual encoding of an obstacle in right visual cortex is suppressed when planning a reach that is interfered with by that obstacle. This visual suppression on trials with interference occurs at the same time as activity in the left pIPS is increasing. We propose that the left pIPS is providing the top down signal to modulate the visual cortical activity. The exact role of the IPS remains an open question, and we have discussed the IPS activity in two separate contexts. On one hand, since it is known that obstacles cause altered hand and finger trajectories (Chapman & Goodale, 2008, 2010a, 2010b; Mon-Williams et al., 2001; Tresilian, 1998) and that the IPS is recruited during visuomotor control (Andersen & Buneo, 2002; Andersen & Cui, 2009; Culham et al., 2006; Culham & Valyear, 2006), the left pIPS activity we observed could reflect its role in the planning and eventual programming of the required adjustments to the grasping movements in the presence of obstacles. On the other hand, the IPS has been shown to be recruited during the directing of spatial attention (Desimone and Duncan, 1995; Corbetta and Shulman, 2002; Pessoa et al., 2003; Serences and Yantis, 2007; Corbetta et al., 2008; Beck and Kastner, 2009) and our results nicely parallel recent work specifically implicating the left IPS in suppressing unwanted visual information (Mevorach et al., 2010).

The left pIPS activity and the concurrent suppression we observed in right visual cortex could therefore, from a traditional standpoint, be due either to the role of the IPS in motor planning or to its role in directing spatial attention; after all, the anatomical overlap between action-planning and attention networks is well established (Andersen & Buneo, 2002; Andersen & Cui, 2009; Astafiev et al., 2003; Culham & Kanwisher, 2001). But, as has been argued elsewhere, perhaps the allocation of spatial attention is equivalent to the selection and partial specification of actions toward that location (Baldauf & Deubel, 2010; Cisek, 2007; Cisek & Kalaska, 2010). In other words, perhaps the IPS activity in our study is performing only one job, and previous work in separate fields has just given it two different names. According to this view, objects in the workspace compete for action-selection (Cisek & Kalaska, 2010) forming an “attentional landscape” (Baldauf & Deubel, 2010) with peaks of activity at the locations of objects of potential interest. The competitive bias that develops in the visual representation of space (Desimone & Duncan, 1995) and the attentional modulations of this bias (Beck & Kastner, 2009; Kastner & Ungerleider, 2000, 2001; Pessoa et al., 2003) are the same representations and biases that exist simultaneously and in parallel throughout the visuomotor parietal-frontal network – representations that are both the encoding of motor plans *and* the directing of attention. Ultimately when one object ‘wins out’ and is selected for processing, this is identical to one motor plan winning out and being fully specified and subsequently executed. Under this framework, one can ask what a visual distractor is in the real world. Given that the end product of object representation is almost always action (action is, after all, the only way we can influence our environment) and that (usually) only one action can be performed at any one time, the visual objects in our workspace that we ignore as targets become potential obstacles to our action. Thus, previous reports of distractor suppression might actually be seen as a special case of a more general visuomotor suppression of unselected action targets. This may also explain why the putative target-selection process we assigned to the activity we observed in the MFG results in a slight positive bias of activity in the visual field contralateral to the obstacle. If positive activations ultimately attract movements, then this left visual cortex / right visual field bias might represent a low grade bias away from the non-target obstacles. Automatically then, the selection of a target inhibits non-targets and may bias movements away from non-target (i.e. potential obstacle) locations.

We propose that parallel to the target selection / non-target inhibition (like that described in Houghton & Tipper, 1994), the IPS is specifically responsible for detecting objects which impede actions and suppressing their neural representation. Note that this does not mean that the responses to other objects that do not interfere with movements are also actively suppressed, but rather, the reduction in the signal in early visual areas only occurs when those objects can potentially interfere with the planned movement. In our experiment, only when the obstacle was likely to interfere with the upcoming reach did we see the suppression of its neural encoding. Here again, our results bridge research demonstrating that the IPS plays a crucial role in the control of action – namely the patient work implicating the dorsal stream in obstacle avoidance (Milner & McIntosh, 2004; Rice et al., 2008; Rice et al., 2006; Schindler et al., 2004) – and research showing that the IPS as crucial to attention – namely that the IPS is specifically recruited when encoding the task relevance of stimuli (Corbetta et al., 2008; Corbetta & Shulman, 2002; Mevorach et al., 2010; Riddoch et al., 2010; Ruff et al., 2008; Serences & Yantis, 2007).

From this unified perspective, the utility of suppressing the cortical activity corresponding to an interfering obstacle is much easier to understand. If an obstacle object competes in an attentional landscape, and interferes with a specified movement (i.e., is task relevant), then the easiest way to implement avoidance is by reducing that the strength of its signal (see Howard & Tipper, 1997; Tipper et al., 1997; Welsh & Elliott, 2004 for a similar argument). The effect of reducing the obstacle encoding (or diverting attention away from it) is to give an advantage to all other simultaneously encoded motor plans (or increase the attentional allocation to all other objects in the workspace) – the net motor result is a trajectory biased away from (or avoiding) that obstacle position. This explanation represents a simple implementation of obstacle avoidance while providing a more grounded interpretation of exactly what relevance might mean in everyday situations.

The visuomotor planning/programming network we defined in the current experiment functions as an elegant feedback loop. Initially, all objects in the workspace are encoded and compete for action-selection. When the specific movement is instructed during the plan phase, the left IPS encodes the task-relevant level of interference of an obstacle, and the activity in early visual areas is suppressed when interference is high. The top-down suppression of activity in early visual cortex is an efficient way of influencing all the other competitive biases that are based on that initial activity. As a consequence, the loop is completed, such that any action selected from those currently encoded in the dorsal stream is inherently biased by the presence of other potentially interfering objects in the workspace.

4.5. Supplemental Results and Discussion

4.5.1. Note on motion artifacts

As was mentioned above, the motion of the hand and arm through the magnetic field is known to introduce artifacts into the fMRI data (Culham, 2006). Evidence of these artifacts is visible in the plots of the time course data in Figure 4.3. Specifically, an examination of the early Execute phase reveals discontinuities in the time courses that are not attributed to any real signal. For example, in the L-Auditory [2], L-Premotor [3], L-Visual [5] and L-IPS [6] time course plots (Figure 4.3) there appears to be a sudden change in BOLD activity between the 2nd and 3rd volume (30 s). But isn't this discontinuity appearing too late to be attributed to the hand movement, which was cued at 24 s? Given that response times and movement times varied across participants, and that participants performed a reach toward the target, grasped and held the object for a moment, then returned their hand to the rest position (right side of the platform), on the majority of trials, participants took more than 2 s to complete the entire movement (this was confirmed from the bore cam video). Thus, motion artifacts were expected for both the volume immediately after the movement was cued (24-26 s) *and* for the next volume (26-28 s). If both of these time points are affected then interpreting them is necessarily problematic, and, any points connected to them in a time course plot may be discontinuous with them. Thus, the activity recorded at the 30 s mark is likely to be veridical, however the two preceding points are likely contaminated by motion artifacts, creating the observed discontinuity.

4.5.2. Preview network

Above we describe and show the results of isolating the network showing activity higher for the Plan phase than the Preview phase (see Figure 4.3). For the theoretical reasons described, we were interested in these areas since we were specifically interested in the planning response. It is interesting, however, to examine other networks that can be extracted – demonstrating the power of the slow event-related design. For example we identified a Preview network that responded more during the Preview phase (average of predictors 1-6) than during Baseline (average of predictors 19-20, see Figure 4.7). As when defining the Plan network, we used a minimum statistical threshold of $p<0.001$ and only analyzed clusters of voxels larger than 294 mm^3 (minimum cluster size estimated by Monte Carlo simulations of $p<0.05$, implemented in the cluster threshold plug-in for BVQX). Not surprisingly the Preview network is characterized by strong visual cortical activity as well as the bilateral activation of the ventral stream structures usually implicated in the construction of rich visual representations of the world (Milner & Goodale, 1995). Interestingly, we do see a largely left lateralized activation of the dorsal visual stream that overlaps with the Plan network shown in Figure 4.3. This suggests that, as predicted by the attentional landscape (Baldauf & Deubel, 2010) and the affordance competition (Cisek, 2007; Cisek & Kalaska, 2010) hypotheses the simple visual presentation of objects in the workspace activates a network of areas not only involved with representation, but also in the competitive coding of potential action targets.

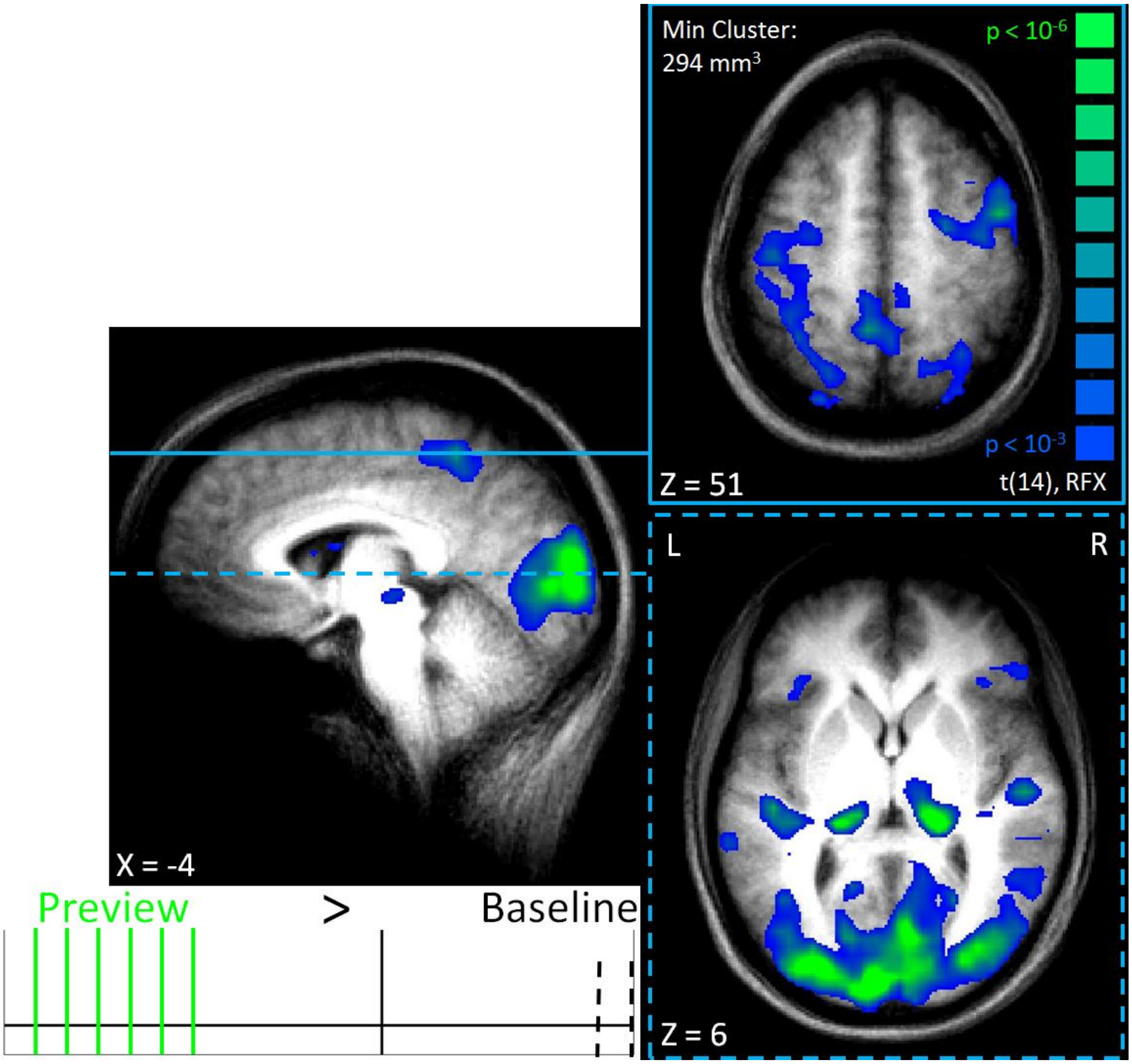


Figure 4.7: Regions active during object preview. A group voxelwise analysis identified areas that were more active (p<0.001, minimum cluster size 294 mm^3) during the Preview phase (average of volumes 1-6) than the Baseline predictors (average of 19-20). The resulting statistical map is presented on an average anatomical MRI of all 15 participants in standardized space with layout to match Figure 4.4. This layout allows for a direct comparison of the Plan and Preview networks. Of note, both the Right Visual and Left pIPS areas are included in this Preview network, while the MFG (and premotor areas) are not.

Moreover, the two distinct areas where we observed Interference effects (Right-visual and Left pIPS, see Figures 4.4, 4.5 and 4.6) overlap with this network (Figure 4.7). This suggests that interference encoding, and its modulation of early visual cortical activity, is likely contingent on the area having a visual response to the object and a motor representation of the planned action. This idea is consistent with previous fMRI studies of action planning showing the IPS to be involved in the integration of visual information of the target position with motor information about the effector required to act on the target (Beurze et al., 2007, 2009). This is intuitive since during planning, interference is defined by the interaction between the purely visual properties of the scene and the planned action – only taken together can these two features combine to determine the task-relevant interference of a given object. Additionally, the lack of overlap between the MFG object-position encoding and the Preview network provides further evidence that the MFG response is tied specifically to the motor representation of the workspace.

4.5.3. Other roles of the IPS – can they all be unified?

In section 4.4.4, we make the argument that the apparently separate roles of the IPS in directing spatial attention (thereby modulating early visual cortex) and planning movements are actually one in the same phenomenon. Of course, we are not the first to have suggested that this might be the case (Baldauf & Deubel, 2010; Cisek, 2007; Cisek & Kalaska, 2010; Ikkai & Curtis, 2008). Moreover, the IPS has been implicated in many tasks outside of attentional direction (e.g. Corbetta et al., 2008; Corbetta & Shulman, 2002) and movement planning (e.g. Andersen & Cui, 2009; Beurze et al., 2009; Culham et al., 2006), including sustained attention (e.g. Ikkai & Curtis, 2008), spatial working memory (e.g. Srimal & Curtis, 2008), decision making (e.g. Gold & Shadlen, 2007) and numerical or magnitude encoding (e.g. Cohen Kadosh & Walsh, 2009; Nieder & Dehaene, 2009) (for reviews see: Culham & Kanwisher, 2001; Duncan & Owen, 2000). It seems unlikely that one brain area is specialized to perform this entire dizzying array of capabilities. More likely, as we and others have argued, the IPS is performing a single task which is central to all of these tasks. As put by Ikkai and Curtis (2008) in a recent paper, “Implicit in this idea is that a unitary mechanism, like a dynamic spatial priority map, could contribute to a variety of cognitive behaviours, like attention, intention and working memory, depending on the afferents used to construct the map and the efferents that readout the map" (pg 1393). Put more generally, and in the context of the current paper, we believe this 'dynamic spatial priority map' is another name for an attentional landscape (Baldauf & Deubel, 2010) which itself is a result of the competitive processes that develop between objects in our environment upon which we might act (Cisek, 2007; Cisek & Kalaska, 2010). If these competitive biases are also the variables in an ongoing decision process, then invariably the same areas will be implicated in decision making. Of course, if the task is to remember the location of an upcoming movement then an area, like the IPS, which codes this information initially, is likely to maintain this encoding across a delay – thus providing a possible explanation of the role of the IPS in spatial working memory. In addition, as the attentional landscape is spread to multiple items in the workspace, the rudiments of a counting system emerge. The catch, of course, is that there must be a limit on the number of items that can be processed in parallel, a reason that we believe a limit of approximately 4 is prevalent in working memory, subitizing and, most recently motor planning tasks (Gallivan et al., 2010).

Of course, trying to paint all of these tasks with a single brush obscures many of the intricacies of the role of the IPS (Andersen & Cui, 2009). For example, many studies show effector specific encoding within the IPS, which would require that more than a single attentional landscape be maintained – at least one for each effector. While much of this is therefore speculation, with continued investigation and – more importantly – a synthesis of information for what appear to be separate research domains, we believe a parsimonious and unified explanation for the role of the IPS, and the fronto-parietal network in general, will emerge.

4.6. References

Andersen, R. A., & Buneo, C. A. (2002). Intentional maps in posterior parietal cortex. *Annu Rev Neurosci, 25*, 189-220.

Andersen, R. A., & Cui, H. (2009). Intention, action planning, and decision making in parietal-frontal circuits. *Neuron, 63*(5), 568-583.

Astafiev, S. V., Shulman, G. L., Stanley, C. M., Snyder, A. Z., Van Essen, D. C., & Corbetta, M. (2003). Functional organization of human intraparietal and frontal cortex for attending, looking, and pointing. *J Neurosci, 23*(11), 4689-4699.

Baldauf, D., & Deubel, H. (2010). Attentional landscapes in reaching and grasping. *Vision Res, 50*(11), 999-1013.

Beck, D. M., & Kastner, S. (2009). Top-down and bottom-up mechanisms in biasing competition in the human brain. *Vision Res, 49*(10), 1154-1165.

Beurze, S. M., de Lange, F. P., Toni, I., & Medendorp, W. P. (2007). Integration of target and effector information in the human brain during reach planning. *J Neurophysiol, 97*(1), 188-199.

Beurze, S. M., de Lange, F. P., Toni, I., & Medendorp, W. P. (2009). Spatial and effector processing in the human parietofrontal network for reaches and saccades. *J Neurophysiol, 101*(6), 3053-3062.

Bressler, S. L., Tang, W., Sylvester, C. M., Shulman, G. L., & Corbetta, M. (2008). Top-down control of human visual cortex by frontal and parietal cortex in anticipatory visual spatial attention. *J Neurosci, 28*(40), 10056-10061.

Castiello, U. (1999). Mechanisms of selection for the control of hand action. *Trends Cogn Sci, 3*(7), 264-271.

Chapman, C. S., & Goodale, M. A. (2008). Missing in action: the effect of obstacle position and size on avoidance while reaching. *Exp Brain Res, 191*(1), 83-97.

Chapman, C. S., & Goodale, M. A. (2010a). Obstacle avoidance during online corrections. *J Vis, 10*(11), 1-14.

Chapman, C. S., & Goodale, M. A. (2010b). Seeing all the obstacles in your way: the effect of visual feedback and visual feedback schedule on obstacle avoidance while reaching. *Exp Brain Res, 202*(2), 363-375.

Chouinard, P. A., & Paus, T. (2006). The primary motor and premotor areas of the human cerebral cortex. *Neuroscientist, 12*(2), 143-152.

Cisek, P. (2007). Cortical mechanisms of action selection: the affordance competition hypothesis. *Philos Trans R Soc Lond B Biol Sci, 362*(1485), 1585-1599.

Cisek, P., & Kalaska, J. F. (2005). Neural correlates of reaching decisions in dorsal premotor cortex: specification of multiple direction choices and final selection of action. *Neuron, 45*(5), 801-814.

Cisek, P., & Kalaska, J. F. (2010). Neural Mechanisms for Interacting with a World Full of Action Choices. *Annu Rev Neurosci*.

Cohen Kadosh, R., & Walsh, V. (2009). Numerical representation in the parietal lobes: abstract or not abstract? *Behav Brain Sci, 32*(3-4), 313-328; discussion 328-373.

Corbetta, M., Patel, G., & Shulman, G. L. (2008). The reorienting system of the human brain: from environment to theory of mind. *Neuron, 58*(3), 306-324.

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci, 3*(3), 201-215.

Culham, J. C. (2006). Functional neuroimaging: experimental design and analysis. In R. Cabeza & A. Kingstone (Eds.), *Handbook of functional neuroimaging of cognition, Ed 2* (pp. 53-82). Cambridge, MA: MIT.

Culham, J. C., Cavina-Pratesi, C., & Singhal, A. (2006). The role of parietal cortex in visuomotor control: what have we learned from neuroimaging? *Neuropsychologia, 44*(13), 2668-2684.

Culham, J. C., & Kanwisher, N. G. (2001). Neuroimaging of cognitive functions in human parietal cortex. *Curr Opin Neurobiol, 11*(2), 157-163.

Culham, J. C., & Valyear, K. F. (2006). Human parietal cortex in action. *Curr Opin Neurobiol, 16*(2), 205-212.

Curtis, C. E., Cole, M. W., Rao, V. Y., & D'Esposito, M. (2005). Canceling planned action: an FMRI study of countermanding saccades. *Cereb Cortex, 15*(9), 1281-1289.

Curtis, C. E., & Connolly, J. D. (2008). Saccade preparation signals in the human frontal and parietal cortices. *J Neurophysiol, 99*(1), 133-145.

Curtis, C. E., & D'Esposito, M. (2003). Persistent activity in the prefrontal cortex during working memory. *Trends Cogn Sci, 7*(9), 415-423.

Curtis, C. E., & D'Esposito, M. (2006). Selection and maintenance of saccade goals in the human frontal eye fields. *J Neurophysiol, 95*(6), 3923-3927.

Curtis, C. E., Rao, V. Y., & D'Esposito, M. (2004). Maintenance of spatial and motor codes during oculomotor delayed response tasks. *J Neurosci, 24*(16), 3944-3952.

Damasio, H. (1995). *Human brain anatomy in computerized images.* Oxford: Oxford UP.

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annu Rev Neurosci, 18,* 193-222.

Duncan, J., & Owen, A. M. (2000). Common regions of the human frontal lobe recruited by diverse cognitive demands. *Trends Neurosci, 23*(10), 475-483.

Fischer, J., & Whitney, D. (2009). Attention narrows position tuning of population responses in V1. *Curr Biol, 19*(16), 1356-1361.

Gallivan, J. P., Chapman, C. S., Wood, D. K., Milne, J. L., Ansari, D., Culham, J. C., et al. (2010). One to four, and nothing more: Non-conscious parallel object individuation in action. *Psychol Sci*.

Gazzaley, A., Cooney, J. W., McEvoy, K., Knight, R. T., & D'Esposito, M. (2005). Top-down enhancement and suppression of the magnitude and speed of neural activity. *J Cogn Neurosci, 17*(3), 507-517.

Gold, J. I., & Shadlen, M. N. (2007). The neural basis of decision making. *Annu Rev Neurosci, 30*, 535-574.

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends Neurosci, 15*(1), 20-25.

Houghton, G., & Tipper, S. P. (1994). A Model of Inhibitory Mechanisms of Selective Attention. In D. Dagenbach & T. H. Carr (Eds.), *Inhibitory Processes in Attention, Memory, and Language* (pp. 53-112). San Diego, California: Academic Press Inc.

Howard, L. A., & Tipper, S. P. (1997). Hand deviations away from visual cues: indirect evidence for inhibition. *Exp Brain Res, 113*(1), 144-152.

Ikkai, A., & Curtis, C. E. (2008). Cortical activity time locked to the shift and maintenance of spatial attention. *Cereb Cortex, 18*(6), 1384-1394.

Kastner, S., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1998). Mechanisms of directed attention in the human extrastriate cortex as revealed by functional MRI. *Science, 282*(5386), 108-111.

