ELECTROENCEPHALOGRAPHIC CORRELATES OF SPATIAL ATTENTION INDEX THE DEGREE OF ONLINE CONTROL IN GOAL-DIRECTED REACHING

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Master of Science

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Abstract

Goal-directed reaches performed with limb vision (i.e., closed-loop: CL) are more accurate than their limb occluded (i.e., open-loop: OL) counterparts. This finding is frequently attributed to the use of online limb vision to effect trajectory amendments. Notably, however, the central planning of CL and OL reaches may also influence trajectory control. To that end, I examined the behavioural and event-related brain potentials (ERP) of reaches in a target perturbation paradigm wherein information regarding the nature of response (CL or OL) was provided prior to response cuing. CL reaches exhibited earlier and more effective trajectory amendments than OL reaches. Moreover, CL and OL reaches differed with regard to ERP components related to the allocation of visuospatial attention (i.e., the N1) and visuomotor integration (i.e., the P2). These results suggest that advanced knowledge related to the availability of online limb vision increases the visuospatial processing of the reaching limb and optimizes trajectory amendments.

Keywords: Action; Electroencephalography; Event-related Potential; Reaching; Pointing; Spatial Attention

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Chapter 1

Introduction

The integration of sensory information into an ongoing movement maximizes the efficiency and effectiveness of motor output. For example, ample studies from the goal-directed reaching literature have shown that actions performed with continuous limb vision (so-called closed-loop [CL] reaches) are more accurate and less variable than their counterparts performed without continuous visual feedback (e.g.,Woodworth, 1899; for review see Elliott et al., 2010; Elliott, Helsen, & Chua, 2001). The basis for this improved performance is thought to underlie the use of dedicated visuomotor networks in the posterior parietal cortex (PPC) of the dorsal visual pathway to effect error-nullifying corrections to the unfolding trajectory (for recent review see Goodale, 2011). In support of this position, CL reaches exhibit more discrete and continuous trajectory modifications than their counterparts performed without continuous visual feedback (Carlton, 1979; Elliott, Carson, Goodman, & Chua, 1991; Heath, 2005; Heath, Westwood, & Binsted, 2004) and such corrections are diminished, or even eliminated, following chronic or transient (i.e., transcranial magnetic stimulation) PPC lesions (Desmurget et al., 1999; Pisella et al., 2000).

Although CL reaches and their no-vision counterparts demonstrate distinct differences in trajectory control, there remains some debate as to whether the availability of visual feedback during a response influences how such actions are planned. In particular, debate centres around the issue of whether unitary or distinct processes characterize the planning of CL reaches and those performed when vision of the limb is occluded at the time of movement onset (so-called open-loop [OL] reaches). On the one hand, Goodale and Milner's (1992; for recent review see Goodale, 2011) perception/action model (PAM) asserts that the integration of visual information for the planning of CL and OL actions takes place at – and not before - the time of response cuing (the real-time control hypothesis: see Westwood & Goodale, 2003). Indeed, the PAM contends that the dedicated real-time visuomotor networks of the dorsal visual pathway are engaged for movement planning *only* after a response has been cued and

only if the target is visible. This real-time control is thought to provide a level of movement flexibility allowing the performer to quickly adapt to an unexpected change in target location that may occur prior to movement onset. In support of the real-time component of the PAM, Westwood and Goodale (2003) employed a size-contrast illusion to assess the impact of illusion-evoking (i.e., relative visual information) visual features on grasping control. In their paradigm, limb and target vision were visible between response cuing and movement onset (vision trials) or concurrently occluded at response cuing (occlusion trials). Notably, vision trials were refractory to the illusion whereas occlusion trials were reliably "tricked" by the illusions relative visual properties (for extensive review of this issue see Bruno, Bernardis, & Gentilucci, 2008; Goodale, 2008; Goodale & Westwood, 2004). Westwood and Goodale interpreted these results to reflect that visual input from the grasping environment at the time of response planning allows for the mediation of the response via the metrical visuomotor centres of the dorsal visual pathway (i.e., real-time control). In turn, results for the occlusion trials indicate that the absence of visual information at the time of response cuing renders motor output that is mediated by relative visual information via the visuoperceptual networks of the ventral visual pathway (e.g., Goodale & Milner, 1992; for review see Goodale, 2011).