Kastner, S., Pinsk, M. A., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1999). Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron, 22*(4), 751-761.

Kastner, S., & Ungerleider, L. G. (2000). Mechanisms of visual attention in the human cortex. *Annu Rev Neurosci, 23*, 315-341.

Kastner, S., & Ungerleider, L. G. (2001). The neural basis of biased competition in human visual cortex. *Neuropsychologia, 39*(12), 1263-1276.

Kwong, K. K., Belliveau, J. W., Chesler, D. A., Goldberg, I. E., Weisskoff, R. M., Poncelet, B. P., et al. (1992). Dynamic magnetic resonance imaging of human brain activity during primary sensory stimulation. *Proc Natl Acad Sci U S A, 89*(12), 5675-5679.

Mevorach, C., Hodsoll, J., Allen, H., Shalev, L., & Humphreys, G. (2010). Ignoring the elephant in the room: a neural circuit to downregulate salience. *J Neurosci, 30*(17), 6072-6079.

Mevorach, C., Humphreys, G. W., & Shalev, L. (2006a). Effects of saliency, not global dominance, in patients with left parietal damage. *Neuropsychologia, 44*(2), 307-319.

Mevorach, C., Humphreys, G. W., & Shalev, L. (2006b). Opposite biases in salience-based selection for the left and right posterior parietal cortex. *Nat Neurosci, 9*(6), 740-742.

Mevorach, C., Humphreys, G. W., & Shalev, L. (2009). Reflexive and preparatory selection and suppression of salient information in the right and left posterior parietal cortex. *J Cogn Neurosci, 21*(6), 1204-1214.

Mevorach, C., Shalev, L., Allen, H. A., & Humphreys, G. W. (2009). The left intraparietal sulcus modulates the selection of low salient stimuli. *J Cogn Neurosci, 21*(2), 303-315.

Milner, A. D., & Goodale, M. A. (1995). *The Visual Brain in Action*. Oxford: Oxford University Press.

Milner, A. D., & McIntosh, R. D. (2004). Reaching between obstacles in spatial neglect and visual extinction. *Prog Brain Res, 144*, 213-226.

Mon-Williams, M., Tresilian, J. R., Coppard, V. L., & Carson, R. G. (2001). The effect of obstacle position on reach-to-grasp movements. *Exp Brain Res, 137*(3-4), 497-501.

Nieder, A., & Dehaene, S. (2009). Representation of number in the brain. *Annu Rev Neurosci, 32*, 185-208.

Ogawa, S., Tank, D. W., Menon, R., Ellermann, J. M., Kim, S. G., Merkle, H., et al. (1992). Intrinsic signal changes accompanying sensory stimulation: functional brain mapping with magnetic resonance imaging. *Proc Natl Acad Sci U S A, 89*(13), 5951-5955.

Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia, 9*(1), 97-113.

Pessoa, L., Kastner, S., & Ungerleider, L. G. (2003). Neuroimaging studies of attention: from modulation of sensory processing to top-down control. *J Neurosci, 23*(10), 3990-3998.

Rice, N. J., Edwards, M. G., Schindler, I., Punt, T. D., McIntosh, R. D., Humphreys, G. W., et al. (2008). Delay abolishes the obstacle avoidance deficit in unilateral optic ataxia. *Neuropsychologia, 46*(5), 1549-1557.

Rice, N. J., McIntosh, R. D., Schindler, I., Mon-Williams, M., Demonet, J. F., & Milner, A. D. (2006). Intact automatic avoidance of obstacles in patients with visual form agnosia. *Exp Brain Res, 174*(1), 176-188.

Riddoch, M. J., Chechlacz, M., Mevorach, C., Mavritsaki, E., Allen, H., & Humphreys, G. W. (2010). The neural mechanisms of visual selection: the view from neuropsychology. *Ann N Y Acad Sci, 1191*(1), 156-181.

Ruff, C. C., Bestmann, S., Blankenburg, F., Bjoertomt, O., Josephs, O., Weiskopf, N., et al. (2008). Distinct causal influences of parietal versus frontal areas on human visual cortex: evidence from concurrent TMS-fMRI. *Cereb Cortex, 18*(4), 817-827.

Schindler, I., Rice, N. J., McIntosh, R. D., Rossetti, Y., Vighetto, A., & Milner, A. D. (2004). Automatic avoidance of obstacles is a dorsal stream function: evidence from optic ataxia. *Nat Neurosci, 7*(7), 779-784.

Serences, J. T., & Yantis, S. (2007). Spatially selective representations of voluntary and stimulus-driven attentional priority in human occipital, parietal, and frontal cortex. *Cereb Cortex*, *17*(2), 284-293.

Serences, J. T., Yantis, S., Culberson, A., & Awh, E. (2004). Preparatory activity in visual cortex indexes distractor suppression during covert spatial orienting. *J Neurophysiol*, *92*(6), 3538-3545.

Silvanto, J., Muggleton, N., Lavie, N., & Walsh, V. (2009). The perceptual and functional consequences of parietal top-down modulation on the visual cortex. *Cereb Cortex*, *19*(2), 327-330.

Smith, A. T., Singh, K. D., & Greenlee, M. W. (2000). Attentional suppression of activity in the human visual cortex. *Neuroreport, 11*(2), 271-277.

Srimal, R., & Curtis, C. E. (2008). Persistent neural activity during the maintenance of spatial position in working memory. *Neuroimage*, *39*(1), 455-468.

Sylvester, C. M., Jack, A. I., Corbetta, M., & Shulman, G. L. (2008). Anticipatory suppression of nonattended locations in visual cortex marks target location and predicts perception. *J Neurosci, 28*(26), 6549-6556.

Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. New York: Thieme Medical.

Tipper, S. P., Howard, L. A., & Jackson, S. R. (1997). Selective Reaching to Grasp: Evidence for Distractor Interference Effects *Visual Cognition*, *4*(1), 1-38.

Tresilian, J. R. (1998). Attention in action or obstruction of movement? A kinematic analysis of avoidance behavior in prehension. *Exp Brain Res, 120*(3), 352-368.

Tresilian, J. R. (1999). Selective attention in reaching: when is an object not a distractor? *Trends Cogn Sci, 3*(11), 407-408.

Welsh, T. N., & Elliott, D. (2004). Movement trajectories in the presence of a distracting stimulus: evidence for a response activation model of selective reaching. *Q J Exp Psychol A, 57*(6), 1031-1057.

Yoon, J. H., Curtis, C. E., & D'Esposito, M. (2006). Differential effects of distraction during working memory on delay-period activity in the prefrontal cortex and the visual association cortex. *Neuroimage, 29*(4), 1117-1126.

Chapter 5

5. General Discussion

5.1. Summary

The goal of the current thesis was to investigate the neural coding of objects that obstructed reaching and grasping behaviour in intact humans and to further specify how these obstacle representations affected movements. In the first experiment (Chapter 2, Chapman & Goodale, 2010b), I extended the findings of my previous behavioural work (Chapman & Goodale, 2008) to demonstrate that obstacle avoidance during reaching persisted: 1) when the reach was made toward a specific location in space, 2) when avoiding one or two obstacles, and 3) when vision of the hand was available during the reach. Furthermore, I directly tested one aspect of expectancy in this experiment by manipulating the predictability of visual feedback. I demonstrated that under the more natural and complex reaching conditions imposed by multi-object environments, there were no effects of the predictability of visual feedback, concluding that in this context the visuomotor system is predisposed to use vision when available. The second experiment (Chapter 3, Chapman & Goodale, 2010a) was designed to test one aspect of obstacle avoidance behaviour that remained inconclusive following the experiment described in Chapter 2. Specifically, the results from Chapter 2 suggested that obstacle avoidance behaviour was the same regardless of whether or not vision of the hand was available during the reach. This could mean that the visuomotor system does not update the reach trajectory in flight, indicating perhaps that obstacle representations are not available to online correction mechanisms. To test this directly, we had participants perform reaches to a target that sometimes switched position at movement onset. Such abrupt target ‘jumps’ are known to induce automatic corrections toward the new location. To test whether or not obstacle information could be incorporated into corrected movements, we placed single objects behind the initial target position (where they have been shown to have significantly reduced interference effects, Chapman & Goodale, 2008) on one side of space. We demonstrated that only when a target jump caused an object to become an obstacle (i.e. the target jumped further in depth and to the right, with an obstacle on the right hand side of space) did we observe spatial avoidance in the reach trajectory. Importantly, this avoidance occurred after the initial response to the jumped target, and could unfold without disrupting the speed of the movement, speaking to the automaticity of these deviations. We did observe, however, significant slowing of the corrected movement when the risk for collision was high. Taken together, the results from Chapter 3 indicate that obstacle representations can be accessed or updated in flight, and that the avoidance system is sensitive to the risks for collision. Finally, in Chapter 4 of this thesis (Chapman, Gallivan, Culham, & Goodale, 2010), we describe results from a neuroimaging study where participants grasped a square target object with an obstacle object either behind or to the side of the target. Importantly, the two obstacle positions interfered differentially with two wrist postures such that for each obstacle position and wrist posture, there were trials where the obstacle interfered and trials where the obstacle did not interfere with the grasp. Using a slow event-related paradigm, we isolated brain areas that were active during the planning of the movement and demonstrated that within this plan network one area in the left IPS exhibited increasing activity on trials where there was interference compared to no-interference trials. This IPS activation was accompanied by suppression in visual cortex, which previous work suggests could indicate the top-down modulation of the visual activity. Importantly, this experiment is the first to show that the neural coding of a non-target object that interfered with a planned action was suppressed.

This thesis was also motivated by theoretical frameworks that suggest objects are encoded in parallel and compete for action specification and selection (see section 1.2, Baldauf & Deubel, 2010; Cisek & Kalaska, 2010; Duncan, 2006). These frameworks all postulate that a frontoparietal network is engaged when competition is being resolved. None of the frameworks, however, propose how the visuomotor system deals with objects that are relevant for action but need to be avoided. I believe my results fit within these frameworks and can extend our understanding of how visuomotor attention is deployed across the workspace. First, the fact that we observed avoidance (movements *away* from obstacles) that precisely scaled with the degree to which an obstacle interferes with movement (Chapter 2 and Chapman & Goodale, 2008) suggests that competitive biases must be sensitive to the nature of interference and that object coding in the brain can result in movements away from the position of non-target objects. Second, the fact that we observed avoidance during online corrections (Chapter 3) suggests the PPC (which has been shown from neuropsychology to be crucial to both tasks in isolation) is involved and that all potential obstacles are at least partially represented, even if they do not interfere with an uncorrected movement. That is, the attentional landscape is flexible and dynamic when deploying visuomotor biases across the workspace. Finally, the fact that we observe simultaneously the activation of the PPC and the suppression of visual cortex (Chapter 4) suggests that the competitive biases are controlled by the PPC and impose their effects by modulating the initial coding of objects in early visual areas.

The remainder of the Discussion is centered on two questions which emerge from my integration of obstacle encoding into a framework of visuomotor competition. First, while all frameworks propose that visuomotor biases are controlled by a frontoparietal network, the specific identification of the PPC in Chapter 4, combined with the PPC's recruitment in a wide array of tasks, raises the question of what exactly the role of this part of the brain is. Second, since the notion of suppression or inhibition of obstacle-related neural activity is critical to the interpretation of my effects, I provide insight into how this inhibitory signal might evolve both spatially and temporally. In combining information pertaining to both these questions, I propose that the PPC is specifically involved in integrating visual scene information from visual cortex with goal-directed motor preparation signals from frontal cortex to produce a visuomotor biasing signal. A crucial component of this PPC-generated bias is the suppression of the neural coding of obstacles (or non-targets). I end with a discussion of the most pertinent outstanding questions and some general remarks.

5.2. What does the PPC do?

Throughout this thesis the PPC has been assigned many different roles. As the primary area responsible for transforming visual cortical information into signals critical to the execution of actions it represents the early part of the dorsal visual stream (Milner &

Goodale, 1995) or, more generally, the frontoparietal network discussed at length in the context of visuomotor selective attentional frameworks (see section 1.2). In this thesis, I have presented evidence that the PPC is involved in obstacle avoidance (Chapman, Gallivan, Culham et al., 2010; Rice et al., 2006; Schindler et al., 2004), online corrections (Chapman & Goodale, 2010a; Desmurget et al., 1999; Pisella et al., 2000), movement planning (e.g. Andersen & Buneo, 2002; Beurze, de Lange, Toni, & Medendorp, 2007, 2009; Chapman, Gallivan, Culham et al., 2010), movement execution (e.g. Andersen & Cui, 2009; Culham, Cavina-Pratesi, & Singhal, 2006; Culham & Valyear, 2006), directed spatial attention (e.g. Corbetta, Patel, & Shulman, 2008; Corbetta & Shulman, 2002) and top-down cortical suppression (e.g. Beck & Kastner, 2009; Mevorach, Hodsoll, Allen, Shalev, & Humphreys, 2010; Pessoa, Kastner, & Ungerleider, 2003). As I discussed in Chapter 4 (section 4.5.3), this list does not include studies showing the involvement of the PPC in spatial working memory (e.g. Srimal & Curtis, 2008), decision making (e.g. Gold & Shadlen, 2007), numerical or magnitude encoding (e.g. Cohen Kadosh & Walsh, 2009; Nieder & Dehaene, 2009) and effector specificity (which by extension includes visuomotor transformations, e.g. Andersen & Buneo, 2002; Andersen & Cui, 2009). I am by no means the first person to realize the incredible number of functions that have been proposed for the PPC or, more generally, for the parietal cortex. As Culham and Kanwisher state in a review of parietal cortex function:

> "…parietal activation has also been reported for a stunningly diverse range of stimuli and tasks. These include motion processing [52•,66•,67,68], stereo vision [69], spatial [70,71] and non-spatial working memory (which shows considerable overlap with visual attention activation [72••]), mental imagery [73], mental rotation [74], response inhibition [75,76], task switching [77], alertness [78], calculation [79,80], and even functions not typically attributed to parietal cortex such as pain processing [81], swallowing [82] or meditation [83]. Clearly, it would be absurd to claim that parietal areas are specialized for any one of these processes and some means of integrating the diversity of findings is required" (2001, p. 159).

John Duncan in collaboration with Adrian Owen provided a systematic meta-analysis of areas involved in 5 cognitive tasks: response conflict, task novelty, number of elements in working memory, working memory delay and perceptual difficulty (2000). Not surprisingly the parietal cortex (and a network of frontal regions) was involved in all tasks (see also Duncan, 2006 for updated review). Culham and Kanwisher (2001) provide some enlightening comments regarding how to make sense of the overwhelming generality of parietal function. They suggest five possible reasons why the parietal cortex is implicated in so many tasks, two of which are specific to neuroimaging and are not discussed here. First, they argue that the parietal cortex might truly be 'association cortex' where, by definition, information specific to all these tasks necessarily converges. Second, the parietal cortex could be serving one purpose that is so general that it is recruited in almost every task (they give examples of attention or coordinate transformation). Finally, third, researchers may be inherently misunderstanding the nature of the parietal cortex, and only with better definitions of its functional organization can we ask the right types of questions to understand its role (Culham & Kanwisher, 2001).

While Culham and Kanwisher perhaps intended for these options to be separate, I believe they are correct on all three points. I also believe the questions they raise pertaining to all of parietal cortex are also relevant when considering only the PPC. Working backwards through their three points, if we have not been asking the right types of questions to tackle the generality of the PPC, then what *are* the right types of questions? At the start of the Introduction, I argued that the 'right' questions for the careful scientist are ones that are specific enough to be experimentally tractable. But perhaps this level of specificity just does not work when one is trying to describe something that by its very nature is not specific. In this case, perhaps the right types of questions to ask when trying to determine the function of the PPC are the big questions: to echo my Introduction, questions like "'Why we are here?' (to shape our environments to our greatest benefit) and 'How do we do it?' (by performing maximally efficient actions)" (section 1.1.1). Seen through this more remote lens, perhaps the role of the PPC is to select the action that accomplishes the current goal most efficiently. This definition matches with Culham and Kanwisher's second speculation that the function of the parietal cortex (and by extension the PPC) is sufficiently general to be involved in the myriad of tasks where it has been shown to be active. How does this general definition of efficient-action-selector fit with the first of Culham and Kanwisher's options that the PPC is associative cortex where specific information relevant to each task converges? Given that the predominant form of information processed in the human brain is visual and the only output (be it verbal report, button pressing or reaching) is a motor response, then the PPC is exactly the region for the association of visual and motor information. Moreover, as the specification of the current goal is likely generated by frontal regions then this information must also flow into the PPC to provide goal direction to the mapping of visual objects and intended actions. The product of this association is the specification of action relevant (or, more generically, response relevant) targets and the partial preparation of movements toward them.

If this interpretation of the function of the PPC sounds familiar, that is because the PPC plays an integral part within the frontoparietal network that was discussed in the context of the three theoretical frameworks of visuomotor selection introduced in section 1.2. Recall that those frameworks each argue that multiple visual objects compete for action relevant neural encoding. The putative result is a bias map or attentional landscape across the workspace with peaks of activation and valleys of inhibition at action-relevant and action-irrelevant (or interfering) locations respectively. Given the above discussion of the PPC, what is its role in the context of a competitive landscape across the visuomotor workspace? I would argue that the PPC is not involved in the generation of the visual map of space – that is a job almost certainly done by early visual areas which we know show retinotopic coding and parse visual scenes into different objects and regions. Nor do I believe the PPC is involved in specifying a particular goal-directed action (i.e. the goal to reach from this start button to that red LED) – that is probably mediated by frontal areas including premotor cortex. Rather, the PPC is the source of the task-relevant bias – controlling which objects and locations in the neural map of the workspace are enhanced and which are inhibited. Ultimately, the PPC integrates visual information and goal intentions to produce selectivity. This conclusion echoes the work of previous researchers, including Bisley and Goldberg (2003), who have argued that the PPC is responsible for creating a map of salient parts of space. In their words (speaking of the activity of LIP in monkeys),

> “Thus one cannot ascertain a monkey’s locus of attention by measuring the activity of a single neuron in LIP, or even by measuring the activity of all the neurons in whose receptive field a given object lies. Instead, one must look at the activity of the ensemble of LIP neurons representing all of the visual field. In this case, we can interpret the graded responses of the discharge at a given site in LIP as providing an attentional priority associated with the object in the subtended receptive field…However, the anatomical projections and graded responses seen in most of these areas suggest that they participate, along with LIP, in a distributed network that drives visual attention. We suggest that it is this distributed network that provides the bias for the biased competition model of attention postulated by Desimone and Duncan…” (Bisley & Goldberg, 2003, p. 85).

Although their interpretation of LIP activity is similar to the role I ascribe to the PPC in this section, Bisley and Goldberg are quick to point out that, a “motor intention interpretation is unlikely for a number of reasons” (2003, p. 85). On this point, I disagree with their explanation. Rather, I believe (in following from the affordance competition hypothesis (Cisek, 2007; Cisek & Kalaska, 2010) and the attentional landscape hypothesis (Baldauf & Deubel, 2010), see section 1.2) that not only does the PPC provide a salience map, but also that this salience map is intrinsically tied to actions. The evidence for this interpretation is found throughout this thesis. To reiterate a few examples, in studies with cats walking over obstacles (see section 1.5.2), it was not the visual presentation of the object that activated the cat PPC, but the movement of the object to a location where it became action relevant (Andujar, Lajoie, & Drew, 2010). Neuroimaging work conducted by Gallivan et al. (2009) showed that the PPC was preferentially activated for objects within reach – again, indicating the PPC is not simply encoding a visual response, but specifically a visual response that is relevant to action. Finally, as mentioned at several points in Chapter 4, Beurze and colleagues (Beurze et al., 2007, 2009) used a partial instruction technique (information about target location or required effector was presented in a random order and separated with a delay) to specifically identify areas of the brain that were crucial to the integration of the two types of information present in each instructional cue. In support of the current interpretation of the PPC, they showed it (along with premotor cortex) had a heightened response to the second of the two cues, regardless of which cue it was, demonstrating that these areas are crucial for visuomotor integration.

The characterization of the PPC as the source of action-relevant biases also explains why this region is critical to obstacle avoidance. As I have argued throughout this thesis (and describe in a detailed mechanistic speculation below, see section 5.4) obstacles are objects whose representations have to be inhibited so that the resulting motor behaviours avoid their location. In many ways then, obstacles are the reciprocal of target objects, whose representations require enhancement so that motor behaviours can be directed toward their location. Not surprisingly, patients with damage to the PPC have trouble with both target-directed reaching (e.g. Perenin & Vighetto, 1988) and obstacle avoidance (Schindler et al., 2004). If a patient is unable to generate a visuomotor bias that integrates the coding of objects conveyed to the PPC by the visual cortex with the generation of goals by the frontal cortex, then there will a fundamental breakdown in the patient's target-directed motor behaviour. It is important to note that it is neither their ability to see nor their ability to execute actions (though this may appear impaired) that is causing the problem. It is instead a failure to integrate the information required to bias behaviour towards and away from action-relevant locations (for a recent detailed account of the neuropsychological implications of impairments to the PPC and the rest of the frontoparietal selection network, see Riddoch et al., 2010).

This account can also help to explain the results of the experiments described in this thesis. The fact that a target-directed action deviates more from obstacles that are closer to the moving limb (Chapter 2 and Chapman & Goodale, 2008) suggests that deviations resulting from putatively PPC-generated biases scale precisely with the degree to which an object could potentially interfere with the intended action. That objects placed past a reach target initially do not interfere with a movement (Chapter 3 and Chapman & Goodale, 2008) but are automatically incorporated into a corrected movement, reveals that biases are 'intelligently' distributed across a defined workspace, and at the same time are flexible enough to incorporate potential changes to the environment. Moreover, the fact that the PPC is implicated in online corrective movements in general (Desmurget et al., 1999; Glover, 2004; Pisella et al., 2000) is not surprising given that moving the hand to a new target location in-flight is easily conceptualized as an updating in real time of the visually defined task demands (i.e. a mismatch between the intended action and new goal location is detected, resulting in the generation of a new bias and a shift in the movement). Together with the findings from Chapter 3, this speaks to the complicated temporal and spatial dynamics of the competitive-bias maps generated by the PPC. Finally, most concretely, the neuroimaging results from Chapter 4, directly implicate the PPC as detecting the task-relevant interference caused by a non-target obstacle. That this interference signal was independent of the object position and the intended action speaks convincingly toward the putative role of the PPC in integrating the visual environment with action demands while remaining separate from each individual process in isolation.

Of course, even if we accept this role for the PPC (which is simplistic and probably incorrect, as scientific hypotheses almost always are), it still leaves open the question of how the bias is implemented and thus affects behaviour. Some clues are evident from the Introduction section on suppression in visual cortex (section 1.3), which resonates with the findings from Chapter 4 of the current thesis. That is, the bias introduced by the PPC manifests in the actual visual coding of space in early visual cortex. The PPC might not code the map of space, but it alters how the map is coded. There is an elegant efficiency to this strategy. If, as argued by the proponents of competitive-bias frameworks (section 1.2), we envision the frontoparietal network as a series of reciprocally connected, nested feedback loops which fill the gap between visual input and motor output, then the easiest way to influence the output (action) is to bias the input (visual map). This way the bias will propagate throughout any areas processing the information that will ultimately determine behaviour. One element that has been lacking in our discussion of the PPC has been its general (though not absolute) division into effector-specific areas (e.g. Andersen & Buneo, 2002; Andersen & Cui, 2009). These subdivisions suggest that rather than a single competitive map (which is how I have discussed its role so far) the PPC may simultaneously code several effector specific maps (e.g. eye and hand). Given that these effector specific maps would be generated from a common input with common or converging outputs (e.g. the eye and hand may arrive at the same target) and rather loosely specified goals, this necessitates that the PPC have the neural machinery to transform information between effector specific coordinate frames (or alternatively from a common frame to each effector independently).

This discussion of the function of the PPC does not appear to relate directly to some of the more purely cognitive roles of the PPC such as its putative role in short term memory and numerical processing. It is beyond the scope of this thesis to elaborate on how these seemingly disparate tasks might actually be explained by the PPC's role in generating visuomotor biases. It is worth noting, however, that in a recent rapid reaching task, we were able to demonstrate that the capacity limit for parallel action planning is approximately four (Gallivan et al., 2010). The fact that this limit is the same as that noted in other cognitive tasks (like subitizing) provides an encouraging link between visuomotor control and higher level cognition.

5.3. How does inhibition work?

A critical component of the hypothesized role of the PPC outlined above is not only to positively bias the visuomotor encoding of target objects, but to negatively bias the visuomotor encoding of objects that are not targets. Moreover, when non-target objects are obstacles that interfere with movements, this inhibitory biasing signal takes on an even greater importance. In the following section, I review three related models which outline how an inhibitory biasing signal might be implemented.

5.3.1. Houghton-Tipper (H&T) model of inhibition

Because the notion of the need to inhibit distracting stimuli is based on the idea that stimuli compete for selection, the Houghton-Tipper model of inhibition argues for many of the same tenets that are central to the competitive frameworks described earlier (see section 1.2). Specifically, it states that, "vision and action systems evolved together to enable successful interactions with the environment" (p. 1385) and that, "the actions which different objects evoke (afford) can automatically be encoded in parallel, and that competition and selection take place between these action representations" (Tipper et al., 1998, p. 1386). What makes their model unique from the more general frameworks is that they propose a mechanism by which inhibition might occur and they tie the predictions of their model to the specific behavioural findings they observe. Upon careful inspection, what is referred to as the Houghton-Tipper model of inhibition is actually two different but related models. The first, forwarded by Houghton and Tipper in 1994, is a properly formalized model that provides a general framework for how inhibition could be implemented to solve many different input-to-output selection problems (referred to here as H&T, Houghton & Tipper, 1994). The second is an application of the original model to the specific case of reaching in the presence of distractors (referred to here as H&T-reach, Houghton & Tipper, 1999; Tipper et al., 1998; Tipper, Howard, & Houghton, 2000). The second model, however, includes additional theoretical components that are not completely formalized, thus leading to some confusion and difficulty in interpretation. In this section, I provide a description of the original model (H&T) and in the following section (5.3.2) I describe the modified version applicable to reaching (H&T-reach).

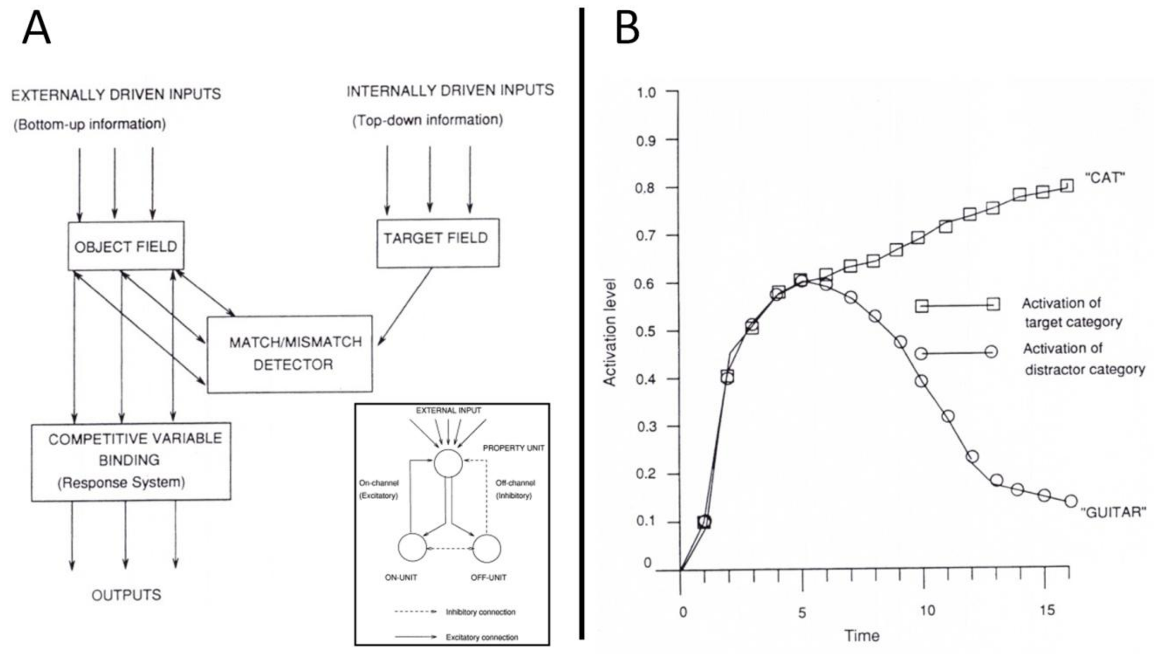


Figure 5.1. Schematic depiction of the H&T model (Houghton & Tipper, 1994) of selection and inhibition. (A) Overall flow of information. External inputs are represented as objects, which are compared (matched) with an internal template of the target. Objects with property units matching the target are enhanced, while those that do not match are inhibited. Ultimately objects are bound to responses which lead to outputs. Inset: diagram of a single property unit. Within the inset a solid line indicates an excitatory connection and a dashed line is an inhibitory connection. The resulting connections mean the property unit functions as a self contained feedback loop, though in the model it is reciprocally connected with all property units defining an object. (B) The modeled timeline of selection/inhibition in a verbal naming task. Both objects / responses give rise to the same initial activation. Once the selection / inhibition has sufficient time to develop, the activity for the object matching the target (in this case “CAT”) is enhanced while the activity for the non-target (“GUITAR”) is inhibited. This model closely matches the actual neural activity for competing targets depicted in Figure 1.2.

The major components of the H&T model (Houghton & Tipper, 1994) are shown in Figure 5.1a. At the highest level of generalization, incoming inputs from the environment are organized into objects (OBJECT FIELD) which are compared with an internally generated representation of the target (TARGET FIELD). Each object is itself comprised of several property units (PROPERTY UNIT, which include colour, location etc, see inset Figure 5.1a) while the target is simply a list of properties (this distinction between property units and properties is explained below). Properties of the target are compared with property units of the objects by a MATCH/MISMATCH DETECTOR. When an object property unit matches with a target property, that property unit is selectively enhanced via feedback mechanisms within the property unit (thus a property unit is actually a feedback circuit that influences the overall strength of signal associated with an object, while a property is simply that – a feature of the target). Importantly, all property units that comprise an object are interconnected such that the enhancement of one property unit will spread to all object properties. Conversely, if there is a mismatch between a target property and an object property unit, then that property unit is selectively inhibited via feedback mechanisms, and this inhibition will spread to all property units of that object. Each object is bound to a specific response and thus competition between objects is ultimately a competition between potential responses (COMPETITIVE VARIABLE BINDING). Eventually, when one of the object-response pairs is sufficiently enhanced (presumably because its property units match the target), it is selected and its response is executed. The H&T model is made clearer when the timeline of activity for two competing object-response pairs is examined (Figure 5.1b). In this example, the competition is an identification problem where the response is to name the object (a CAT versus a GUITAR). Importantly, the initial activation of both responses is identical. Only after enough time has elapsed for the relevant object features to have been compared with the internal CAT target do we see the selective enhancement of the CAT response and inhibition of the GUITAR response (at approximately time point 6). The pattern of model activation bears a striking resemblance to that shown in Figure 1.2 of neural data supporting the notion of parallel encoding and selection in the attentional frameworks.

5.3.2. Houghton & Tipper model of reaching (H&T-reach)

In applying the H&T model to reaching data (which I refer to as H&T-reach), Houghton, Tipper and colleagues (Houghton & Tipper, 1999; Tipper et al., 1998, 2000) introduced some significant additions. First, they assume that the direction of a target-directed reach is coded by a neural population (for which there is abundant evidence, e.g. Georgopoulos, Schwartz, & Kettner, 1986). The result for any reach is a distributed encoding of preferred direction across a number of cells (see Figure 5.2). Second, they assume that a population of cells can code for more than one target-directed reach (i.e. parallel encoding of a reach toward a distractor) at a time (as was shown by Cisek & Kalaska, 2005, see Figures 1.2, 5.2c and 5.2g). Finally – and most importantly – they argue that there are two separate inhibitory processes which are engaged differentially depending on the relative salience of a distractor. If the salience of the distractor is low relative to the target, then no top-down inhibitory signal is generated (top-down inhibition is the type explained in the H&T model), and the distractor-related activity is filtered out by a version of lateral inhibition (see Figure 5.2 left panel). That is, cells with a preferred direction toward the target are amplified (on-center) and cells with a preferred direction away from the target (including the distractor) are inhibited (off-surround). The result of this ‘weak’ form of inhibition is distractor-related activity that is not completely inhibited, resulting in trajectories that deviate toward distractors (see Figure 5.2d). Conversely if the salience of a distractor is high relative to the target, and thus demands a large inhibitory response, then the process described in the H&T model is engaged (which they refer to as reactive inhibition). That is, a match/mismatch detector compares an internal template of the target to the distractor which generates a strong top-down suppressive signal toward the distractor (that also should enhance the target, but this is never specified). The result of this ‘strong’ form of inhibition is a suppression of the distractor population code *below* baseline, resulting in deviations away from the distractor (see Figure 5.2h).

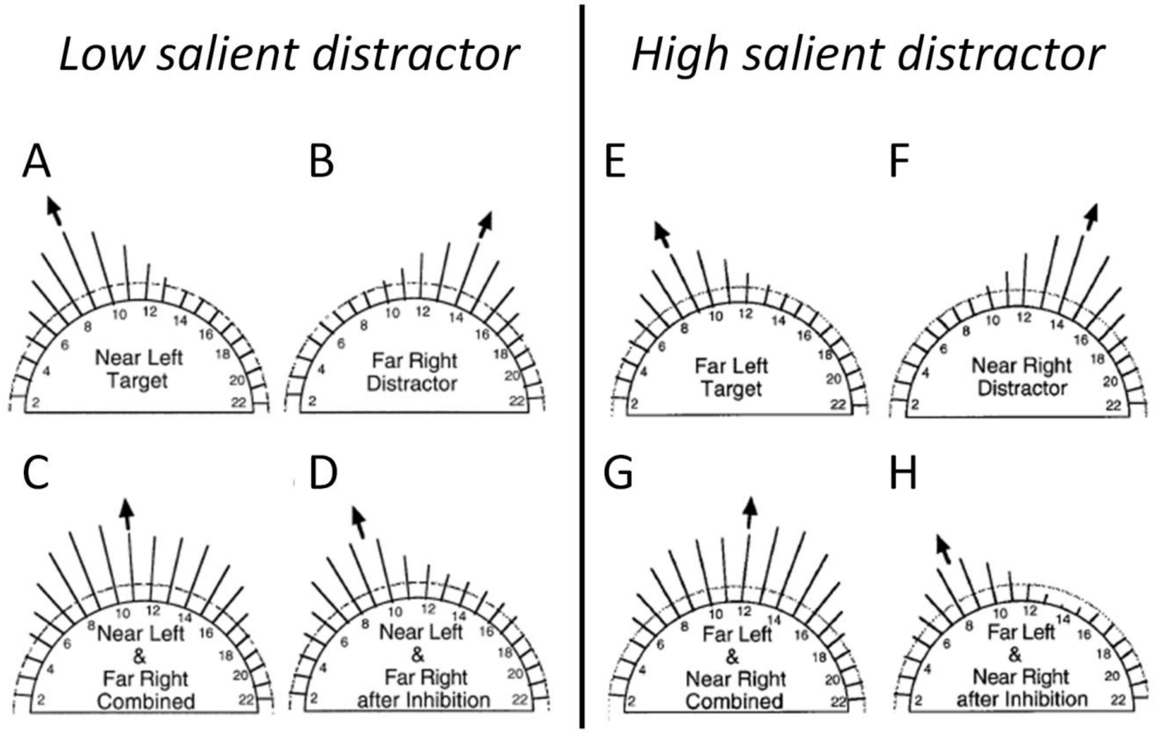


Figure 5.2. Schematic depiction of the H&T-reach model (Houghton & Tipper, 1999; Figure from Tipper et al., 1998) of reaching in the presence of distractors. Reach direction is depicted as the peak of a distribution of activity across a population (direction indicated with black arrows). Targets (A,E) and distractors (B,F) presented in isolation lead to unimodal distributions with a reach directed toward the target. Summing the target and distractor distributions (C,G) gives a bimodal distribution with a reach direction in the middle of the two peaks, suggestive of parallel encoding. Inhibitory processes lead to shifts in reach direction either toward (D) or away (H) from the distractor. Left Panel: (A) a strong response to a near target and (B) a weak response to a far distractor results in (D) incomplete inhibition of the distractor and deviations toward its location. Right panel: (E) a weak response to a far target and (F) a strong response to a near distractor results in (H) reactive inhibition which suppresses the distractor below baseline and results in deviations away from its location.

Unfortunately, the H&T-reach model, which is obviously the most applicable to the current thesis, is not properly formalized (like the H&T model) and is rife with inconsistencies which make applying it to other tasks difficult. Most problematic is the notion that the relative salience of the distractor determines which of two independent inhibitory mechanisms is engaged. Tipper and colleagues (2000) seem to acknowledge this point. In an adapted version of the distractor reach paradigm, participants were now required – on some trials – to reach toward the distractor LED. Regarding their model's predictions, they state:

> "Unfortunately, it is not possible to predict the effect of this new procedure on reaching trajectory. We have argued that the weakly activated reaching response does not trigger reactive inhibition. Rather, selection can be resolved via lateral inhibition between cells in the activated populations. We simply did not know whether the increased salience of the reaching response to the LED would be sufficient to trigger reactive inhibition, and thus reduce deviations toward, or even cause deviations away from, the LED." (Tipper et al., 2000, p. 236)

This comment illustrates that the notion of relative salience is poorly understood. In fact, I would argue that it is not defined at all, but rather is interpreted for each experiment differently to account for the observed results. The only clear variable that Tipper and colleagues argue directly affects relative saliency is 'visuomotor processing efficiency' (for summary see Meegan & Tipper, 1999; Tipper, Meegan, & Howard, 2002). They argue that targets or distractors presented closer to the responding hand (proximity-to-hand effect, Meegan & Tipper, 1998) or on the same side of space as the responding hand (ipsilateral effect, Meegan & Tipper, 1998; Tipper, Lortie, & Baylis, 1992) are processed more quickly (that is, reaches toward them are planned more efficiently). Since distractor inhibition is tied to relative salience, this leads to the following argument, "Because near distractors win the race for the control of action, they interfere more, and hence require greater levels of inhibition" (Tipper et al., 2002, p. 593). The authors make the opposite argument when a distractor location is obstructed by a clear obstacle, "In the obstacle condition...the hand has to deviate around the transparent surface. Therefore this action is far more complex, and hence will lose the race for the control of action" (Tipper et al., 2002, p. 599). By extension, the more complex (i.e. less efficient) action toward the obstacle location requires less inhibition. If this sounds confusing, that is because it is.

The confusion arises because ‘visuomotor processing efficiency’ is as nebulous a term as salience was in the first place. I agree that there are likely stronger biases toward objects within reach of the acting (and/or dominant) hand, and thus distractors occupying that space may require additional inhibition. But to base a non-formalized model on these concepts where ‘salience’ of a distractor or ‘efficiency’ of visuomotor planning response provides the (arbitrarily determined and relatively unknown) switch between ‘weak’ and ‘strong’ inhibition is quite simply a formula that will not work for describing behaviour.

Less severe but equally troubling problems are strewn throughout the descriptions of the H&T-reach model. The most problematic for the current thesis is their treatment of obstacles. As indicated in the quote above (from a 2002 paper describing the H&T-reach model), an obstacle is something other than a non-target object in the environment. This is a departure from the original description of the H&T model, where it was argued, “...we propose that to achieve the behavioural goal [reaching for a bag of chips on a cluttered coffee table], the accommodation of a detailed form of an action to the nontarget objects is required, such as when reaching around or over obstacles” (Houghton & Tipper, 1994, p. 56). Here, clearly, obstacles are non-target objects to be avoided, and thus, according to the H&T model, require inhibition. If, as argued in the original formulation of the H&T model, obstacles do require inhibition, then it would seem necessary to account for that suppressive effect when trying to interpret the distractor-at-obstacle-location effects reported in their later study (Tipper et al., 2002).

5.3.3. Welsh & Elliot’s Response Activation Model (RAM)

Overall, the application of the H&T-reach model to describe the neural suppression and avoidance behaviour in the current thesis does not look promising. There is, however, an alternative theory posited by Welsh and Elliot (2004). In their Response Activation Model (RAM), Welsh and Elliot agree that competing motor plans (coded by populations of neurons) are automatically initiated in parallel. However, rather than relying on the postulation of two inhibitory mechanisms to explain behaviour, they argue that deviations-toward or deviations-away from distractors are a result of timing. That is,

> “The critical difference between the response vector [H&T-reach] and the response activation models, however, is that the latter acknowledges that inhibitory processes require time to develop. As such, the initial characteristics of the movement are dependent upon how complete selection is at the moment of response initiation, not solely on the salience of the competing stimulus. Indeed, we predict the opposite effects of salience—objects of greater action relevance (salience) will initiate responses that are more difficult to inhibit because of a tighter and more efficient perception–action link. The result of this tighter link is that the responses to stimuli of greater action relevance will remain in an active state for a longer period of time, resulting in more of the competing action being incorporated into the initial response and, in this case, causing deviation towards the nontarget location.” (Welsh & Elliott, 2004, p. 1035)

Thus, according to the RAM, deviations toward distractors are the result of actions initiated before inhibition of distractor responses has had time to completely develop (resulting in behaviour like that depicted in Figure 5.2, left panel). Deviations-away, however, represent cases where inhibition has reduced activation at the distractor location below baseline, inducing shifts in population codes away from its position (as in Figure 5.2, right panel). In a more recent finding, Welsh and Elliot also demonstrate that information presented prior to the presentation of targets and distractors (so called pre-cues) can also influence behaviour (Welsh & Elliot, 2005). They interpret these findings as evidence that the visuomotor system can develop and maintain biases across an experiment, not just within a given trial. My discussion of these models of inhibition and their implications and potential application to obstacle avoidance is discussed in the next section where I outline my own ideas for a model of reaching behaviour in the presence of non-target objects.

5.4. Obstacle Inhibition Model

The RAM forwarded by Welsh and Elliot (2004) and described above (see section 5.3.3) definitely improves upon the H&T-reach model (see section 5.3.2) in that separate inhibitory processes are not required to account for the difference between deviations toward and away from distractors. Rather, Welsh and Elliot argue this difference is due to the development of the inhibitory signal across time. Despite the improvement, there are still two points of contention I have with the RAM model. First, it quite clearly asserts that distractor inhibition is not the same as obstacle avoidance. Second, it hypothesizes that deviations away from distractors occur only when the response to a non-target is reduced below baseline. Both these points are evident in the following passage:

> "In sum, what is proposed to be the important determining factor of movement trajectories, under competitive conditions in which obstacle avoidance is not at issue, is the completeness of inhibitory process intervention on the competing nontarget responses. If the nontarget response is in an active state (above baseline levels), the combination of the active target and nontarget response population codes will result in initial movement trajectories that deviate towards the nontarget location. On the other hand, if a competing response has been inhibited (activation levels returned to below baseline) prior to movement initiation, then the resulting combination of codes should result in a trajectory that veers away from the nontarget location" (Welsh & Elliott, 2004, p. 1036).

Hopefully by now, I have managed to make it clear why I believe treating obstacles as separate from distracting stimuli is a problem. Provided that real-world distracting stimuli have three-dimensional shape, then their identification as non-targets renders them as obstacles. Similar to what I argued in Chapter 4 (section 4.4.4), two-dimensional LED distractors (like those used by both Tipper and Welsh) are therefore likely the exception rather than the rule. Since humans evolved to interact in a dynamic three-dimensional environment, then an account of visuomotor selection and inhibition should be applicable to the demands of such an environment.

My concern with deviations away from distractors requiring that those locations be deactivated (i.e. drop below baseline) is that the experimental evidence does not support this premise. In the work described in Chapter 4, as well as that reviewed in the Introduction (see section 1.3), the noted suppressive effects are always *relative* suppression. That is, the initial response to a visual object is always positive (or activated, to use Welsh and Elliot's terminology). This is clear in Chapter 4 (see Figure 4.4) where the response to the obstacle object during the Preview phase was robust. In the following two sections, I first outline a modified version of a response activation model that is extended to include the inhibition of obstacles and incorporate the notion of relative inhibition. Second, I focus on evidence across a number of studies which provide a suggestion of the precise timeline for these selective/inhibitory processes to unfold.

5.4.1. Stages of obstacle inhibition

I hesitate to use the word ‘model’ since what I describe here is not mathematically formalized (though, potentially it could be, which would be an interesting avenue to pursue). Rather, it is a model in the sense that Welsh and Elliot (2004) and Tipper et al. (i.e. H&T-reach, Houghton & Tipper, 1999; Tipper et al., 1998, 2000) use the term – a descriptive definition of how visuomotor selection might occur. It borrows heavily from the competitive frameworks described in the Introduction (see section 1.2), and my choice to depict task relevant objects with ‘peaks and valleys’ of activity distributed across the workspace is taken directly from Baldauf and Deubel’s attentional landscapes hypothesis (2010). I use in my examples the type of obstacle avoidance we tested in Chapter 2. Specifically, I consider trials with a single object present (e.g. on the left in the Figures for this section) when reaching toward a localized target (e.g. red LED). The described processes should extend to all the studies I describe in the current thesis (though the nature of grasping avoidance may differ), as well as to my previous behavioural study with obstacles (Chapman & Goodale, 2008).