Further evidence supporting the real-time component of the PAM is derived from Hu, Eagleson, and Goodale (1999). In their study, participants were instructed to grasp target objects in CL and OL conditions, as well as in a condition including a visual delay between target viewing and movement onset. Notably, CL and OL trials exhibited comparable grasp kinematics such that the magnitude and timing of peak grip aperture - as well as overall movement duration – did not differ between visual conditions. In contrast, delay trials produced longer overall movement durations and were associated with larger and later occurring peak grip apertures. These results support the real-time hypothesis' contention that the visuomotor networks of the dorsal visual pathway are engaged for movement planning only at the time of response cuing, and only when vision of the movement environment is available to the performer.

On the other hand, Rizzolatti, Riggio, and Sheliga's (1994) pre-motor theory of attention (PMTA) contends that attention and action are linked and are implemented by common control structures (see also Cisek, 2007; Cisek & Kalaska, 2010). Thus, the

PMTA asserts that the attentional properties of a to-be-performed motor task (e.g., the presence or absence of online visual feedback) may influence early movement planning. In support of this view, a number of studies from the oculomotor control literature have shown that attentional shifts toward a target are triggered during saccade planning (Hoffman & Subramaniam, 1995; Irwin & Gordon, 1998). Notably, this pre-motor shift of attention results in increased saccade efficiency and effectiveness. In addition, more recent work involving manual responses have shown a similar link between attention and response planning. In particular, directing visuospatial attention towards a cued target location has been linked to movement planning and control processes (Boulinguez & Nougier, 1999; Welsh, 2011; Welsh & Pratt, 2008). For example, Tipper, Lortie, and Baylis (1992) had participants reach to target objects cued in concert with the presentation of semantically similar non-target distractors in conditions wherein distractors were located between the movement start location and target, or placed in a location adjacent to the target. Results showed increased interference effects (i.e., longer response times) when the distractor fell within the path of the reaching response (i.e., when the distractor was adjacent to the target). Tipper et al. interpreted these results as evidence that attention accesses action-centered representations. In particular, the movement plan for a target-directed response creates an attentional field that extends outwards from the hand to the cued target location (Rizzolatti et al., 1994; Tipper et al., 1992). In turn, the distractor specifies a competing response that must be actively inhibited, resulting in action-centred interference between target and distractor. Moreover, increased competition (i.e., interference) is thought to arise when the distractor is within the attentional field of the target-directed response (i.e., between the hand and cued target) because of a greater overlap between the target and the actively inhibited distractor-directed motor program (Rizzolatti et al., 1994; Tipper et al., 1992). In line with Tipper et al., recent non-human primate electrophysiology studies have shown the simultaneous activation of multiple target-directed cell populations when monkeys were presented with several potential reaching targets (Cisek & Kalaska, 2005; see Cisek & Kalaska, 2010 for review). Subsequently, when a single target-directed response was cued from among the potential targets, directional signals associated with the cued target were amplified whereas signals for the uncued targets were suppressed.

Recent work by Neely and colleagues has also provided indirect evidence of a behavioural link between attentional demands and task-based movement requirements. Specifically, Neely, Tessmer, Binsted, and Heath (2008) had participants complete CL and OL reaches when visual conditions were performed in separate blocks (blocked schedule) and when randomly interleaved on a trial-by-trial basis (random schedule). CL reaches in the blocked schedule produced shorter reaction times and increased trajectory amendments relative to their matched schedule OL counterparts. In contrast, CL and OL reaches in the random schedule were comparable and demonstrated reaction time values and online trajectory amendments commensurate with OL trials in the blocked schedule (see also Elliott & Allard, 1985; Zelaznik, Hawkins, & Kisselburgh, 1983). In other words, advanced knowledge related to the availability of visual feedback (i.e., CL blocked schedule trials) resulted in decreased movement planning times and increased online trajectory corrections. In turn, advanced knowledge that visual feedback would be unavailable (i.e., OL blocked schedule trials), or unpredictable prior to movement onset (i.e., CL and OL random schedule trials), resulted in increased planning times and decreased online trajectory corrections. Neely et al. proposed that the absence of online visual feedback or the inability to predict its presence during a response increased the attentional demands of encoding limb and target properties (i.e., location) prior to movement onset, thereby rendering longer planning times and decreased online corrections. In other words, knowledge of the availability of visual feedback influenced the extent to which actions were specified in advance of movement onset.