The first step in the model is to acknowledge one of its inherent limitations – namely that the workspace appears as a visual transient, and requires that only a single reach be performed per trial. As Cisek and Kalaska argue, “…interaction with a complex and ever changing environment…cannot be broken down into a sequence of distinct self-contained events that start with a discrete stimulus and end with a specific response” (2010, p. 275). Of course, they recognize, as I do, that this trial-based approach allows for us to test specific questions, but they caution that, “…the apparent serial order of these events [responses to objects, followed by their selection] is largely the result of the experimental strategy of dividing behaviour into a sequence of discrete and independent trials” (Cisek & Kalaska, 2010, p. 288). With the caveat that the visuomotor selective processes that are discussed rarely, if ever, occur discretely during natural behaviour, we start with the onset of the visual stimulus. In the specific case in question, this would be produced by the LCD goggles opening, revealing the workspace (a black table, with red LED target, tall grey obstacle and start button see Figure 5.3a). As Cisek and Kalaska state: “When the stimulus is first presented, we should expect an initial fast feedforward sweep of activity along the dorsal stream, crudely representing the potential actions that are most directly specified by the stimulus" (Cisek & Kalaska, 2010, p. 285). In our example, there are two objects which are visually salient and could potentiate actions – the red LED target and the grey obstacle. Assuming there are no biases introduced prior to visual onset (i.e. expectation or trial history – this is a point I return to later in this section), both the LED and obstacle would therefore have a positive activation. This initial activation is depicted in Figure 5.3b as two Gaussian hills of activity centered on both the target and obstacle locations (this is identical to how activity was presented by Baldauf & Deubel, 2010). For convenience, I depict the attentional landscape as overlaid on the workspace and the objects therein. Of course, these hills of activity are meant to represent the theoretical neural activity associated with the objects and workspace, and thus are unlikely to be mapped to space in the way implied by the figure. This format, however, allows for a convenient and easily interpretable correspondence between the objects and my proposed evolution of the response to each object. For the purposes of the present example, the amount of initial positive activity at each location is somewhat irrelevant, so I have made the two activations equal. However, an argument could be made that the larger, more salient, more proximal grey object would have a stronger initial response (though this would be strongly affected by pre-trial biases, which I discuss below). Before proceeding with a description of the evolution of the inhibitory response, I first focus on the idea of relative salience; an idea that I feel must be introduced to solve what I refer to as the obstacle paradox, which is explained below.

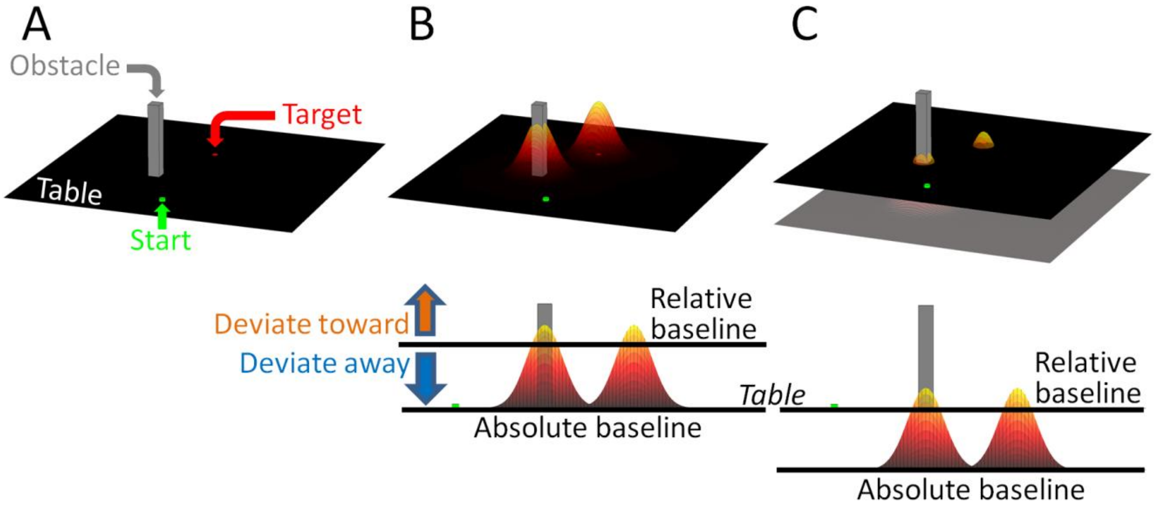


Figure 5.3. Proposed initial activations following visual presentation in a typical obstacle avoidance study. Where theoretical activity is shown, a 3D view of the workspace is presented above a side-on view of the workspace. (A) Layout prior to visual onset. Participants are asked to make reaches from the start button to the target without contacting the obstacle. (B) At visual onset both the target and obstacle objects are represented with positive activation (theoretical activation overlaid on workspace). For graphical convenience, the lower limit of activation (absolute baseline) is at the plane of the table. An arbitrary relative baseline is shown; objects with activations above this limit at movement onset result in deviations toward their location, while objects with activations below this limit result in deviations away from their location. C) To be consistent with other figures in the section (Figures 5.4 and 5.5), the plane of the table is shown as the relative baseline.

The obstacle paradox is simply the fact that visual objects (including obstacles) always give rise to positive activity, yet obstacles (and sometimes distractors) result in movements away (i.e. negative or repulsive effects) from their location. According to the implications from a model like the affordance competition hypothesis (Cisek, 2007; Cisek & Kalaska, 2010), objects resulting in positive responses should act as attractors to movement. This is clearly not the case for obstacles which have positive activity but repulsive effects. In order to account for the obstacle paradox, I introduce the notion of a relative baseline (depicted in Figure 5.3). In Figures 5.3b and 5.3c I show equal initial-activation hills centered on the target and obstacle locations. For graphical convenience, in Figure 5.3b these hills reach their minimum (which I refer to as absolute baseline) at the plane of the table. I believe that for every visual scene, in addition to the initial crude specification of potential actions, there is also a baseline of activity established between the competitive encoding of objects. Activations of objects higher than this relative threshold result in movements that deviate toward those locations, while those objects with activations lower than this relative threshold result in movements that deviate away from those locations. Critically, however, objects whose activations are inhibited below the relative baseline can still remain above some absolute baseline – thus allowing for a positively activated object to result in deviations away from its location. In the bottom panel of Figure 5.3b I select an arbitrary relative baseline. In Figure 5.3c I show that, for graphical convenience, you can let the plane of the table represent the relative rather than absolute baseline (as I do for Figures 5.4 and 5.5). You can imagine that the relative baseline for any given workspace might be related to the number of competing objects, or the range of initial activations (i.e. some sort of mean activation). I admit that this idea is somewhat arbitrary, and perhaps is not much better of a solution than introducing a second type of inhibition as Houghton and Tipper did in their H&T-reach model (see section 5.3.2). It does, however, have the benefits of proposing a single mechanism and of matching with experimental evidence for positive activations resulting in negative (deviate-away) consequences. As an extremely speculative neural correlate of the notion of a relative baseline, it has been shown that a subset of neurons in the superior colliculus (a structure critical to controlling eye-movements) show reduced ‘build-up’ activity as the number of potential eye-movement targets increases (Basso & Wurtz, 1997, 1998). The authors conclude that this activity is representative of a motor set, and here I (very tentatively) suggest that this motor set might in part establish a relative baseline across the set of potential targets (as the number of targets increases, by virtue of a limited capacity system, the activity to each individual target decreases – thus the relative baseline would also decrease).

Having established the specification of initial activations and the idea of a relative baseline, I now describe how the inhibitory processes might unfold (see Figure 5.4). I agree with the fundamental premise forwarded by Welsh and Elliot in the RAM (2004) that these inhibitory processes take time to develop. I also agree, therefore, that should one be forced to act at different stages of inhibition, then different reach behaviours will be observed (a possible reach for each stage of inhibition is therefore indicated with a green line in the bottom panels of Figure 5.4). Consider the stage immediately after the initial encoding of the salient objects (Figure 5.4a). Here I represent that both the target LED and obstacle have positive initial activations. Should an action be required before *any* selective process has been engaged, then both positively activated locations compete as potential targets, and this model predicts a trajectory that is initially aimed toward the midpoint of the two targets. Of course, participants take at least 200ms to initiate an action, so at least 200ms of selective processing will be brought to bear on the activity associated with the target and obstacle, which means that the noted hand path at this stage is unlikely to be produced. Experimentally, however, we can force participants to treat all objects in a visual scene as potential targets until they initiate a movement. Under these conditions, participants are essentially prevented from progressing further down the selection pathway (though some enhancement at all potential target locations is likely). In this case, we have shown that participants do indeed initiate trajectories toward the midpoint of the two targets (Chapman, Gallivan et al., 2010a).

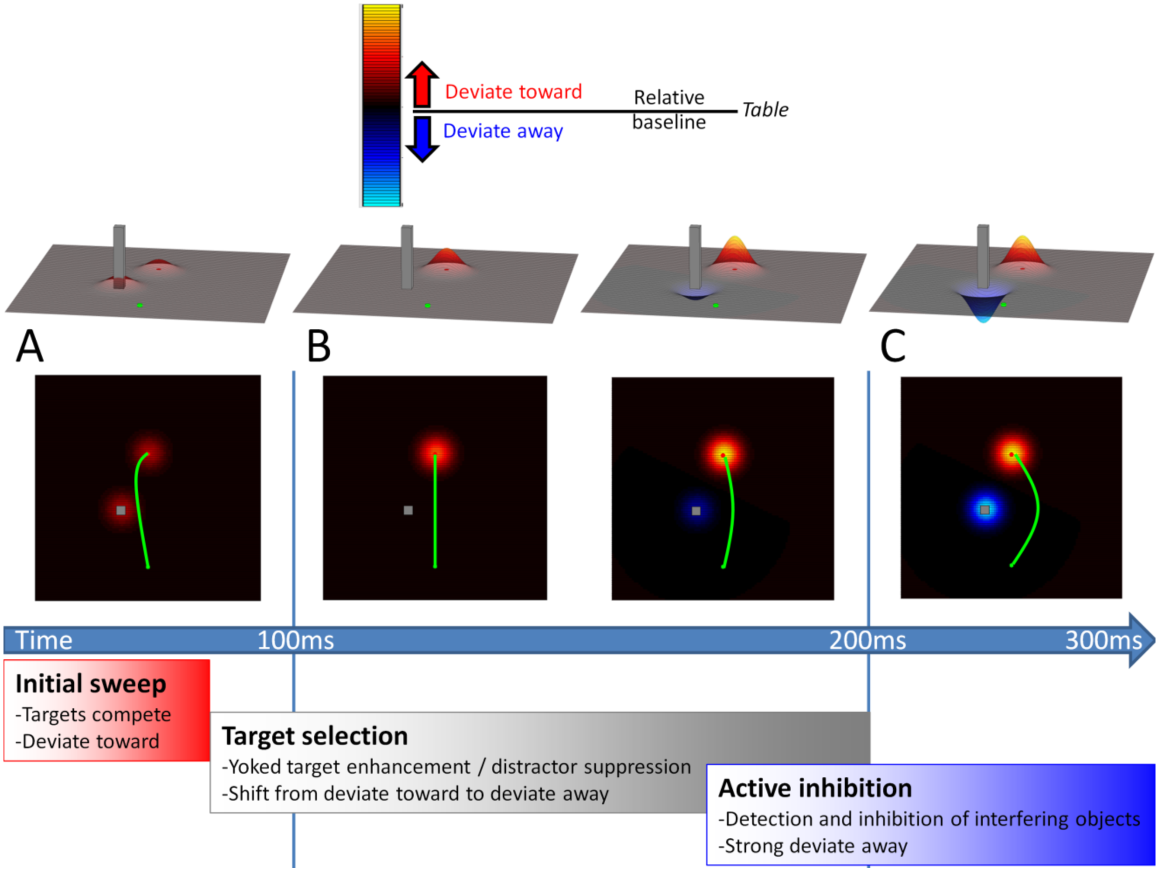


Figure 5.4. Proposed evolution of activity related to target selection and obstacle inhibition. 3D plots of the workspace and activity appear in the top row, overhead view in the second row and along the bottom a theoretical timeline is shown. The relative baseline is at the plane of the table – positive activations relative to this baseline attract movements while negative activations relative to this baseline repel movements. In the overhead view, green traces correspond to hypothetical trajectories if reaches were initiated with the depicted activity. (A) Initially, both the target and obstacle are positively represented, and a reach would aim for a midpoint between them. (B) Due to the target matching the desired stimulus and obstacle not matching the desired stimulus there is a yoked enhancement of the target and inhibition of the non-target. Reaches executed during this phase would shift from slight deviations-toward to deviations-away from distractors. (C) Because the obstacle interferes with the desired reach, it receives additional active inhibition, resulting in strong deviations away from its location.

Immediately following the initial specification of potential action targets, a “slower selection process should begin to sculpt the neural activity patterns by introducing a variety of task-relevant biasing factors” (Cisek & Kalaska, 2010, p. 285). For my example, I consider two biasing factors, target selection *and* the detection of object interference. I stress the ‘and’ since the second major modification I propose to make to previous models of inhibition is that the inhibition of distracting stimuli (including, and potentially most importantly, obstacles) is tied not only to their status as not matching the target but also to their role as physical stimuli interfering with a movement. Admittedly, this again introduces a further complication to inhibition that may prove difficult to implement, but presuming systems exist to identify the degree to which competing visual stimuli match an internal representation of the goal target (the MATCH/MISMATCH detector from the H&T model, see section 5.3.1) then it does not seem too much of a stretch to suggest that a similar system exists to compare the internal representation of a desired movement *trajectory* to an objects physical dimensions to detect where there may be interference. The experimental evidence discussed in Chapter 4 suggests that this type of selective process must be occurring. That is, given that the target-selection demands in that experiment stayed identical across trials (always grasp the square rectangle) then the interference activity we find in the PPC is indicative exclusively of planning a grasp where the non-target object functions as an obstacle. Moreover, since we find this effect across both obstacle positions, but only when the wrist posture yields an interfered reach, the reported activity is not merely the result of selecting a target in the presence of a specific object, but must be tied to the detection (and visual cortical suppression) specifically of interfering stimuli.

With these two stages of selection / inhibition (target selection and interference detection) in mind, I return to my model example. I first show how the target selection process might affect the activity at both the target and obstacle locations. Here I borrow from the idea put forward by the Houghton-Tipper model of inhibition (H&T model, Houghton & Tipper, 1994) of target selection as a process of matching object properties perceived from the environment with an internal representation of the target (see Figure 5.1). Objects in the environment sharing critical features with the target (MATCH) are selectively enhanced, and objects whose features do not overlap with the target (MISMATCH) are selectively inhibited. Moreover, given that all objects encoded in parallel compete for selection and that we assume a limited capacity system (that is, one can encode only a finite number of objects with a finite positive activity) the enhancement (or inhibition) of an object's activity is necessarily yoked to the inhibition (or enhancement) of all others. That is, in order to keep a system-wide equilibrium (determined by capacity) as the activity associated with one object goes up, activity associated with another must go down. I represent this type of yoked-target enhancement / non-target inhibition in Figure 5.4b. Since the red LED clearly matches the internal representation of the target, activity at its location is enhanced. Concurrently, the mismatch between the internal target representation and the tall grey obstacle drive the activity at the obstacle location down. For simplicity, to represent that these two processes are necessarily linked, I show the activations changing by equivalent amounts, though this might not necessarily be the case since the system could independently weight the enhancement or the inhibition as being more important (or more than one object location may need inhibiting, resulting in differing amounts of enhancement and inhibition to each object). Examining the resulting theoretical reach trajectories (green lines in overhead plots), we see that during this process of MATCH/MISMATCH enhancement/inhibition we would predict a graded response of deviations that gradually shift away from non-target locations – precisely as observed by Tipper's and Welsh's group (Tipper et al., 1998, 2000; Welsh & Elliott, 2004; Welsh, Elliott, & Weeks, 1999). In situations where the non-target is not a physical object but a distracting LED, the inhibition at its location is likely to develop relatively slowly – both because the urgency to avoid (see next paragraph) is low and because it shares many characteristics with the target (same shape, size etc.). Given that experimenters using these types of distractors usually demand rapid responses, in some experiments partial deviations toward distractors (closer to behaviour depicted in Figure 5.4a) and in some partial deviations away from distractors (closer to Figure 5.4b, right panel) will be observed, dependent on the exact timing and configuration of the target and distractor. As Welsh and Elliot

(2004) showed, giving more time to allow the inhibitory process to develop fully resulted in deviations away from distractors (see section 5.4.2 and Figure 5.6).

What is lacking in the experimental evidence of reaches deviating away from inhibited distractors are the large scale deviations induced by obstacles. It is likely for this reason that both Welsh et al. and Tipper et al. elected to leave this behaviour as separate from the behaviours explained by their models. However, I find this unsatisfying. The plain fact is that we do avoid obstacles, that they must be encoded in the brain, and that somehow this encoding must result in large deviations away from their position. Importantly, as I have argued above, obstacles are likely the most commonly encountered non-target objects. Therefore, I introduce in my model the idea that the degree to which an object interferes with a desired trajectory is a separate (but parallel) process whereby an internal template of the desired reach is compared with an object’s physical position. Objects whose physical shape interferes with the desired movement are subject to an additional inhibitory response, which I label active inhibition (see Figure 5.4c). For simplicity, I show the target selective process as occurring prior to the interference detection and active inhibition process. As mentioned, however, these processes likely occur in parallel and thus no specific order should be presumed from my ordering of them (but see section 5.4.2 for speculation on the timing of these events). Of course, this active inhibition requires that participants have an internal template of a desired reach (in the same way that the target selection phase requires an internal template of the target). I do not propose to specify how this desired reach might be computed, but I believe the overwhelming consistency of target directed reaches speaks to the existence of such a template. That is, given that the degrees of freedom of the reaching arm allow for an infinite number of solutions for how the hand could arrive at a target, the remarkable consistency both within and across participants (generally straight (relative to the workspace) trajectories with some biomechanical curvature) suggests that an internal template would be accessible. This idea of a trajectory template is supported by the evidence from obstacle avoidance in reaching tasks with monkeys (see section 1.5.1) where the spatial path of a reach around an obstacle remained incredibly stable from the first reach trial across thousands of repetitions (Torres & Andersen, 2006). In my example (Figure 5.4c), the activity at the obstacle location receives additional active inhibition due to its proximity along the desired reach trajectory (e.g. straight from start position to target). The result is a reach that strongly deviates away from the obstacle position. It is worth mentioning that in the preceding discussion of active inhibition, I specified only that the physical shape of an object would influence how much it would interfere with a desired reach. One could imagine that other features (like harmful properties such as extreme heat or sharp edges) could also factor into this avoidance; this remains a testable question.

The evolution of the target selection and non-target (obstacle) inhibition described above and depicted in Figure 5.4 starts from the inaccurate assumption of null activity prior to visual onset. Not only will this never occur in the real world (as described above) but it also fails to account for the fact that across an experiment, participants will develop biases to act at particular locations, or expect obstacles to appear in specific parts of the workspace. This was indeed the motivation for Welsh and Elliot to demonstrate how these biases can emerge prior to action specification using pre cues (2005). These biases are likely maintained without a visual signal and thus have profound influences on selection, inhibition and behaviour. Two recent experiments prove how important previous trial history is on reaching movements. In one study, Jax and Rosenbaum (2007) had participants perform many fast reaches outward from a central target to one of 12 eccentric targets (like positions on a clock) then inward back to the middle. On some trials, a virtual obstacle was placed between the target and goal position and avoidance was noted. Importantly, on the trial *after* the participant had avoided an obstacle residual curvature was still present in the reach, even though no obstacle was present. This indicates that previously executed paths will create biases in the attentional landscape that carry over to subsequent trials (though with time, these biases fade, see Jax & Rosenbaum, 2009). In a similar vein, we recently used our rapid reach paradigm where there are multiple potential targets present prior to movement onset to test for the biasing effects of acting at one location repeatedly across up to five trials (Chapman, Gallivan et al., 2010b). Here, two targets were always present on the screen prior to movement onset, one to the left and another to the right of midline and one was selected as the target for action when the reach was initiated. Embedded within the pseudo-randomized sequence of trials were sets of trials where one target (e.g. the left side) was consecutively selected as the target for action for up to 5 trials. We observed the clear build-up (and eventual saturation) of an initial trajectory bias toward the previously cued target. In my example, modeling the attentional landscape that develops during an obstacle avoidance trial, I would predict there would therefore be several sources of bias that participants would carry across trials. I give an example of some of these biases as applied to the example that has been used throughout this section (see Figure 5.5). Given that the position of the target (Figure 5.5a) and depth of obstacles (Figure 5.5b) remains constant across the experiment, one would expect biases of these locations to be maintained. I have depicted the relative bias toward the target location to be positive, thus aiding in enhancement, while the relative bias toward obstacles is negative, thus aiding in inhibition. Because the biases are relative, however, these particular locations are likely still preferentially attended (i.e. result in positive activations). It is also worth noting that I have intentionally caused the bias at the right-hand obstacle locations to be slightly larger than the bias on the left hand side. This is to account for the fact that right-hand reaches (as was performed in this task) are more interfered with by right-hand obstacles – thus these positions may require, and retain, additional inhibition. Finally both the start position of the hand (Figure 5.5c) and the possible path of the hand through space (Figure 5.5d) are potential sources of bias. It has been shown that perceptual processing is better near the location of the hand (Brown, Kroliczak, Demonet, & Goodale, 2008; Kao & Goodale, 2009), and, as has been discussed, interference effects of distractors (Meegan & Tipper, 1998), or detection of perceptual targets (Deubel & Schneider, 2004) is increased near the hand and close to the upcoming trajectory. Even considering only this small selection of biasing factors, it is clear that the pre-trial attentional landscape is complex (see Figure 5.5e where a simple sum of the bias templates is presented). Moreover, this account does not deal with the fact that the biases are likely to have interactive relationships (i.e. a sum is unlikely to be the method by which biases are integrated) nor does it reflect the fact that the environment and agent are rarely static, meaning that the workspace itself is constantly shifting.