Human neuroimaging and non-human primate electrophysiology studies further support a reliable link between attention and response planning (Astafiev et al., 2003; Filimon, 2010; Filimon, Nelson, Huang, & Sereno, 2009; Rizzolatti, Luppino, & Matelli, 1998; Rizzolatti et al., 1994; Ruge, Braver, & Meiran, 2009). Indeed, Astafiev et al.'s (2003) functional magnetic resonance imaging (fMRI) study of human participants reported overlapping activation of parietofrontal regions when participants covertly attended to a region of space and when participants implemented goal-directed saccades and reaches to that same region of visual space. In particular, activation within intraparietal regions, frontal eye fields and the dorsal pre-motor area were observed

across all tasks: an overlapping pattern of results supporting the link between attention and response planning (Astafiev et al., 2003; Rizzolatti et al., 1994; Ruge et al., 2009).

In the context of the present study, I acknowledge that some recent neuroimaging work has contrasted the neural substrates of CL reaches and reaches completed in the absence of concurrent limb and target vision (i.e., occlusion trials) (e.g., Filimon et al., 2009; Thaler & Goodale, 2011). In particular, Filimon et al.'s (2009) non-event related fMRI study contrasted CL and occluded (i.e., in darkness) reaches to peripherally cued target locations. CL and occlusion trials produced a similar activation of frontoparietal networks (including regions of the dorsal and ventral pre-motor area, the supplementary motor area, primary motor cortex and superior, medial and intraparietal sulcus); however, the left superior parietal-occipital sulcus (sPOS) showed greater activation in CL reaches as compared to their occluded counterparts. Importantly, however, due to the concurrent removal of limb and target vision during occlusion trials, Filimon et al., along with other neuroimaging studies, are unable to disentangle the neural activation associated with limb and target vision. Moreover, to prevent disruption of the magnetic field, fMRI-based studies are limited to small amplitude wrist or finger movements. As a result, current neuroimaging work may not accurately characterize the neural substrates supporting goal-directed reaching in peripersonal space (Culham et al., 2003; Culham, Cavina-Pratesi, & Singhal, 2006; Previc, 1998).

My thesis examined the behavioural and electroencephalographic properties associated with the planning of CL and OL reaches in peripersonal space. To my knowledge no previous electroencephalographic or human imaging studies have directly examined this issue. Specifically, my work examined the concurrent behavioural and event-related brain potentials (ERPs) associated with CL and OL reaches performed in an environment wherein participants were provided advanced information regarding the nature of the response (i.e., CL vs. OL). Importantly, this advanced information was used to determine whether knowledge related to the availability of online limb vision influences movement planning processes. In particular, prior to target presentation, participants were provided a colour-dependent fixation cross denoting whether a to-be-performed response was to be completed in a CL (i.e., green cross) or OL (i.e., red cross) environment. In addition, I used a target perturbation paradigm wherein initial target

position remained stationary or 'jumped' to a new target location following movement onset: a paradigm requiring participants to make in-flight amendments to their trajectories. In other words, I created a situation in which participants were unable to reliably predict the physical location of the to-be-reached target in advance of movement onset. As such, the online monitoring of the movement trajectory was required to maximize endpoint accuracy.

Previous target perturbation studies have found that the initial kinematic parameterization of reach trajectories scale to the properties (i.e., extent) of the target object presented at movement onset and subsequently demonstrate later trajectory amendments to account for the target jump (Bridgeman, Lewis, Heit, & Nagle, 1979; Elliott, Binsted, & Heath, 1999; Goodale, Pelisson, & Prablanc, 1986; Gréa et al., 2002; Heath, Hodges, Chua, & Elliott, 1998; Krigolson & Heath, 2006; Prablanc, Desmurget, & Grea, 2003; Prablanc & Martin, 1992). For example Heath et al., (1998) found that peak velocity of reach trajectories scaled to the amplitude of the originally presented target whereas the timing of the deceleration phase scaled to the amplitude of the perturbed target location. In other words, online monitoring of target information is used to modify the latter stages of a reaching response. Furthermore, studies contrasting the adaptations of CL and OL reaches to a target perturbation have shown that trajectory amendments in the former condition are implemented earlier and with greater precision than in the latter condition (Reichenbach, Thielscher, Peer, Buelthoff, & Bresciani, 2009). In other words, concurrent visual feedback of limb and target optimizes the efficiency and effectiveness of online corrections (Elliott et al., 1999; Prablanc & Martin, 1992; Reichenbach et al., 2009). In terms of behavioral predictions, CL reaches should exhibit greater accuracy and less variability than OL reaches, due to the implementation of more effective and efficient trajectory based modifications.