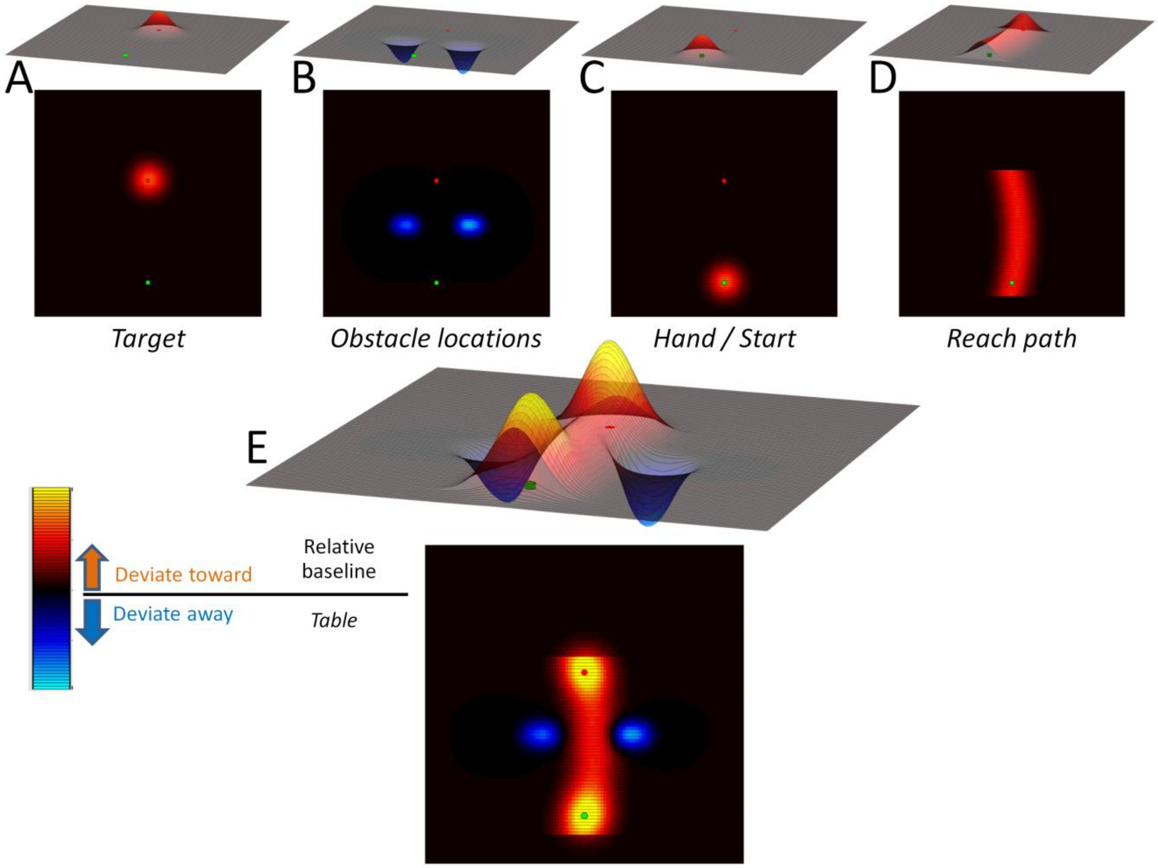


Figure 5.5. Possible sources of between-trial bias and the potential distribution of activity that may result. Overhead views shown below 3D plots. The plane of the table is the relative baseline. (A) Positive bias at the target location. (B) Negative bias at the obstacle locations, with an even larger bias on the right when participants reach with their right hand. (C) and (D) Positive biases at the hand start position and along the reach path respective. (E) A simple sum of the biases depicted in A-D, demonstrating what is an overwhelmingly complicated workspace bias even prior to task demands being incorporated.

Despite the obvious shortcomings, this model provides some tentative first steps toward understanding how non-target objects – which can often become obstacles – might influence our movements. It also suggests that the inhibition of a non-target is as automatic as, and is intrinsically linked to, the selection of a target. Moreover, the inhibition of non-targets and the resulting movement trajectories away from their location implies that the visuomotor system is predisposed to treat non-targets as potential obstacles and veer away from their location.

5.4.2. Temporal evolution of obstacle inhibition

Critical to the inhibition model of obstacle avoidance I described above (and to the RAM from which it is derived, Welsh & Elliott, 2004) is the idea that target selection and non-target inhibition evolve across time. However, while I provided some insight into what events might occur in this process (see Figure 5.4), the specific timing remains largely an open question. In this section, I provide a brief survey from experiments which provide some insight into the temporal aspect of selection and inhibition (a tentative time course of these events appears in the bottom panel of Figure 5.4). Many of the conclusions I make regarding the timing of inhibition can actually be derived from Figure 1.2 from the Introduction. In that section (1.2 and specifically in that figure), I present data from each of three attentional frameworks that describe competitive processes between relevant visuomotor stimuli. Figure 1.2a, shows average spiking data from 88 neurons in IT cortex when the target (thick black line) versus non-target (thin black line) is in the receptive field of the neuron (Desimone, 1998). Figure 1.2b shows data from a population of cells in dorsal premotor cortex when a monkey was required to remember two possible targets before selecting one based on a cued colour (Cisek & Kalaska, 2005). Finally Figure 1.2c shows data from a population of parietal cortex cells when one of two to-be-reached targets was inside (red and blue traces) or outside (black trace) the cells receptive field prior to movement execution (Baldauf, Cui, & Andersen, 2008). Across all three we can extract at least two properties of target selection. First, as suggested in the description of the model presented earlier (see Figures 5.3 and 5.4), all visual stimuli are initially represented with a positive activation. This initial sweep of activation can be seen in Figure 1.2 as the sharp rise of traces that occurs within 50 ms of the onset of the visual array and is equivalent for targets and non-targets. From 50 to 100 ms after visual onset, target selection processes are likely being carried out (i.e. the matching of target features to object features etc.), such that targets are selectively enhanced and non-targets are selectively inhibited. I referred to this as yoked selection/inhibition in the model description (see Figure 5.4b). This appears as the abrupt separation of target from non-target activity that occurs somewhere between 100-200 ms after visual onset (see Figure 1.2). After ~200 ms (approximately the same time that the earliest behavioural reports of a decision could be seen) it is unclear exactly what happens. From the data presented in Figure 1.2, it appears that activity for both the target and non-target remains above their initial (i.e. prior to visual onset) state, with the target activity steadily increasing and the non-target activity steadily decreasing. Many other studies have confirmed that the timeline of target selection follows the above description (e.g. McPeek, 2006; Schall, 2001; Song & McPeek, 2010). Only a few experiments, however, have revealed clues about how long the inhibitory response, potentially responsible for deviations away from distractors and obstacles, takes to develop. It is possible that as soon as the target and non-target activity begins to diverge (e.g. at ~150 ms) then behaviour executed with competitive encoding in this state would move away from non-targets. This interpretation is not supported, however, by studies showing that non-targets with residual positive activations (but less than target activation) still result in deviations toward the distractor location (McPeek, 2006; Welsh & Elliott, 2004). Thus, it appears as if it does take some time for the non-target suppression and target enhancement to evolve, and that deviations away from non-target locations will only occur if enough time has passed such that the non-target activity is suppressed below a *relative* baseline. I present data from four studies which suggest that what I refer to as active inhibition emerges at least 200 ms and up to 500 ms after the presentation of the visual array (see Figure 5.6).

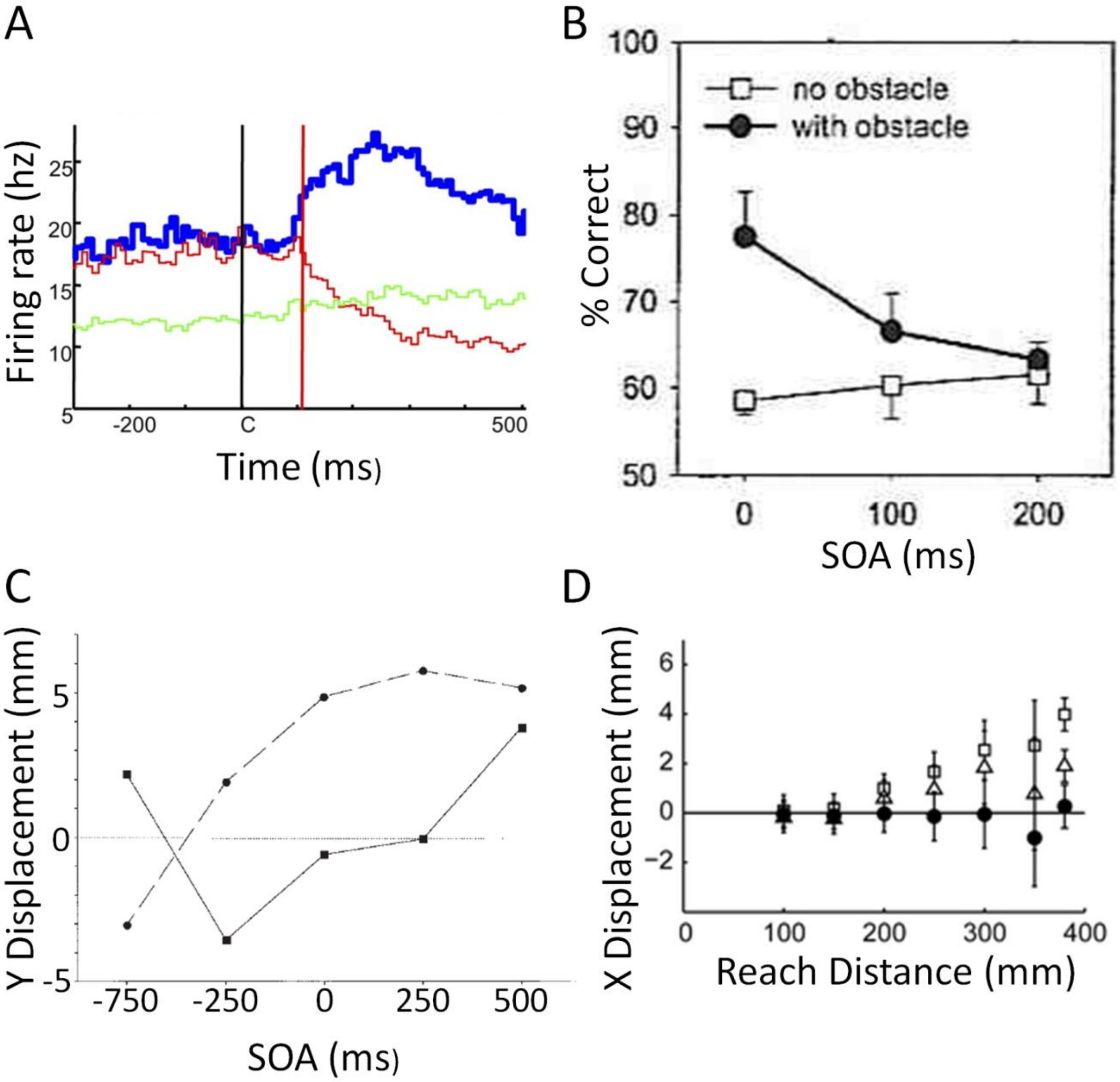

A
Firing rate (hz)
25
20
15
10
5
-200
C
500
Time (ms)
B
100
90
80
70
60
50
no obstacle
with obstacle
% Correct
0
100
200
SOA (ms)
C
Y Displacement (mm)
5
0
-5
-750
-250
0
250
500
SOA (ms)
D
X Displacement (mm)
6
4
2
0
-2
0
100
200
300
400
Reach Distance (mm)

Figure 5.6. Data from previous experiments providing insight into the timeline of inhibition. (A) From Cisek and Kalaska (2005). Dorsal premotor neural activity in macaque monkeys for selected targets in a cells preferred direction (thick blue line) selected targets in the opposite direction (red line) and selected targets in an orthogonal direction (green line). Immediately after the cue selects the target for action (‘C’ in figure) both target and non-target activity is high. After ~100 ms the target activity is enhanced and non-target activity is reduced. Eventually (~200 ms) the non-target activity falls below the visual baseline activity. (B) From Duebel and Schneider (2004). Perceptual identification performance at the obstacle location (see Figure 1.3) on trials where cross-workspace reaches were planned. When the stimulus was presented concurrently with (0-ms SOA) or just after (100-ms SOA) the signal to move identification was superior on trials with an obstacle was present (black symbols) than on trials with no obstacle (white symbols). After 200 ms, the identification performance with an obstacle present was comparable to performance without an obstacle, but was still above chance. (C) From Welsh and Elliot (2004). Endpoint difference from target (in reach direction, Y) for reaches made in the presence of a distractor. Distractors presented from 250 ms before (-250-ms SOA) to 500 ms after (500-ms SOA, occurring during the movement) the cue to act led to deviations toward their location (landing further in depth for far targets, dashed line, and nearer in depth for near targets, solid line). Distractors presented 750 ms before (-750-ms SOA) the cue to act received sufficient inhibition to result in deviations away from their location. (D) From Trommershauser et al. (2006). Lateral (X) deviations from midline at different points along the reach distance for rapid reaches made in the presence of a penalty region. Penalty regions presented concurrently with the cue to go (open square symbols) result in deviations away from their location as early as 200 mm into the reach. Penalty regions presented 200 ms after the cue to go (open triangle symbols) still led to significant deviations away from their location by the end of the reach. Penalty regions presented 400 ms after the cue to go (filled square symbols) did not affect the reach.

First I focus on additional data from the Cisek and Kalaska (2005) experiment in which a monkey was required to retain two possible target locations across a memory delay before making a reach toward the one that matched a colour cue. The new data I present in Figure 5.6a show the PMd population activity for targets in a cells preferred direction (blue trace), for targets opposite to the cells preferred direction (red trace), and for space located orthogonal (90°) to a cell's preferred direction. Critically, activity here is aligned such that 0 ms (denoted with a 'C') corresponds to the onset of the colour cue. It is worth noting that the population response to both potential targets (red and blue traces) is higher than the response to a location where no target was present (green trace) confirming parallel encoding. In agreement with the estimate of 100-200 ms required to select a target, the red vertical bar in Figure 5.6a is placed where a significant difference between the target (blue) and non-target (red) emerges, in this case, 110 ms after cue onset. Interestingly, the inhibited red trace does not fall below the relative baseline offered by the green trace (a visual response to no target) for at least another 100 ms. This is the first evidence suggesting that a possible lower limit for noting negative inhibitory behaviour (i.e. deviations away) would be 200ms following cue onset. This 200-ms limit resonates with the perceptual identification during obstacle avoidance data that was discussed in section 1.2.2 of the Introduction (Deubel & Schneider, 2004). Recall that in this task, participants made reaches where an obstacle either interfered (reaches across the workspace) or did not interfere (straight reaches, see Figure 1.3). A stimulus was briefly presented at the obstacle location and required identification. Critically, identification of this stimulus was improved only when the obstacle interfered with the reach. In that study, Duebel and Schneider (2004) also manipulated when the to-be-identified stimuli was presented. The resulting data are shown in Figure 5.6b. When the perceptual stimulus was flashed concurrently with the visual presentation of the scene (0-ms stimulus onset asynchrony (SOA)) or immediately after (100-ms SOA) the reported enhancement at the obstacle position was observed. With an SOA of 200 ms, however, the enhancement effect was gone. Importantly, perceptual identification performance had returned to a level that was comparable to presenting an item at the obstacle location even when the obstacle was not there. So, from Cisek and Kalaska's (2005) data we see that

~200 ms after target specification, non-target information matches then moves below a visual-stimulation-only baseline and from Duebel and Schneider's (2004) data we see that ~200 ms after target specification perceptual enhancement at an obstacle also returns to a relative baseline (though not absolute, which would be 50% performance). The critical test, of course, would be to use the Duebel and Schneider perceptual identification task and extend the time window beyond 200 ms. I would make the prediction that past this range, the identification at the obstacle location should actually go below the relative baseline performance, consistent with active inhibition (for further discussion of this and other potential future experiments, see section 5.5).

These experiments indicate that the effects of active inhibition take at least 200 ms and probably more to develop. Welsh and Elliot (2004) provide some of the only evidence I could find for what happens to information that has been inhibited for longer than this amount of time prior to movement onset. In this study, non-targets (green LEDs) were presented either before, concurrently with, or after targets (red LEDs). Consistent with their previous work (Welsh et al., 1999), Welsh and Elliot found that non-targets presented concurrently with a target resulted in deviations toward them, a result they attribute to residual competition due to incomplete inhibition (Welsh & Elliott, 2004). This is seen in Figure 5.6c where the dashed line represents data from trials with distractors further in depth and the solid line data from trials with distractors closer in depth. In both cases, at the 0-ms SOA time point the reach ends closer to the distractor (dashed line, further in depth, solid line, closer in depth). The critical finding from their new study was that this deviation-toward extended to non-targets presented even 250 ms prior to the target. They argued therefore, that even 250 ms was not enough time for suppression of the non-target response (and 250 ms is a very low estimate, given that they present endpoint data from a movement with a ~250-ms reaction time and ~350-ms movement time). If the non-target preceded the target by 750 ms, however, the observed behaviour was reversed, such that now reaches deviated away from the distractor location. From this evidence, the timeline for active inhibition to be observable in reach behaviour is somewhere from 250 to 750 ms (plus reaction and possibly movement time). Welsh and Elliot (2004) also included trials where the distractor did not come on until approximately the same time as the target (SOA of 250 ms which is roughly equal to reaction time) as well as trials where the distractor did not come on until near the end of the reach (SOA of 550 ms). In both cases, there was some evidence for deviations toward, suggesting that in this study, the abrupt onset of a visual item during the reach functioned to attract the movement.

How well does the above timeline for active inhibition apply to the obstacle avoidance effects I have reported before (Chapman & Goodale, 2008), and in the current thesis (Chapman & Goodale, 2010a, 2010b)? For the experiment described in Chapter 2, reaction times were, on average greater than 350 ms (comparable to the ~300-ms reaction times I reported in 2008). Therefore, the avoidance we observe (which is evident from the very earliest part of the trajectory) could definitely be the result of inhibitory processes engaged from 200 to 300 ms after stimulus onset. Not only does this put a potential cap on the time required for active inhibition to result in deviations-away (~300 ms), it also suggests that under natural reaching conditions (participants were encouraged to reach quickly, accurately and comfortably) reaction times might exactly correspond to how long it takes for visuomotor competition to resolve – including target selection and the active inhibition of non-targets. The finding that active inhibition takes ~300 ms to evolve also allows for some speculation of what might be occurring in Chapter 3 where we observed obstacle avoidance during online corrections. In that experiment, the earliest corrections to a jumped target position occurred ~275 ms into the reach. Recall that these initial corrections were independent of the obstacle location, a point key to our argument that avoidance we observed was restricted to the corrected portion of the reach. A careful examination of Figure 3.4 from this study reveals that the first deviations *due to obstacles* after a correction occur as quickly as within 100 ms. Given the preceding argument that inhibition resulting in avoidance should take at least 300 ms to develop this presents at least two options (which are not mutually exclusive) for what might be happening. First, as I argued in Chapter 3, we believe the potential obstacle was represented at least partially prior to movement onset. Thus, the moment a correction was initiated toward a new target position, this representation was already in place (or needed little further suppression) to cause the observed avoidance. With respect to the proposed model of inhibition, this suggests that all relevant objects within the current and potential workspace are at least partially encoded. This seems to conflict with our previous work (Chapman & Goodale, 2008) where obstacles placed past the reach target no longer influenced movements. In that study, however, the target never changed depth and the reach distance was close to most participants' comfortable reach extent. That is, because the obstacles in the experiment described in Chapter 3 were both within reach, and because targets sometimes jumped to depths further than the initial target position, I believe all obstacles were coded as being potentially relevant, and hence received at least some inhibitory signal prior to movement onset (unlike the objects placed past the reach target in the 2008 study which were not action relevant at any point during the experiment). This argument also gives credence to and extends the notion of an automatically specified desired reach trajectory (discussed in section 5.4.1) by suggesting that this trajectory template is flexible and could specify more than one potential reach (as would be expected if two separate movements were to be coded in parallel, each being affected by an obstacle).

An alternative and perhaps complementary explanation for the rapidity of the deviations around obstacles after the initiation of an online correction comes from the idea that biases established prior to the movement might influence how information from different objects is used. Welsh and Elliot argue a similar point when discussing some observed evidence for eye-movements that deviated away from distractors, "Specifically, because participants were *never* required to complete a saccade to the cued location, an inhibitory code may have been placed on that location, thus biasing a movement in the direction opposite to the cue before response programming processes began" (Welsh & Elliott, 2004, p. 1053). This is a point they extend in their later study using pre-cues (Welsh & Elliot, 2005). Exactly this type of bias was not at play in the results described in Chapter 3, since corrected trajectories when obstacles were not present, or were present on the side opposite the correction did not result in avoidance (see Figure 3.3). That is, if a strong bias had been established at all potential obstacle locations across the entire experiment, it should have resulted in deviations even when the obstacle was not there. An alternative use of this bias, however, may be to expedite the inhibition of an obstacle if it occurs at a location where *only* an obstacle is expected. Under this framework, an inhibitory bias may serve more as a filter, labelling locations where targets will not occur, thus allowing active inhibition to proceed as soon as an object in that location becomes task relevant. This interpretation is supported by evidence from a recent experiment by Julia Trommershauser and colleagues (Trommershauser et al., 2006). Recall that in studies by this group, a goal region is presented with a penalty region and participants' reach endpoints avoid the penalty based on its value and position (discussed in section 1.4.2, Trommershauser, Maloney, & Landy, 2003a, 2003b). In the more recent study, these researchers also manipulated when the penalty region appeared on the screen (Trommershauser et al., 2006). In the data shown in Figure 5.6d, the penalty region (at a location and negative value shown to induce avoidance) was presented either concurrently with the target (open squares), 200 ms after the target (open triangles, approximately coincident with reach onset) or 400 ms after the target (closed circles). What is plotted is the lateral reach deviation at several positions along the reach distance. What can be noted from this single subjects data (which extended to all subjects in the experiment) is that penalty regions presented even at reach onset were able to be incorporated into these rapid reaches (total movement durations of ~300 ms) and that this deviation occurred as early as 50% through the movement (or ~150 ms). By comparison, penalty regions presented 400 ms after the trial start were not successfully avoided – suggesting that the last 100 to 200 ms of a reach is not enough time to use penalty information. This leaves an estimate of ~150 to 200 ms for active inhibition resulting in deviations away, less than that suggested earlier. However, if the penalty information is subject to a bias that improves the speed with which inhibition can evolve, then the estimate is flexible.

Thus, as with the model of inhibition, there are at least two contributing components to the time line of its evolution – inhibition with and without the effects of expectancy and bias. When considering active inhibition in the absence of expectancy and bias (e.g. when the location of the non-target object changes from trial to trial), inhibition sufficient to cause deviations away from non-target objects likely takes ~300 ms from visual stimulus onset to develop. However, in cases where a bias develops prior to movement onset (as in Chapter 3 when participants knew a target jump occurred on 1/3 of trials, or in Trommershauser et al., 2006 where participants knew a penalty region would always appear at one of two locations) active inhibitory processes can proceed in parallel with target selection and affect movement as quickly as 100 ms after an initiated correction (see Chapter 3) or 150 ms after reach onset (Trommershauser et al., 2006). It is worth noting that we directly tested a form of expectancy in the experiment described in Chapter 2 of this thesis where we manipulated (with blocked, random or alternating trial orders) whether participants could predict the availability of visual feedback. The results from that experiment indicated that it was the availability of vision, not its predictability that influenced behaviour – that is, participants behaved similarly any time vision was available, regardless of whether or not it was expected. This suggests that the visuomotor system, while having the ability to flexibly adapt expectancies of environmental features which are likely to change (such as target and obstacle positions), is hardwired to use basic information (such as online visual information) regardless of the context.

5.5. Future directions

In the course of writing a thesis, one typically generates a large number of ideas for further experiments. Here I focus on three potential future directions that directly follow from my thesis and the mechanisms predicted in my model.