In terms of ERP outcomes, I identified the N1 and P2 as candidate ERP components sensitive to the locus of visuospatial attention and response programming, respectively. In particular, the N1 presents as a negative amplitude component with a lateralized topography over posterior-occipital electrode sites and has been linked to the orientation of visuospatial attention and the allocation of attentional resources (Handy & Mangun, 2000; Hillyard, Vogel, & Luck, 1998; Mangun & Hillyard, 1987; Vogel &

Luck, 2000; van Elk, van Schie, Neggers, & Bekkering, 2010). For example, Mangun and Hillyard (1987) found that visual probes presented at locations on the same side as overt attention engendered an increased N1 component in comparison to visual probes presented at unattended locations. Moreover, Handy and Mangun (2000) found a greater N1 for targets with high perceptual load (i.e., difficulty to discriminate) at cued locations as compared to targets with easier discriminability. Furthermore, the N1 has been linked to the attentional modulations associated with manual response planning (Eimer, Cockburn, Smedley, & Driver, 2001; Eimer, Van Velzen, Gherri, & Press, 2006; Gherri & Eimer, 2010; Gherri, Van Velzen, & Eimer, 2009; for review see Baldauf & Deubel, 2010). Specifically, Eimer et al. (2006) provided a visual cue directing participants to use their left or right hand for a manual response. Notably, visual probe stimuli were presented either to the cued "relevant" hand or to the opposite uncued hand during response planning. Results demonstrated an enhanced N1 for visual probes presented adjacent to the cued hand. These results were interpreted to support the link between attention and response planning. Furthermore, Gherri and Eimer (2010) proposed an obligatory link between manual response planning and spatial attention. In their study, ERP components were measured to visual probe stimuli presented near the cued and uncued response hand in two conditions. In one condition, directed attention and the cued response hand were spatially compatible (i.e., located on the same side of visual space) whereas in the other condition attention and the cued hand were located on opposite sides (i.e., spatially incompatible). In line with the above-described research by Eimer and colleagues, Gherri and Eimer showed an enhanced N1 for visual probes presented adjacent to the cued hand, as compared to probes presented to the uncued hand, with this N1 modulation only present when attention and response planning were spatially compatible. Gherri and Eimer interpreted these results as evidence for an obligatory link between response planning and visuospatial attention (i.e., the PMTA).

The P2[1] presents as a positive amplitude component at roughly 200 ms following stimulus onset, with a bilateral activation over frontal areas (Adrover-Roig & Barceló, 2010; Fritzsche, Stahl, & Gibbons, 2011; Kim, Kim, Yoon, & Jung, 2008; Nikolaev,

[1] Also termed the anterior P2 (P2a), frontal P3 (P3f) and frontal selection positivity (FSP).

Ziessler, Dimova, & van Leeuwen, 2008; Potts, Patel, & Azzam, 2004). The P2 has been shown to index response relevant processes, with previous studies eliciting increased P2 components for task relevant stimuli (Potts, 2004; Potts et al., 2004), and for task environments requiring increasing attentional demands (Fritzsche et al., 2011; Kim et al., 2008; Lenartowicz, Escobedo-Quiroz, & Cohen, 2010; Makeig et al., 1999). In particular, the P2 has been shown to correlate with reaction and response time, suggesting its role in the planning, and execution of a motor response (Fritzsche et al., 2011; Kim et al., 2008; Makeig et al., 1999). These results suggest that differences in the P2 may serve to index putative attention-linked preparatory processes in CL and OL actions.

In terms of research predictions, if responses are structured in real-time (i.e., the PAM) then CL and OL reaches should elicit comparable ERP components in advance of response cuing (Westwood & Goodale, 2003). In contrast, if advanced knowledge regarding the availability of online visual feedback influences the manner in which a response is structured, then differences in ERP components should underlie CL and OL reaching. More specifically, if knowledge of the availability of online visual feedback increases the attentional resources directed to the reaching limb (i.e., the PMTA), then CL and OL reaches should exhibit differences in the N1 and P2 components prior to response cuing.