5.5.1. Attention scales with interference

One critical postulate of my model (see section 5.4) is that the amount of attention and inhibition an object receives is contingent not only on its visual salience, but also on its action relevance. Support from this idea has come from researchers demonstrating that potential targets gain an attentional enhancement, as indicated by a perceptual identification at upcoming target locations (see section 1.2.2 and Baldauf & Deubel, 2010). Moreover, research from this group has indicated that objects that interfere with a movement also receive an attentional boost (Deubel & Schneider, 2004). Given the findings reported in the current thesis – specifically those from Chapter 2 – where obstacles in different positions exert differential effects (i.e. obstacles close to midline on the right cause the most reach deviation), I would predict that perceptual identification should scale with obstacle interference. That is, it should be possible to correlate the deviation observed during the movement to the identification of stimuli presented at the location of the obstacle prior to the movement. This type of experiment could include both single-obstacle and two-obstacle trials (as described in Chapter 2) – the two obstacle trials being particularly interesting since their asymmetry about midline (i.e. one close to midline on the left and one further from midline on the right) should result in differential identification performance at the two different locations within the same visual display. The nature of the results would allow for a direct test of whether the additional avoidance induced by some obstacles is due to a between-trial bias or an inhibitory bias that is applied in real time every trial. If it were a between-trial bias, then perceptual identification at those locations (relative to other obstacle locations) should be impaired from the moment the visual scene is presented. If the bias develops strictly within a trial, however, the objects that cause increased interference may initially have more attention diverted toward them, followed by a more sudden reduction. It is therefore a distinct possibility that the differences in identification induced by interference would not emerge initially, but would be characterized by the timeline of the inhibitory response. I discuss this type of experiment in the next section.

Assuming identification performance does correlate with interference (be it a positive or negative correlation), this task could then be used to test for the effects of obstacle properties other than location. That is, properties such as the perceived potential for harm (i.e. a sharp or fragile object) could affect reaching, which in turn, could be reflected in the perceptual identification performance. All other factors being equal, an object that is perceived as harmful likely attracts more attention but requires more inhibition, and thus a characteristic perceptual identification response curve could be predicted. Another interesting use of this technique would be to systematically vary the degree to which an object was to be treated as a target or a non-target and measure the identification response at its location. For example, in a reaching task with a red and blue cube always present, one could vary the number of times the red cube was the target, or was to be ignored (and thus avoided). In blocks where the red cube was never the target, identification responses at its location should match what would be observed for an obstacle. However, in blocks where the red cube is sometimes the target, or likely the target, then identification responses at its location should improve. In general, I would argue attentional enhancement should scale with the number of features that overlap between the expected target template and the objects in the environment. Moreover, as was mentioned above, it should be possible to correlate the identification performance with the actual reach deviations – as an object increasingly competed as a potential target, not only would you predict an increase in identification at its location, but also that this identification boost would persist up until movement onset and result in deviations toward its position (as in the predicted trajectory in Figure 5.4a).

5.5.2. Timeline of inhibition

As mentioned in the previous section, it should be possible to use perceptual identification in conjunction with a reaching task to identify *if* and *where* attentional enhancement occurs across the workspace. Equally important is to consider *when* this enhancement occurs. To date, experiments using the dual-task identification technique have examined only perceptual events occurring during the period from visual onset to movement onset (~200 ms at the minimum, Deubel & Schneider, 2004; Schiegg, Deubel, & Schneider, 2003). As explained in section 5.4.2, however, if active inhibition engages only after 200 ms, then it is critical to present the perceptual identification stimuli after this time point. I would make the strong prediction that identification performance at an obstacle location would initially be facilitated (up to ~200 ms, as shown by Deubel & Schneider, 2004) but that after 200 ms, this performance should be reduced below a relative baseline (but remain above the absolute baseline of chance performance). In addition to presenting the identification stimulus prior to movement onset, it would be interesting to measure the identification performance at different locations during the reach itself. While Chapter 3 of the current thesis indicates that obstacle representations can be accessed or updated in flight, it is unknown if (though I speculate that) this is accompanied by an alteration in the distribution of attention. By presenting to-be-identified stimuli during the reach itself, it would be possible to more conclusively determine the dynamics of the attentional landscape during the movement.

Ultimately, the most powerful use of combining reaching with an identification task would be to examine how both the spatial (previous section) and temporal (current section) effects unfold. It should be possible to test if there are initial biases at the hand, target and obstacle locations as well as on a desired reach path (as hypothesized in my model, see section 5.4 and Figure 5.5). It would be interesting to see how the layout and magnitude of these attentional biases shift as the identification of targets and obstacles reshape the desired movement. As mentioned in the previous section, manipulating the degree to which an object is to be treated as a target or as an obstacle should also alter not only its initial representation but also how this representation changes across time – objects sharing characteristics with the target may show attentional enhancement for much longer (extending even into the reach movement) than those that are clearly identified as non-targets.

5.5.3. fMRI of reaching (vs. grasping)

In order to alleviate constraints imposed by the fMRI environmental and potential motion artifacts, the fMRI study of obstacle avoidance described in Chapter 4 employed a grasping task. Of course, the other work described in this thesis (Chapter 2 and Chapter 3) examined obstacle effects on the reach (or transport) component in tasks where grasping was not required. It therefore remains an open question if the same area of the PPC identified for the grasping task in Chapter 4 would be responsible for coding obstacles that interfered with the transport phase of a movement. A strong argument from studies examining differences in reach and grasp networks (e.g. Culham et al., 2006; Culham & Valyear, 2006) suggest that there may be functional subdivisions within the PPC for these two tasks – fitting with the notion of effector specificity mentioned in section 5.2. While an fMRI experiment testing reach transport avoidance would require a redesign of the apparatus described in Chapter 4, other recent experiments have successfully employed outward reaching in the scanner (for example by using targets and obstacles that hang from above, rather than platforms that straddle the hips). Even if a design was restricted to lateral movements (as for the study in Chapter 4), it would be possible to introduce obstacles that needed avoiding vertically. Technical issues aside, to test for obstacle encoding, I would adapt the slow event related paradigm we used in the study described in Chapter 4 to one resembling the partial instruction methodology used by Beruze and colleagues (2007; 2009). In those experiments, researchers presented two pieces of information (target location and effector, in a random order) separated by a short delay. By jittering the delay timing (unlike in our study, where the delays between visual presentation, planning instruction and execute instruction were longer and constant), they were able to increase their experimental power by increasing the number of trials. In an obstacle task using this technique, the two pieces of information that would be presented randomly and separated by a delay would be the target location and the obstacle location. As Beurze et al. (2007; 2009) did with effector and target, this would give a measure of areas that preferentially responded to the target or obstacle in isolation, and critically, would identify areas that integrated these two pieces of information. More importantly, I would predict that on trials where the integration of this information indicated that an obstacle would interfere with the target-directed movement, there would be an even greater signal in these integration areas.

5.6. Conclusions and Implications

As basic scientists, we invariably face the question of what purpose our research serves. The answer, by the nature of our work, has to be ‘not very much’. Precise questions afford precise answers, and therefore, any one experiment, or any single thesis will have little that is directly applicable to everyday life. Of course, the quest of basic science is knowledge and the accumulation of knowledge is something that can have real-world impact. Where might the knowledge of obstacle avoidance mechanisms take us should a sufficient understanding of its implementation allow for its application to other tasks? If a Google search is any indication, then the answer is likely that understanding obstacle avoidance will help us design more intelligent machines. The top 28 hits (followed by a hit to one of our own papers, Striemer, Chapman, & Goodale, 2009) when searching ‘obstacle avoidance’ pertain to the control of robots (or algorithms to control artificial agents). As an example of how important obstacle avoidance is in the domain of robotics, consider space exploration. As we extend our scientific reach beyond Earth's gravitational pull, and onto other planets, 'intelligent' robots are becoming an incredibly important part of exploration science. Consider a robotic probe exploring an unfamiliar planet with a mandate to collect soil samples. Under these conditions if the robot successfully identifies and collects 70% of the intended samples, the mission is likely to be considered a success. However, if the robot fails to correctly identify and avoid a *single* obstacle, resulting in a serious collision, or a restriction of movement, then the mission is an utter failure.

Of course, space exploration is not the only domain where robots or algorithms are designed to deal with obstructing objects. Most advanced automobiles now come equipped with collision detection systems, engaged most often when backing the car up. Advances in surgery are allowing telerobotic operations, and some of the most sophisticated systems automatically engage avoidance strategies. In these cases, however, the system (e.g. a car) can treat every object in the environment as an obstacle, and the strategy is relatively simple – do not allow for contact with any object. By comparison, in the current thesis, like the planetary exploration robot, the participant must be able to encode both targets and obstacles. Moreover, targets should attract movement and obstacles should repel them. Thus, the problem of obstacle avoidance becomes very complicated only when there is a requirement to perform flexibly determined goal-directed behaviours. As I have reiterated throughout this thesis, this is an extraordinarily difficult problem. As a final example, consider your current environment. If your desk (or table, or couch, depending on where you are) has even one-tenth the clutter of mine, there will be multiple objects, and they almost certainly got there by you putting them there. And when you next need to pick up one of those objects, your brain will automatically represent all objects on the surface, select only the one you want to act upon, and plan and execute an action toward it that avoids all other objects. That we perform these actions without effort makes clear what should be apparent – these things seem easy because humans come with a brain designed by evolution to solve precisely this problem. The consequences of failing to perform actions that get to the target while avoiding obstacles are obvious. In fact, I would argue that missing the target is less catastrophic than colliding with an obstacle. You can perform a second movement to the target if required, but you may not be able to recover from a particularly brutal collision.

I feel the preceding discussion makes two key points regarding why the study of obstacles is important. First, in environments with more than two objects, the number of obstacles we deal with far outweighs the number of targets. Second, the consequences of failed avoidance are more dire than the consequences of failed target directed action. I have argued throughout this thesis that to solve the problem of visuomotor selection, and therefore to study goal direction actions, it is imperative to consider how the brain represents all objects within the workspace. Three theoretical frameworks for visuomotor attention served as providing guiding principles to this work (see section 1.2). In each, an emphasis was put on how objects encoded in the brain competed for selection. In the current thesis, I have demonstrated why it is equally important within these competitive frameworks to consider how encoded objects compete for inhibition. In considering how exactly these inhibitory mechanism might be engaged, I introduced my own version of a model of inhibition (see section 5.4) which outlined how, after an initial phase where all potential objects give rise to a positive response, those not matching a target template are automatically inhibited. Moreover, this inhibitory response is truly competitive in that the activity associated with those objects whose properties (in the case of the current thesis, location and size) interfere more with the desired reach require additional inhibition. I have provided evidence that this inhibitory response is automatically engaged, but takes time - approximately 300 ms - to complete. This evolution can account for the apparently disparate results showing deviations toward and away from non-target distractors – as non-targets are inhibited they move from competing targets (thus acting as attractors) to suppressed non-targets (thus repelling movement) to inhibited obstacles (thus resulting in large deviations away from their location). Additionally, I discussed how expectancy and between-trial bias might influence the distribution of attention across the workspace and interact with these processes to produce the behaviour I report. Finally, I argued that the PPC, as a crucial part of a frontoparietal network responsible for goal directed action specification and selection, plays the critical role of biasing the attentional landscape with action relevant weights.

Moving forward, as we basic scientists make our small contributions to the edifice of knowledge, those of us who study visuomotor control must ultimately recognize the role of non-target objects: they are everywhere, and their successful avoidance is vital to adaptive behavior.

5.7. References

Andersen, R. A., & Buneo, C. A. (2002). Intentional maps in posterior parietal cortex. *Annu Rev Neurosci, 25*, 189-220.

Andersen, R. A., & Cui, H. (2009). Intention, action planning, and decision making in parietal-frontal circuits. *Neuron, 63*(5), 568-583.

Andujar, J. E., Lajoie, K., & Drew, T. (2010). A contribution of area 5 of the posterior parietal cortex to the planning of visually guided locomotion: limb-specific and limb-independent effects. *J Neurophysiol, 103*(2), 986-1006.

Baldauf, D., Cui, H., & Andersen, R. A. (2008). The posterior parietal cortex encodes in parallel both goals for double-reach sequences. *J Neurosci, 28*(40), 10081-10089.

Baldauf, D., & Deubel, H. (2010). Attentional landscapes in reaching and grasping. *Vision Res, 50*(11), 999-1013.

Basso, M. A., & Wurtz, R. H. (1997). Modulation of neuronal activity by target uncertainty. *Nature, 389*(6646), 66-69.

Basso, M. A., & Wurtz, R. H. (1998). Modulation of neuronal activity in superior colliculus by changes in target probability. *J Neurosci, 18*(18), 7519-7534.

Beck, D. M., & Kastner, S. (2009). Top-down and bottom-up mechanisms in biasing competition in the human brain. *Vision Res, 49*(10), 1154-1165.

Beurze, S. M., de Lange, F. P., Toni, I., & Medendorp, W. P. (2007). Integration of target and effector information in the human brain during reach planning. *J Neurophysiol, 97*(1), 188-199.

Beurze, S. M., de Lange, F. P., Toni, I., & Medendorp, W. P. (2009). Spatial and effector processing in the human parietofrontal network for reaches and saccades. *J Neurophysiol, 101*(6), 3053-3062.

Bisley, J. W., & Goldberg, M. E. (2003). Neuronal activity in the lateral intraparietal area and spatial attention. *Science, 299*(5603), 81-86.

Brown, L. E., Kroliczak, G., Demonet, J. F., & Goodale, M. A. (2008). A hand in blindsight: hand placement near target improves size perception in the blind visual field. *Neuropsychologia, 46*(3), 786-802.

Chapman, C. S., Gallivan, J. P., Culham, J. C., & Goodale, M. A. (2010). Mental Blocks: fMRI reveals top-down modulation of early visual cortex when obstacles interfere with grasp planning. *Neuropsychologia*.

Chapman, C. S., Gallivan, J. P., Wood, D. K., Milne, J. L., Culham, J. C., & Goodale, M. A. (2010a). Reaching for the unknown: Multiple target encoding and real-time decision-making in a rapid reach task. *Cognition, 116*(2), 168-176.

Chapman, C. S., Gallivan, J. P., Wood, D. K., Milne, J. L., Culham, J. C., & Goodale, M. A. (2010b). Short term motor plasticity revealed in a visuomotor decision-making task. *Behav Brain Res*.

Chapman, C. S., & Goodale, M. A. (2008). Missing in action: the effect of obstacle position and size on avoidance while reaching. *Exp Brain Res, 191*(1), 83-97.

Chapman, C. S., & Goodale, M. A. (2010a). Obstacle avoidance during online corrections. *J Vis, 10*(11), 1-14.

Chapman, C. S., & Goodale, M. A. (2010b). Seeing all the obstacles in your way: the effect of visual feedback and visual feedback schedule on obstacle avoidance while reaching. *Exp Brain Res, 202*(2), 363-375.

Cisek, P. (2007). Cortical mechanisms of action selection: the affordance competition hypothesis. *Philos Trans R Soc Lond B Biol Sci, 362*(1485), 1585-1599.

Cisek, P., & Kalaska, J. F. (2005). Neural correlates of reaching decisions in dorsal premotor cortex: specification of multiple direction choices and final selection of action. *Neuron, 45*(5), 801-814.

Cisek, P., & Kalaska, J. F. (2010). Neural Mechanisms for Interacting with a World Full of Action Choices. *Annu Rev Neurosci*.

Cohen Kadosh, R., & Walsh, V. (2009). Numerical representation in the parietal lobes: abstract or not abstract? *Behav Brain Sci, 32*(3-4), 313-328; discussion 328-373.

Corbetta, M., Patel, G., & Shulman, G. L. (2008). The reorienting system of the human brain: from environment to theory of mind. *Neuron, 58*(3), 306-324.

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci, 3*(3), 201-215.

Culham, J. C., Cavina-Pratesi, C., & Singhal, A. (2006). The role of parietal cortex in visuomotor control: what have we learned from neuroimaging? *Neuropsychologia, 44*(13), 2668-2684.

Culham, J. C., & Kanwisher, N. G. (2001). Neuroimaging of cognitive functions in human parietal cortex. *Curr Opin Neurobiol, 11*(2), 157-163.

Culham, J. C., & Valyear, K. F. (2006). Human parietal cortex in action. *Curr Opin Neurobiol, 16*(2), 205-212.

Desimone, R. (1998). Visual attention mediated by biased competition in extrastriate visual cortex. *Philos Trans R Soc Lond B Biol Sci, 353*(1373), 1245-1255.

Desmurget, M., Epstein, C. M., Turner, R. S., Prablanc, C., Alexander, G. E., & Grafton, S. T. (1999). Role of the posterior parietal cortex in updating reaching movements to a visual target. *Nat Neurosci, 2*(6), 563-567.

Deubel, H., & Schneider, W. X. (2004). Attentional selection in sequential manual movements, movements around an obstacle, and in grasping. In G. W. Humphreys & M. J. Riddoch (Eds.), *Attention in action : advances from cognitive neuroscience* (pp. 69-91). Hove, East Sussex: Psychology Press.

Duncan, J. (2006). EPS Mid-Career Award 2004: brain mechanisms of attention. *Q J Exp Psychol (Colchester), 59*(1), 2-27.

Duncan, J., & Owen, A. M. (2000). Common regions of the human frontal lobe recruited by diverse cognitive demands. *Trends Neurosci, 23*(10), 475-483.

Gallivan, J. P., Cavina-Pratesi, C., & Culham, J. C. (2009). Is that within reach? fMRI reveals that the human superior parieto-occipital cortex encodes objects reachable by the hand. *J Neurosci, 29*(14), 4381-4391.

Gallivan, J. P., Chapman, C. S., Wood, D. K., Milne, J. L., Ansari, D., Culham, J. C., et al. (2010). One to four, and nothing more: Non-conscious parallel object individuation in action. *Psychol Sci*.

Georgopoulos, A. P., Schwartz, A. B., & Kettner, R. E. (1986). Neuronal population coding of movement direction. *Science, 233*(4771), 1416-1419.

Glover, S. (2004). Separate visual representations in the planning and control of action. *Behav Brain Sci, 27*(1), 3-24; discussion 24-78.

Gold, J. I., & Shadlen, M. N. (2007). The neural basis of decision making. *Annu Rev Neurosci, 30*, 535-574.

Houghton, G., & Tipper, S. P. (1994). A Model of Inhibitory Mechanisms of Selective Attention. In D. Dagenbach & T. H. Carr (Eds.), *Inhibitory Processes in Attention, Memory, and Language* (pp. 53-112). San Diego, California: Academic Press Inc.

Houghton, G., & Tipper, S. P. (1999). Attention and the control of action: An investigation of the effects of selection on population coding of hand and eye movement. In D. Heinke, G. W. Humphreys & A. Olson (Eds.), *Connectionist Modles in Cognitive Neuroscience*. London: Springer-Verlag.

Jax, S. A., & Rosenbaum, D. A. (2007). Hand path priming in manual obstacle avoidance: evidence that the dorsal stream does not only control visually guided actions in real time. *J Exp Psychol Hum Percept Perform, 33*(2), 425-441.

Jax, S. A., & Rosenbaum, D. A. (2009). Hand path priming in manual obstacle avoidance: rapid decay of dorsal stream information. *Neuropsychologia, 47*(6), 1573-1577.

Kao, K. L., & Goodale, M. A. (2009). Enhanced detection of visual targets on the hand and familiar tools. *Neuropsychologia, 47*(12), 2454-2463.

McPeek, R. M. (2006). Incomplete suppression of distractor-related activity in the frontal eye field results in curved saccades. *J Neurophysiol, 96*(5), 2699-2711.

Meegan, D. V., & Tipper, S. P. (1998). Reaching into Cluttered Visual Environments: Spatial and Temporal Infuences of Distracting Objects. *Q J Exp Psychol A, 51a*(2), 225-249.

Meegan, D. V., & Tipper, S. P. (1999). Visual Search and Target-Directed Action. *J Exp Psychol Hum Percept Perform, 25*(5), 1347-1362.

Mevorach, C., Hodsoll, J., Allen, H., Shalev, L., & Humphreys, G. (2010). Ignoring the elephant in the room: a neural circuit to downregulate salience. *J Neurosci, 30*(17), 6072-6079.

Milner, A. D., & Goodale, M. A. (1995). *The Visual Brain in Action*. Oxford: Oxford University Press.

Nieder, A., & Dehaene, S. (2009). Representation of number in the brain. *Annu Rev Neurosci, 32*, 185-208.

Perenin, M. T., & Vighetto, A. (1988). Optic ataxia: a specific disruption in visuomotor mechanisms. I. Different aspects of the deficit in reaching for objects. *Brain, 111 (Pt 3)*, 643-674.

Pessoa, L., Kastner, S., & Ungerleider, L. G. (2003). Neuroimaging studies of attention: from modulation of sensory processing to top-down control. *J Neurosci, 23*(10), 3990-3998.

Pisella, L., Grea, H., Tilikete, C., Vighetto, A., Desmurget, M., Rode, G., et al. (2000). An 'automatic pilot' for the hand in human posterior parietal cortex: toward reinterpreting optic ataxia. *Nat Neurosci, 3*(7), 729-736.

Rice, N. J., McIntosh, R. D., Schindler, I., Mon-Williams, M., Demonet, J. F., & Milner, A. D. (2006). Intact automatic avoidance of obstacles in patients with visual form agnosia. *Exp Brain Res, 174*(1), 176-188.

Riddoch, M. J., Chechlacz, M., Mevorach, C., Mavritsaki, E., Allen, H., & Humphreys, G. W. (2010). The neural mechanisms of visual selection: the view from neuropsychology. *Ann N Y Acad Sci, 1191*(1), 156-181.

Schall, J. D. (2001). Neural basis of deciding, choosing and acting. *Nat Rev Neurosci, 2*(1), 33-42.

Schiegg, A., Deubel, H., & Schneider, W. X. (2003). Attentional selection during preparation of prehension movements. *Visual Cognition, 10*(4), 409-431.

Schindler, I., Rice, N. J., McIntosh, R. D., Rossetti, Y., Vighetto, A., & Milner, A. D. (2004). Automatic avoidance of obstacles is a dorsal stream function: evidence from optic ataxia. *Nat Neurosci, 7*(7), 779-784.

Song, J. H., & McPeek, R. M. (2010). Roles of narrow- and broad-spiking dorsal premotor area neurons in reach target selection and movement production. *J Neurophysiol*.

Srimal, R., & Curtis, C. E. (2008). Persistent neural activity during the maintenance of spatial position in working memory. *Neuroimage, 39*(1), 455-468.

Striemer, C. L., Chapman, C. S., & Goodale, M. A. (2009). "Real-time" obstacle avoidance in the absence of primary visual cortex. *Proc Natl Acad Sci U S A, 106*(37), 15996-16001.

Tipper, S. P., Howard, L. A., & Houghton, G. (1998). Action-based mechanisms of attention. *Philos Trans R Soc Lond B Biol Sci, 353*(1373), 1385-1393.

Tipper, S. P., Howard, L. A., & Houghton, G. (2000). Attention and Performance XVIII: Behavioral Consequences of Selection from Neural Population Codes. In S. Monsell & J. Driver (Eds.), *Control of Cognitive Processes*. Cambridge: The MIT Press.