Methods

Participants

Twelve self-declared right-hand dominant individuals (8 male, 4 female: age range 20-40 years) with normal or corrected-to-normal vision were recruited to participate in this project. This project was approved by the Office of Research Ethics, University of Western Ontario, and was carried out according to the Declaration of Helsinki.

Apparatus and Procedure

Participants sat at an aiming apparatus consisting of three shelves supported by an aluminum frame (for schematic see Figure 5 from Neely & Heath, 2010). The top shelf of the apparatus supported a monitor (DELL: 3007WFP, 11ms response rate; Austin, TX,

USA; 2560 x 1600 resolution at 60Hz) and was used to project visual stimuli onto a one-way mirror that composed the middle shelf of the apparatus. The bottom shelf of the apparatus was a solid surface wherein participants completed reaching movements. The distance between the top shelf and the middle shelf, and middle shelf and reaching surface was 315 mm. Thus, the optimal geometry of this setup created a situation wherein participants perceived visual stimuli projected by the monitor as being located on the lower (i.e., reaching surface) of the apparatus. The lights in the experimental suite were extinguished throughout data collection. As a result, the one-way mirror occluded direct vision of the reaching limb. In place of veridical limb vision, a light emitting diode (LED) was affixed to a splint complex and secured to the participant's reaching (i.e., right index) finger. A head-chin rest was positioned at the participant's midline and was used to maintain a constant optical geometry. All experimental events were controlled via MATLAB (The MathWorks, Natick, MA, USA) and Psychophysics Toolbox extensions (Brainard, 1997).

In advance of each trial participants used their reaching finger to depress a microswitch (henceforth referred to as start location) that was positioned 300 mm from the front edge of the aiming apparatus and 285 mm left of participant's midline. Following this, the LED attached to the participants finger was illuminated. Subsequently, a white fixation cross (10 mm by 10 mm) was projected, and participants were required to maintain their gaze on this position for the duration of a trial (see figure 1 for schematic). Following a randomized foreperiod (i.e., 500 to 1000 ms), a colour change of the fixation cross (green or red) was provided for 1,000 ms and was used to signal whether vision of the limb would be available (i.e., closed-loop: CL) or unavailable (i.e., open-loop: OL) during the to-be-completed response. A green fixation cross indicated a CL response; that is, the LED attached to the reaching finger would remain illuminated during the response. In turn, a red fixation cross indicated an OL trial such that the LED would be extinguished upon release of pressure from the start location (i.e., at movement onset). Following cuing of the reaching condition (CL vs. OL), a target (3 mm by 3 mm white circle) was projected 285 mm (i.e., middle target) to the right of the start location for a randomized foreperiod (i.e., 1,000 to 2,000 ms) after which an auditory tone cued participants to initiate their response (i.e., a left to right reaching

movement). For 33% of trials, the location of the target remained stationary (i.e., non-perturbed trial) throughout the reaching response. For the remaining 66% of the trials, the position of the target was perturbed 40 mm left (i.e., near target) and right (i.e., far target) of the original (i.e., middle) target location; that is, the target 'jumped' to a location nearer to, and farther away, from the original target position. In total, participants completed 140 trials to the non-perturbed target and the same number of trials to each of the near and far target perturbations. Participants were instructed to keep their movement times between 300 and 500 ms and were provided with visual feedback for reaches with lower and higher movement times. Trials that fell outside this bandwidth were added randomly back into the trial sequence and repeated. The ordering of visual condition (CL vs. OL) and the presentation of perturbed and non-perturbed targets was randomized. In order to prevent ocular artefacts in the electroencephalogram data, a trial wherein a saccadic or smooth pursuit eye movement was detected after fixation of the home position was discarded and entered back into the randomized trial matrix.

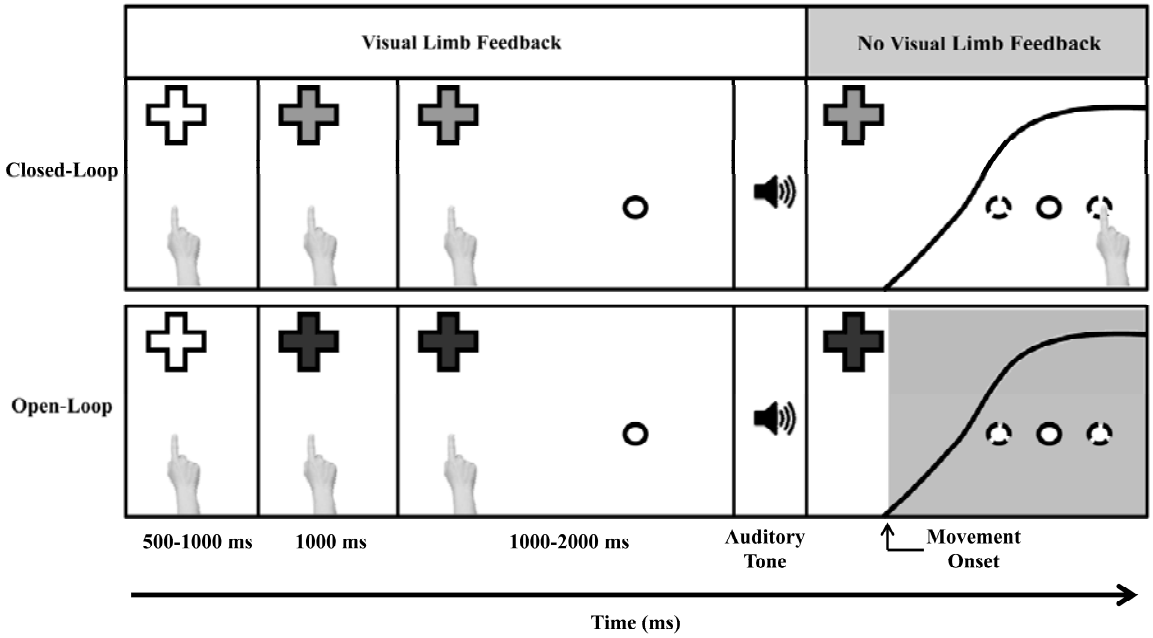

Figure 1: Schematic representation of the closed- and open-loop reaching conditions. For each reaching condition vision of the limb was available until movement onset. In this schematic the curvilinear line represents the reaching trajectory and white and gray backgrounds represent when vision of the limb was available (i.e., LED on) and unavailable (i.e., LED off), respectively. Prior to response cuing, the middle target was always presented for a randomized preview period, while at movement onset the target could remain stationary, or be perturbed to the left (i.e., near) or right (i.e., far) target locations. In the above schematic non-perturbed and perturbed targets are denoted by solid- and dash-lined circles, respectively.

Behavioral Analysis

In addition to the LED, the splint complex attached to the reaching finger contained an infrared emitting diode (IRED). The position of the IRED was sampled at 500 Hz via an OPTOTRAK Certus (Northern Digital, Inc.; Waterloo, ON, Canada). IRED position data were filtered offline with a second-order dual-pass Butterworth filter using a low-pass cut-off frequency of 15 Hz. Displacement data were differentiated using a three-point central finite difference algorithm to obtain instantaneous velocities. Movement onset was defined as the frame coinciding with release of pressure from the start location whereas movement offset was defined as the first frame wherein resultant velocity fell below 50 mm/s for 10 consecutive frames (i.e., 20 ms).

Dependent variables included: reaction time (RT: the time from the onset of the auditory tone to movement onset), movement time (MT: time between movement onset and offset), and the spatial distribution of movement endpoints in the primary (i.e., horizontal) movement direction (i.e., 100% of MT). The aforementioned variables were examined via 2 (visual condition: CL, OL) by 3 (target eccentricity: near, middle, far) repeated-measures ANOVA. Additionally, displacement of the reaching limb in the primary movement direction was computed at decile increments of normalized MT, and was examined by adding the variable Time (i.e., 10%, 20% … 80%, 90% and 100% of MT) to the ANOVA model. Main effects and interactions were decomposed via simple effects planned comparisons.

Electroencephalographic Analysis

The electroencephalogram (EEG) was continuously recorded and referenced to a common ground from 64 electrodes mounted in a fitted cap according to the International 10/20 system using Brain Vision Recorder software (Version 1.10, Brain Products, GmbH, Munich, Germany). The vertical and horizontal electrooculograms were recorded from electrodes above and below the right eye and on the outer canthi of both eyes, respectively. Electrode impedances were kept below 20kΩ at all times. The EEG data was sampled at 1000 Hz and amplified (Brain Vision BrainAmp DC, Brain Products, GmbH, Munich, Germany).