Tipper, S. P., Lortie, C., & Baylis, G. C. (1992). Selective reaching: evidence for action-centered attention. *J Exp Psychol Hum Percept Perform, 18*(4), 891-905.

Tipper, S. P., Meegan, D. V., & Howard, L. A. (2002). Action-centered negative priming: Evidence for reactive inhibition. *Visual Cognition, 9*(4), 591-614.

Torres, E., & Andersen, R. (2006). Space-time separation during obstacle-avoidance learning in monkeys. *J Neurophysiol, 96*(5), 2613-2632.

Trommershauser, J., Maloney, L. T., & Landy, M. S. (2003a). Statistical decision theory and the selection of rapid, goal-directed movements. *J Opt Soc Am A Opt Image Sci Vis, 20*(7), 1419-1433.

Trommershauser, J., Maloney, L. T., & Landy, M. S. (2003b). Statistical decision theory and trade-offs in the control of motor response. *Spat Vis, 16*(3-4), 255-275.

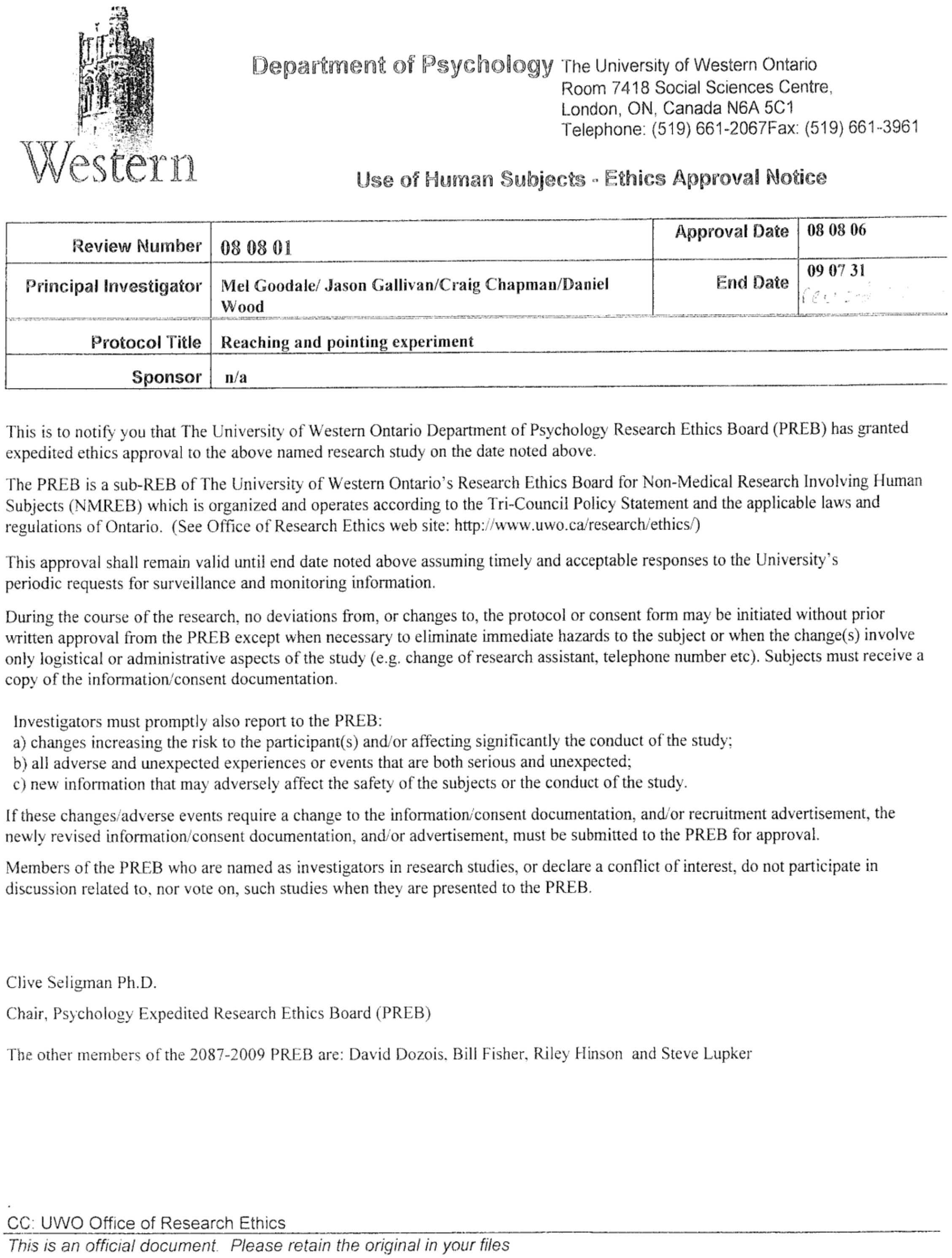
Trommershauser, J., Mattis, J., Maloney, L. T., & Landy, M. S. (2006). Limits to human movement planning with delayed and unpredictable onset of needed information. *Exp Brain Res, 175*(2), 276-284.

Welsh, T. N., & Elliot, D. (2005). The effects of response priming on the planning and execution of goal-directed movements in the presence of a distracting stimulus. *Acta Psychologica, 119*, 123-142.

Welsh, T. N., & Elliott, D. (2004). Movement trajectories in the presence of a distracting stimulus: evidence for a response activation model of selective reaching. *Q J Exp Psychol A, 57*(6), 1031-1057.

Welsh, T. N., Elliott, D., & Weeks, D. J. (1999). Hand deviations toward distractors. Evidence for response competition. *Exp Brain Res, 127*(2), 207-212.

Appendix A



Western

Department of Psychology The University of Western Ontario
Room 7418 Social Sciences Centre,
London, ON, Canada N6A 5C1
Telephone: (519) 661-2067Fax: (519) 661-3961

Use of Human Subjects - Ethics Approval Notice

Review Number	**08 08 01**	**Approval Date**	**08 08 06**
Principal Investigator	**Mel Goodale/ Jason Gallivan/Craig Chapman/Daniel Wood**	**End Date**	**09 07 31** [illegible]
Protocol Title	**Reaching and pointing experiment**		
Sponsor	**n/a**		

This is to notify you that The University of Western Ontario Department of Psychology Research Ethics Board (PREB) has granted expedited ethics approval to the above named research study on the date noted above.

The PREB is a sub-REB of The University of Western Ontario's Research Ethics Board for Non-Medical Research Involving Human Subjects (NMREB) which is organized and operates according to the Tri-Council Policy Statement and the applicable laws and regulations of Ontario. (See Office of Research Ethics web site: http://www.uwo.ca/research/ethics/)

This approval shall remain valid until end date noted above assuming timely and acceptable responses to the University's periodic requests for surveillance and monitoring information.

During the course of the research, no deviations from, or changes to, the protocol or consent form may be initiated without prior written approval from the PREB except when necessary to eliminate immediate hazards to the subject or when the change(s) involve only logistical or administrative aspects of the study (e.g. change of research assistant, telephone number etc). Subjects must receive a copy of the information/consent documentation.

Investigators must promptly also report to the PREB:
a) changes increasing the risk to the participant(s) and/or affecting significantly the conduct of the study;
b) all adverse and unexpected experiences or events that are both serious and unexpected;
c) new information that may adversely affect the safety of the subjects or the conduct of the study.

If these changes/adverse events require a change to the information/consent documentation, and/or recruitment advertisement, the newly revised information/consent documentation, and/or advertisement, must be submitted to the PREB for approval.

Members of the PREB who are named as investigators in research studies, or declare a conflict of interest, do not participate in discussion related to, nor vote on, such studies when they are presented to the PREB.

Clive Seligman Ph.D.

Chair, Psychology Expedited Research Ethics Board (PREB)

The other members of the 2087-2009 PREB are: David Dozois, Bill Fisher, Riley Hinson and Steve Lupker

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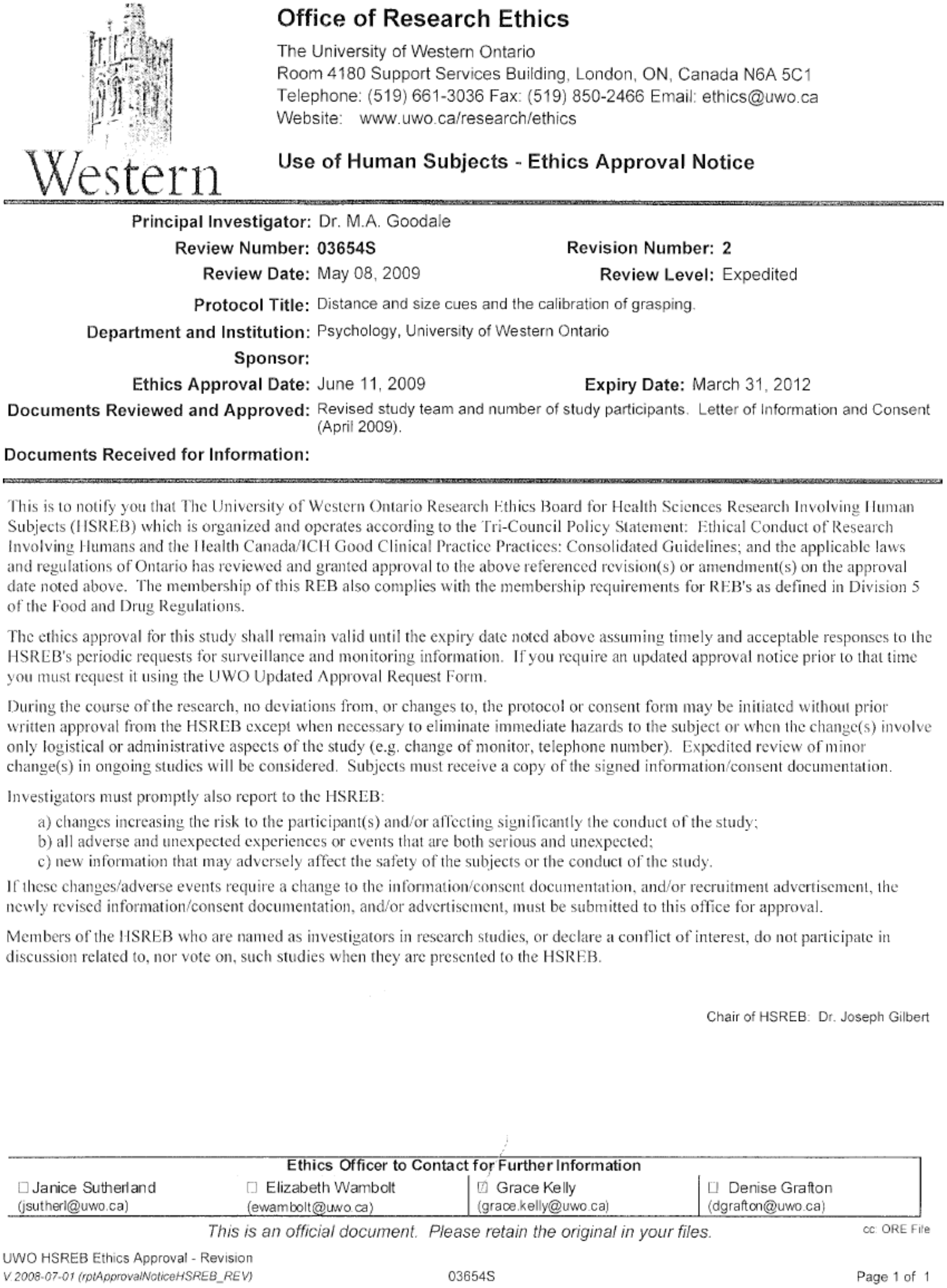

Office of Research Ethics
The University of Western Ontario
Room 4180 Support Services Building, London, ON, Canada N6A 5C1
Telephone: (519) 661-3036 Fax: (519) 850-2466 Email: ethics@uwo.ca
Website: www.uwo.ca/research/ethics

Use of Human Subjects - Ethics Approval Notice

Principal Investigator: Dr. M.A. Goodale
Review Number: **03654S** **Revision Number:** **2**
Review Date: May 08, 2009 **Review Level:** Expedited
Protocol Title: Distance and size cues and the calibration of grasping.
Department and Institution: Psychology, University of Western Ontario
Sponsor:
Ethics Approval Date: June 11, 2009 **Expiry Date:** March 31, 2012
Documents Reviewed and Approved: Revised study team and number of study participants. Letter of Information and Consent (April 2009).
Documents Received for Information:

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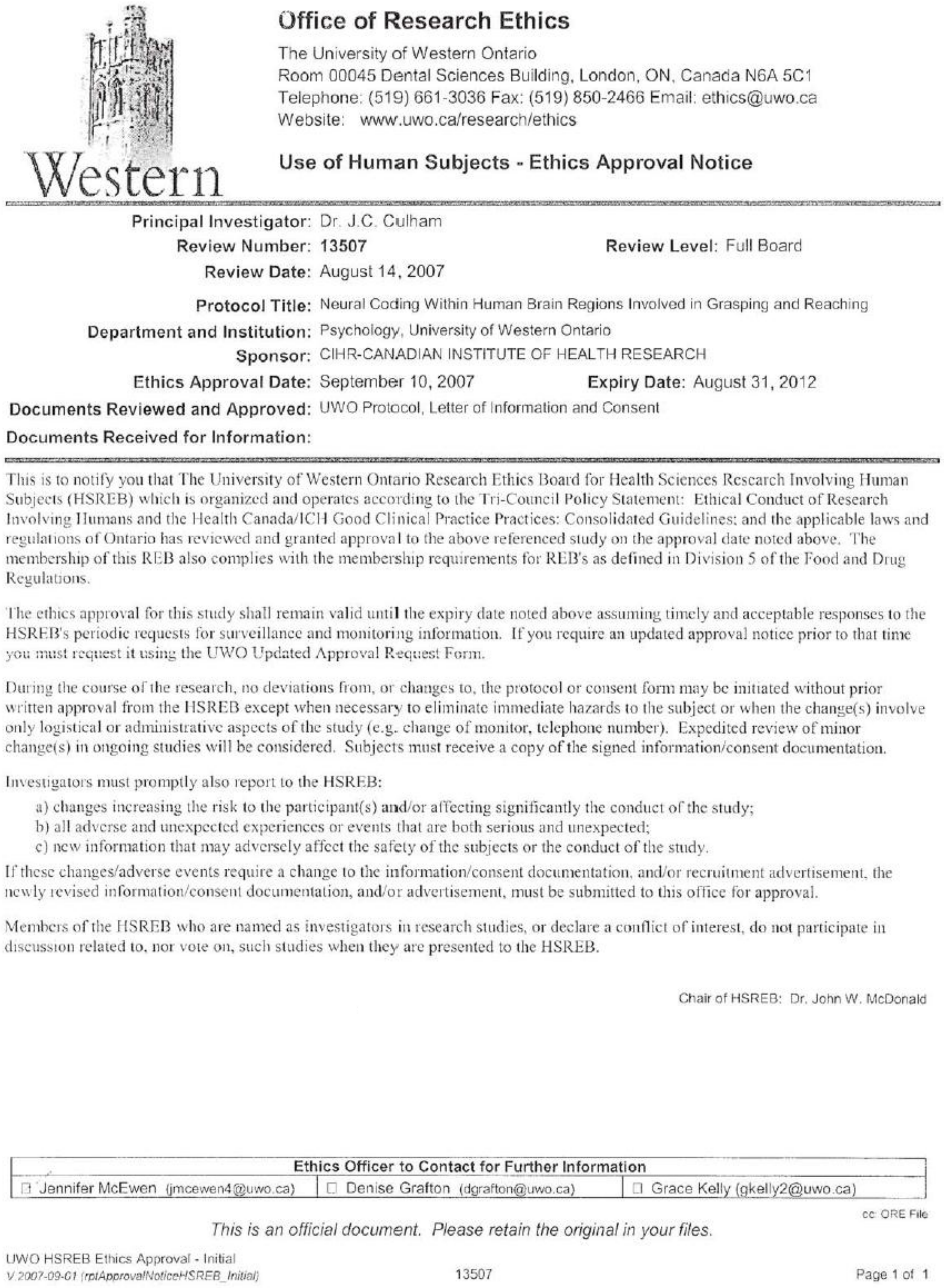

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Use of Human Subjects - Ethics Approval Notice

Principal Investigator: Dr. J.C. Culham
Review Number: 13507 **Review Level:** Full Board
Review Date: August 14, 2007
Protocol Title: Neural Coding Within Human Brain Regions Involved in Grasping and Reaching
Department and Institution: Psychology, University of Western Ontario
Sponsor: CIHR-CANADIAN INSTITUTE OF HEALTH RESEARCH
Ethics Approval Date: September 10, 2007 **Expiry Date:** August 31, 2012
Documents Reviewed and Approved: UWO Protocol, Letter of Information and Consent
Documents Received for Information:

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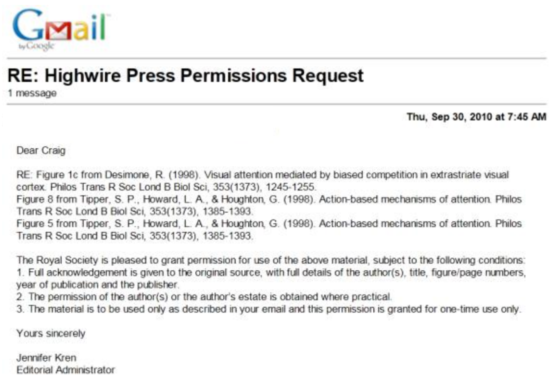
Appendix B



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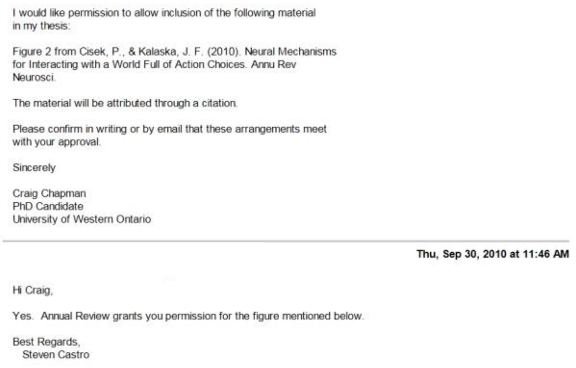

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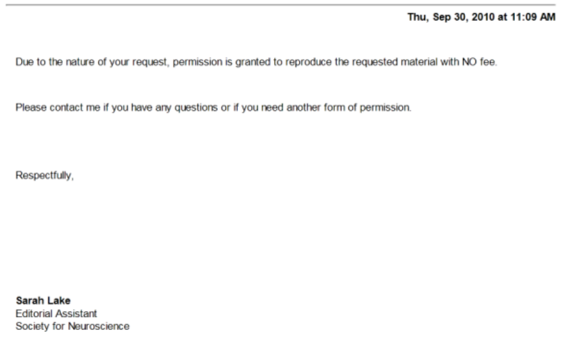

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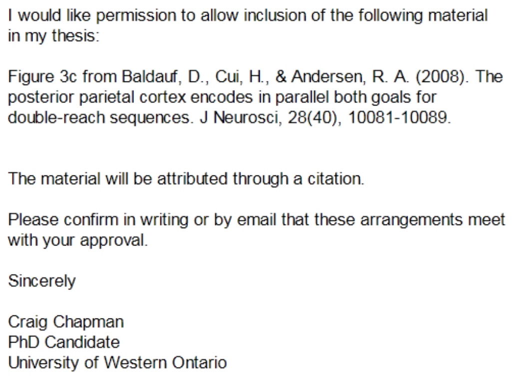

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PhD Candidate
University of Western Ontario

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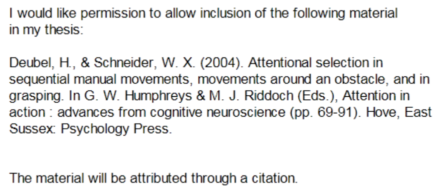

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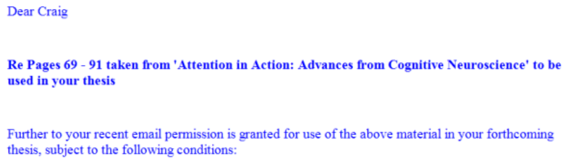

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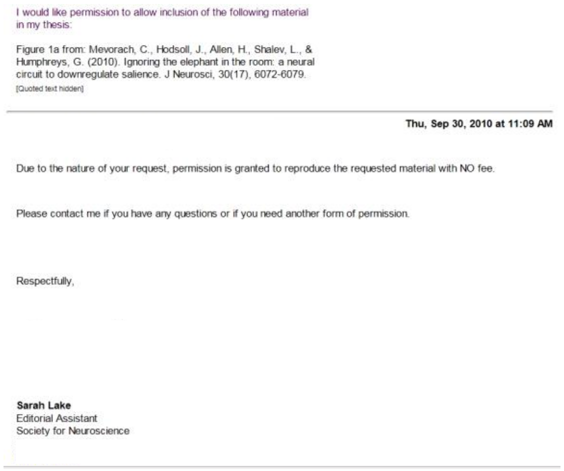

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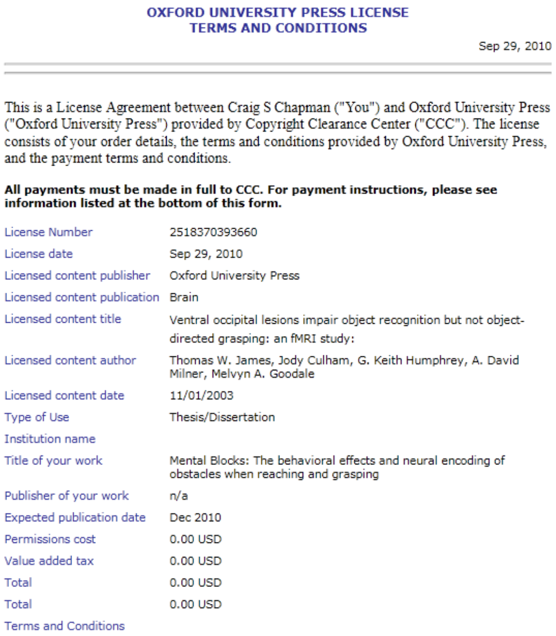

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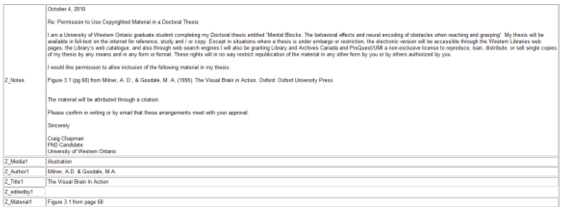

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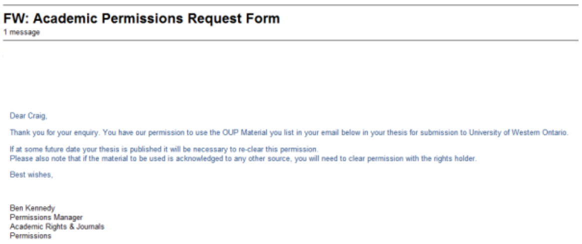

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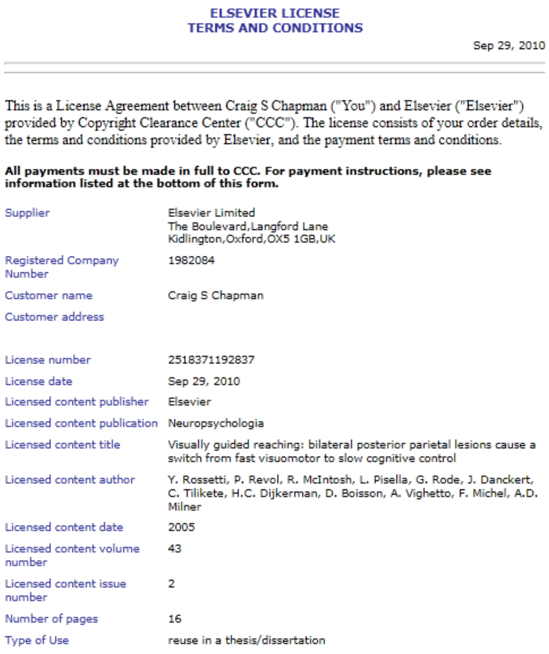

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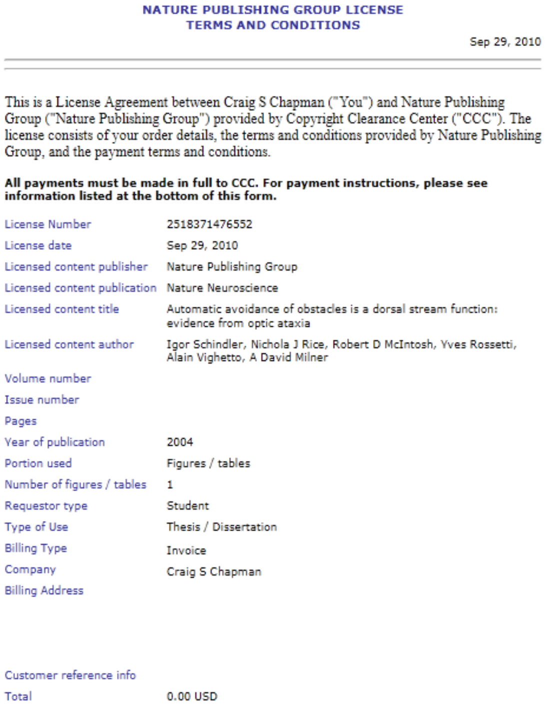

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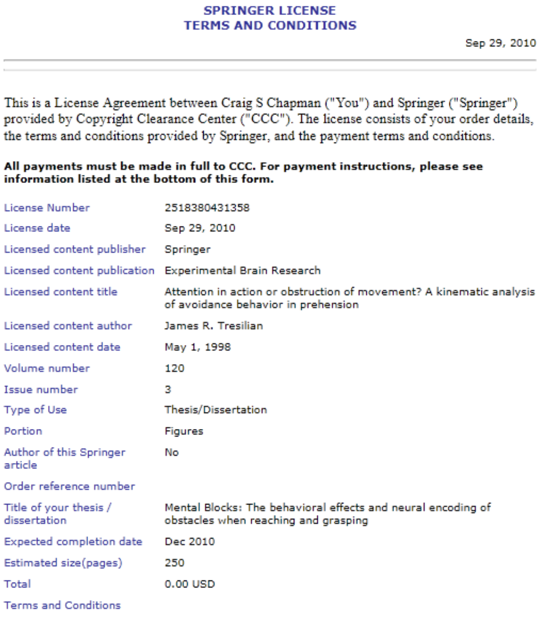

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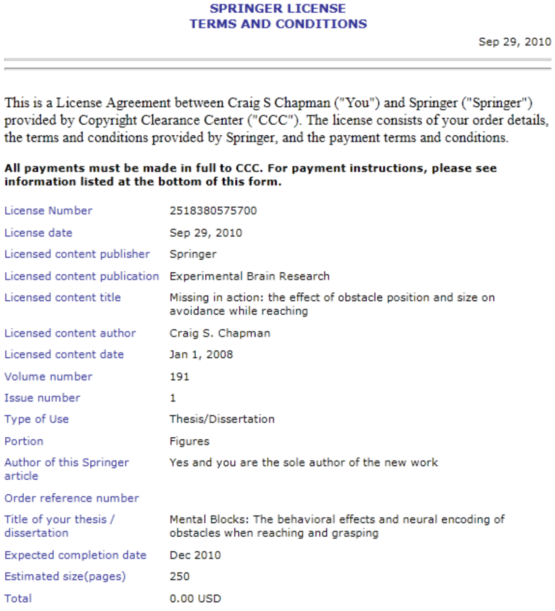

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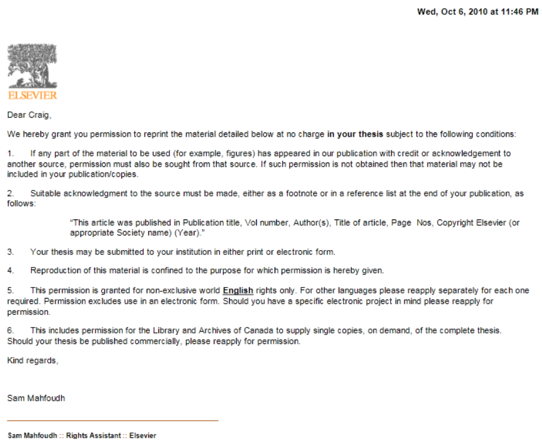

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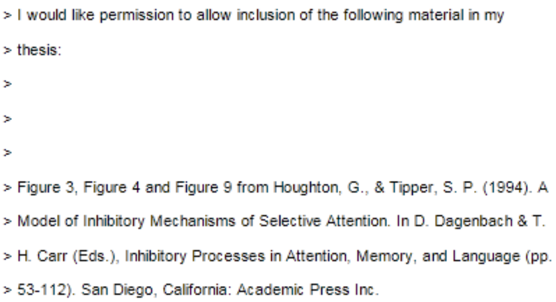

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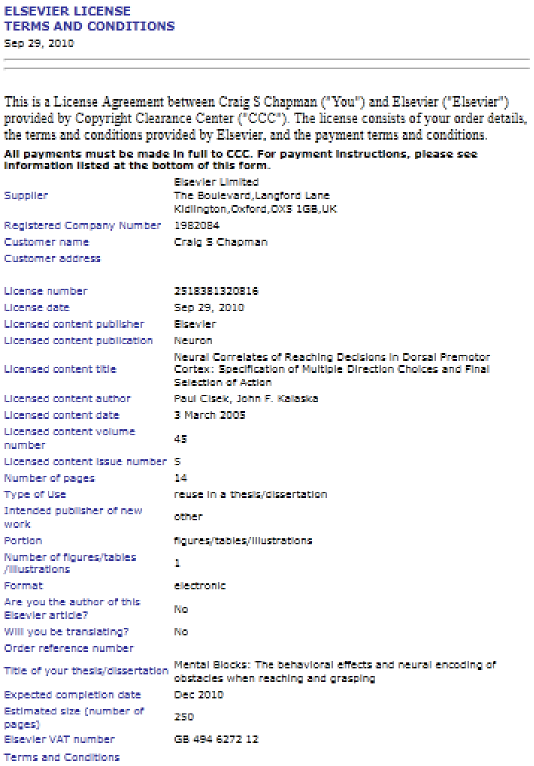

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Overall Average: 92.3%

University of British Columbia
Bachelor of Science in Cognitive Systems: Brain and Behaviour Option, minor in English Literature
Conferred May 2004
Overall Average: 85.3%

Relevant Coursework

Graduate:

Course in Graduate Statistics
Seminar in Behavioural and Cognitive Neuroscience
Seminar in Decision Theory
Seminar in Biological Timing Mechanisms
Seminar in Philosophy of Mind
Seminar in Neuroimaging of Cognition
Seminar in Cognitive Neuroscience of Event Related Potentials
Seminars in Computational Neuroscience
Course in Multivariate Statistics

Undergraduate:

5.5 full courses in Psychology (faculty of Science)
3.5 full courses in Computer Science
2 full courses in Philosophy (Knowledge and Cognition)

Employment

Research

Brain and Attention Research Lab, UBC — Sept. 2004 – May 2005
Research Assistant
Supervisor: Dr. Alan Kingstone

- Designed, implemented and conducted independent research projects on Categorization and Theory of Mind
- Collaborated with fellow researchers, and contributed to the lab group dynamic
- Presented and reported research findings

Brain and Attention Research Lab, UBC — May 2003 – Aug. 2004
Student Research Assistant
Supervisors: Dr. Alan Kingstone, Amelia Hunt

- Designed, implemented and conducted research projects on saccadic illusions in collaboration with other students
- Participated in all lab activities
- Presented research findings

Ophthalmology Research Lab, UBC / BC Children's Hospital — Jan. 2002 – May 2003
Student Research Assistant
Supervisor: Dr. Deborah Giaschi

- Implemented and conducted research projects on low level motion and developmental dyslexia
- Programmed visual stimuli experiments, including fMRI stimuli design
- Presented and reported research findings

Teaching / Mentoring

Honours Thesis Student Supervision, Faculty of Science, UWO — Sept.2009 – Apr.2010
Student: Maria Khami
Supervisor: Dr. Mel Goodale

- Led student through the experimental process: designed experiment, assisted with data collection, statistical analysis and reporting of results

Honours Thesis Student Supervision, Faculty of Science, UWO — Sept.2008 – Apr.2009
Student: Jennifer Milne
Supervisor: Dr. Mel Goodale

- Collaborated on developing research project, collecting and analyzing data, and reporting results.
- Continued to collaborate as student moved onto MSc

Honours Thesis Student Supervision, Faculty of Science, UWO Sept.2008 – Apr.2009
Student: Ravi Doobay
Supervisor: Dr. Mel Goodale

- ❑ Led student through the experimental process: designed experiment and background reading list.
- ❑ Met weekly to assist with data collection, statistical analysis and reporting of results

Honours Thesis Student Supervision, Faculty of Social Science, UWO Sept.2007 – Apr.2008
Student: Dustin Kirshen
Supervisor: Dr. Mel Goodale

- ❑ Led student through the experimental process: designed experiment, assisted with data collection, statistical analysis and reporting of results

Department of Psychology, Faculty of Social Science, UWO Sept. 2006 – Apr. 2006
Teaching Assistant, Psychology 281 (Statistics)
Supervisor: Dr. Patrick Brown

- ❑ Led weekly tutorial covering assignments from lecture
- ❑ Graded midterms and finals

Department of Psychology, Faculty of Social Science, UWO Jan. 2006 – Apr. 2006
Teaching Assistant, Psychology 215 (Sensation and Perception)
Supervisor: Dr. Brian Timney

- ❑ Met with students on a regular basis
- ❑ Graded midterms and finals

Department of Psychology, Faculty of Social Science, UWO Sept. 2005 – Dec 2005
Teaching Assistant, Psychology 115a (Introduction to Sensation and Perception)
Supervisor: Dr. Terrence Biggs

- ❑ Delivered lecture on introduction to Perception
- ❑ Corresponded with students
- ❑ Assisted with grading

Department of Cognitive Systems, Faculty of Science, UBC Sept. 2004 – May 2005
Teaching Assistant, Cognitive Systems 300 (Integration of Topics in Cognitive Systems)
Supervisor: Dr. Ron Rensink

- ❑ Designed lab component of the course using LEGO robotics to explore progressively intelligent systems
- ❑ Instructed and evaluated students, primarily in the lab component of course

- Assisted in the creation of course material and topics

Department of Integrated Science, Faculty of Science, UBC — Sept. 2003 – Dec. 2003
Teaching Assistant, Integrated Science 333 (Artificial and Biological Control Systems)
Supervisor: Gillian Gerhard

- Collaborated with a fellow student to design lab component of course using LEGO robotics to explore the definition of systems
- Instructed and evaluated students, primarily in the lab component of course
- Administered exams and was available for meetings outside of scheduled time

Department of Housing and Conferences, UBC — Sept. 2001 – May 2002
Residence Advisor
Supervisor: Chad Hyson

- Provided floor leadership to younger students in junior residence
- Enforced standards to maintain a positive learning and social environment
- Programmed activities to promote floor camaraderie

Awards and Scholarships

Governor General’s Gold Medal Award Nominee, Psychology – 2008
Keith Humphrey Memorial Award - 2008
NSERC Canadian Graduate Scholarship – Doctoral, 2007-2010
Ontario Graduate Scholarship, 2006/07
Western Graduate Research Scholarship, 2007
NSERC Canadian Graduate Scholarship – Master’s, 2005/06
Master's Scholarship - University of Alberta, Declined
Lacey Scholarship - University of British Columbia, Declined
Killam Predoctoral Scholarship Dalhousie University, Declined
NSERC Undergraduate Student Research Award, 2004
Multidisciplinary Undergraduate Research Conference Award for Outstanding Presentation, 2004
NSERC Undergraduate Student Research Award, 2003
NSERC Undergraduate Student Research Award, 2002
Undergraduate Scholarship Program Scholarship, 2003 – 2004
Chancellor’s Major Entrance Scholarship, 1999 – 2003
Top Academic Student, Abbotsford Senior Secondary, 1999
Top All-Around Student, Abbotsford Senior Secondary, 1999

Publications

Chapman, C.S., & Goodale, M.A. (2010). Obstacle avoidance during online corrections. Journal of Vision. 10(11), 1-14.

Chapman, C.S., Gallivan, J.P., Wood, D.W., Milne, J.L., Culham, J.C., & Goodale, M.A. (2010). Short-term motor plasticity revealed in a visuomotor decision-making task. Behavioral Brain Research. 214(1), 130-134.

Chapman, C.S., Gallivan, J.P., Wood, D.W., Milne, J.L., Culham, J.C., & Goodale, M.A. (2010). Reaching for the unknown: Multiple target encoding and real-time decision-making in a rapid reach task. Cognition. 116(2), 168-176.

Chapman, C.S. & Goodale, M.A. (2010). Seeing all the obstacles in your way: The effect of visual feedback on obstacle avoidance. Experimental Brain Research, 202(2), 363-375.

Striemer, C.L., Chapman, C.S. & Goodale, M.A. (2009). ‘‘Real-time’’ obstacle avoidance in the absence of primary visual cortex. Proceedings of the National Academy of Science. 106, 15996-16001.

Chapman, C.S. & Goodale, M.A. (2008). Missing in Action: The effect of obstacle position and size on avoidance while reaching. Experimental Brain Research. 191(1):83-97

Hunt, A.R., Chapman, C.S. & Kingstone, A. (2008). Chronostasis: Taking a long look at action and time perception. Journal of Experimental Psychology: Human Perception and Performance. 34(1):125-36

Chapman, C. S., Hunt, A.R. & Kingstone, A. (2007). Squeezing Uncertainty from Saccadic Compression. Journal of Eye Movement Research, 1(1):2, 1-5, http://jemr.org/.

Chapman, C., Hoag, R. & Giaschi, D. (2004). The Effect of Disrupting the Human Magnocellular Pathway on Global Motion Perception. Vision Research. 44: 2551–2557.

Research Submitted

Chapman, C.S., Gallivan, J.P., Culham, J.C., & Goodale, M.A. Mental Blocks: fMRI reveals top-down modulation of early visual cortex when obstacles interfere with grasp planning. *Submitted*. Neuropsychologia, August 2010.

Gallivan, J.P., Chapman, C.S., Wood, D.W., Milne, J.L., Ansari, D.A., Culham, J.C., & Goodale, M.A. One to four, and nothing more: Non-conscious parallel object individuation in action. *Submitted*. Psychological Science, July 2010.

Valyear, K.F., Chapman, C.S., Gallivan, J.P., Mark, R.S., & Culham, J.C. To use or to move: Goal-set modulates priming when grasping real tools. *Submitted.* Experimental Brain Research, July 2010.

Presentations and Posters

Chapman, C.S., Gallivan, J.P., Wood, D.W., Milne, J.L., Culham, J.C., Ansari, D.A., & Goodale, M.A. (2010). Rapid reaching task 'points' toward different representations of number. Poster given at the 40th Annual Meeting of the Society for Neuroscience, November 2010.

Wood, D.W., Chapman, C.S., Gallivan, J.P., Milne, J.L., Culham, J.C., & Goodale, M.A. (2010). Visual salience of potential targets overrides spatial probabilities in a rapid reach task. Poster given at the 40th Annual Meeting of the Society for Neuroscience, November 2010.

Valyear, K. F., Gallivan, J. P., McLean, A., Chapman, C. S., & Culham, J.C. (2010). Neural priming of tool use. Poster given at the 40th Annual Meeting of the Society for Neuroscience, November 2010.

Rossit, S., Chapman, C.S., Milne, J., Fraser, J.A., Teasell, R., Donais, J., Howson, S., Moran, R., McIntosh, R. D., & Goodale, M. A. (2010). Memory-guided obstacle avoidance in patients with left visual neglect. Poster given at the 2010 European Society of Neuropsychology conference, September 2010.

Chapman, C.S., Gallivan, J.G., Culham, J.C. & Goodale, M.A. (2009). Mental blocks: Using fMRI to reveal the encoding of obstacles during reach-to-grasp movements. Talk given at the 39th Annual Meeting of the Society for Neuroscience, October 2009.

Valyear, K.V., Chapman, C.S., Gallivan, J.G. & Culham, J.C. (2009).Tool identity can prime grasping, but only when the goal is to use. Talk given at the 39th Annual Meeting of the Society for Neuroscience, October 2009 .

Chapman, C.S., Doobay, R. & Goodale, M.A. (2009). Looking Forward to a Correction: Obstacle avoidance during online correction. Talk given at the 9th Annual Meeting of the Vision Sciences Society, May 2009.

Striemer, C.L., Chapman, C.S. & Goodale, M.A. (2009). Implicit processing of obstacles for immediate but not delayed reaching in a case of hemianopic blindsight. Talk given by first author at the 9th Annual Meeting of the Vision Sciences Society, May 2009.

Gallivan, J.P., Chapman, C.S., Wood, D.K., Milne, J.L., Culham, J.C. & Goodale, M.A. (2009). Stuck in the middle: Kinematic evidence for optimal reaching in the presence of multiple potential reach targets. Poster presented by the first author at the 9th Annual Meeting of the Vision Sciences Society, May 2009.

Chapman, C.S., Kirshen, D. & Goodale, M.A. (2009). Seeing all the obstacles in your way: The effect of visual feedback on obstacle avoidance. Poster presented at the 8th Annual Meeting of the Vision Sciences Society, May 2008.

Chapman, C.S., Kirshen, D. & Goodale, M.A. (2008). Seeing all the obstacles in your way: The effect of visual feedback on obstacle avoidance. Poster presented at the 8th Annual Meeting of the Vision Sciences Society, May 2008.

Goodale, M.A., Wolf, M.E., Whitwell, R.L., Brown, L.E., Cant, J.S., Chapman, C.S., Witt, J.K., Arnott, S.R., Khan, S.A., Chouinard, P.A., Culham, J.C. & Dutton, G.N. (2008). Preserved motion processing and visuomotor control in a patient with larger bilateral lesions of occipitotemporal cortex. Talk given by the first author at the 8th Annual Meeting of the Vision Sciences Society, May 2008.

Wolf, M.E., Whitwell, R.L., Brown, L.E., Cant, J.S., Chapman, C.S., Witt, J.K., Arnott, S.R., Khan, S.A., Chouinard, P.A., Culham, J.C., Dutton, G.N., & Goodale, M.A. (2008). Preserved visual abilities following large bilateral lesions of the occipitotemporal cortex. Poster presented by the first author at the 8th Annual Meeting of the Vision Sciences Society, May 2008.

Chapman, C.S., Goodale, M.A. (2008). The effect of visual feedback on obstacle avoidance during reach-to-point movements. Poster presented at the 2nd annual meeting of the Canadian Association for Neuroscience, May 2008.

Gallivan, J.P., Chapman, C.S. & Culham, J.C. (2008). Do objects within reach prime the visuomotor system for action?. Poster presented by the first author at the 2nd annual meeting of the Canadian Association for Neuroscience, May 2008.

Chapman, C.S. & Goodale, M.A. (2007). Missing in Action: Obstacle Avoidance While Reaching. Talk given at the 7th Annual Meeting of the Vision Sciences Society, May 2007.

Chapman, C.S. & Goodale, M.A (2007). Obstacle Avoidance While Reaching: Effects of Obstacles and Non-Obstacle Objects on Reach Trajectory. Poster presented at the 1st annual meeting of the Canadian Association for Neuroscience, May 2007.

Hunt, A.R., Chapman, C.S. & Kingstone, A. (2006). Distortions of Space (and Time?) During Saccadic Eye Movements. Talk given by the first author at the 16th meeting of BBCS, June 2006.

Chapman, C.S., Hunt, A.R., Hungr, C. & Kingstone, A. (2005). Squeezing response uncertainty out of the compression effect. Presented poster at the 12th Annual Meeting of CNS, April 2005.

Fairbairn, N., Chapman, C.S., Bischof, W., Smilek, D & Kingstone, A. (2005). Redefining Perspective: An Application of Cognitive Ethology. Presented poster at the 12th Annual Meeting of CNS, April 2005.

Hunt, A.R., Chapman, C.S., Hungr, C., & Kingstone, A. (2004). Taking a long look at voluntary action and time perception. Poster presented by first author at 11th Annual Meeting of the Cognitive Neuroscience Society, April 2004

Chapman, C.S., Hunt, A.R. & Kingstone, A. (2004). Does Time Fly When You Move Your Eyes?: Examining Temporal Judgments Triggered by Voluntary Action. Talk given at the 2nd Annual Multidisciplinary Undergraduate Research Conference, March 2004

Hoag, R., Chapman, C.S., & Giaschi. (2003). Motion Coherence Thresholds Can Be Elevated by Flicker Adaptation or Red Background. Presented poster at the 5th Annual Meeting of the Vision Science Society, May 2003

Current Research Interests

Obstacle avoidance: what defines an obstacle to this system, what brain mechanisms underlie this identification, and how does its neural encoding result in deviations away from its location

Multiple target encoding: Goal directed reaching in cases where non-target objects act as possible reach targets, or afford actions

Timeline of non-target inhibition: Evolution of target selection and non-target inhibition responses in visuomotor tasks

University Activities

UWO Intramurals Participant (Soccer, Ball Hockey, Squash) September 2005 – Present

UWO Brain Bee volunteer – March 2009

Psychology Graduate Students Association elected member, September 2006 – May 2007

UBC / UWO Debate Club Member, September 1999 – May 2007

UBC Intramurals Participant (Ball Hockey, Ice Hockey, Soccer, Football) September 1999 – May 2004

UBC Tae Kwon Do Club Member, September 1999 – May 2003

UBC Residence Floor Representative, Totem Park Residence Association, September 2000 – May 2001