Offline, the EEG data was filtered through a (0.1 Hz – 25 Hz) passband phase shift-free Butterworth filter, re-referenced to the mean-mastoid electrodes, and ocular artefacts were algorithm-corrected using the Gratton and Coles algorithm (Gratton, Coles, & Donchin, 1983). Subsequent to this, epochs where the change in voltage between samples (at any channel) exceeded 35 μVs, or where the difference between the epoch maxima and minima exceeded 150 μVs, were discarded. Epochs locked to the fixation cross color change were baseline corrected using an interval immediately preceding the event of interest. ERP waveforms for CL and OL visual conditions were then constructed by averaging the epochs for each participant. ERP components were then quantified by taking the mean voltage across a 100 ms window (+/- 50ms) centered on peaks of interest for each participant, electrode channel and visual condition. Mean voltages were then submitted to paired sample t-tests to contrast each visual condition time-locked to the fixation cross color change. For display purposes, grand-averaged ERP waveforms were constructed by averaging epochs across all participants for each electrode channel and visual condition. In addition, for the plotting of scalp topographies, a difference waveform was generated through a subtraction of visual condition grand-averaged ERP waveforms.

Results

Behavioural Results

The grand mean for RT was 280 ms (SD=48) and this variable did not produce any manipulation related effects. In terms of MT, results yielded a main effect of target eccentricity, $F(2,22) = 5.08$, $p < 0.02$, as well as a visual condition by target eccentricity interaction, $F(2,22) = 6.78$, $p < 0.01$. MTs for CL and OL reaches to the middle target (i.e., the non-perturbed target) were equivalent (p = ns) whereas MTs for CL reaches to the near and far targets (i.e., the perturbed targets) were respectively shorter and longer than their OL counterparts (ps < 0.001) (see Figure 2 and Table 1 for details). Moreover, and as shown in Figure 2, CL trials elicited a temporal scaling to veridical target eccentricity whereas OL trials did not.

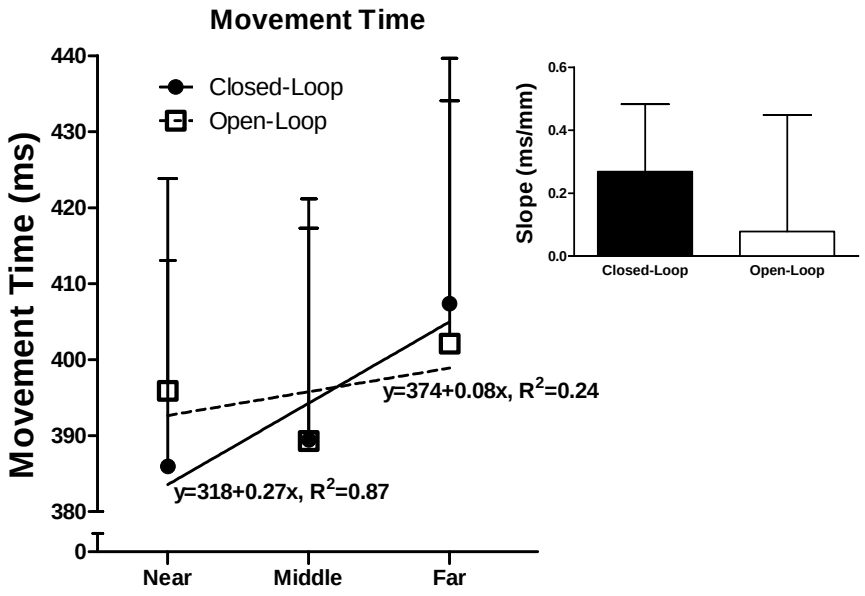

Figure 2: Mean values of movement time as a function of visual condition (closed- and open-loop) and target eccentricity (near, middle, and far). Regression lines show the scaling of movement time to target eccentricity for each visual condition, with associated regression line slopes in the inset panel. Error bars represent between participant standard deviations. Note: regression equations were also calculated via index of difficulty ($ID=\log_2[(2A/W)]$) (Fitts, 1954): where A = movement amplitude and W = target width. MT by ID scaling for CL= ($y=6+51.29x$, $R^2=0.84$), and MT by ID scaling for OL = ($y=290+14.05x$, $R^2=0.20$).

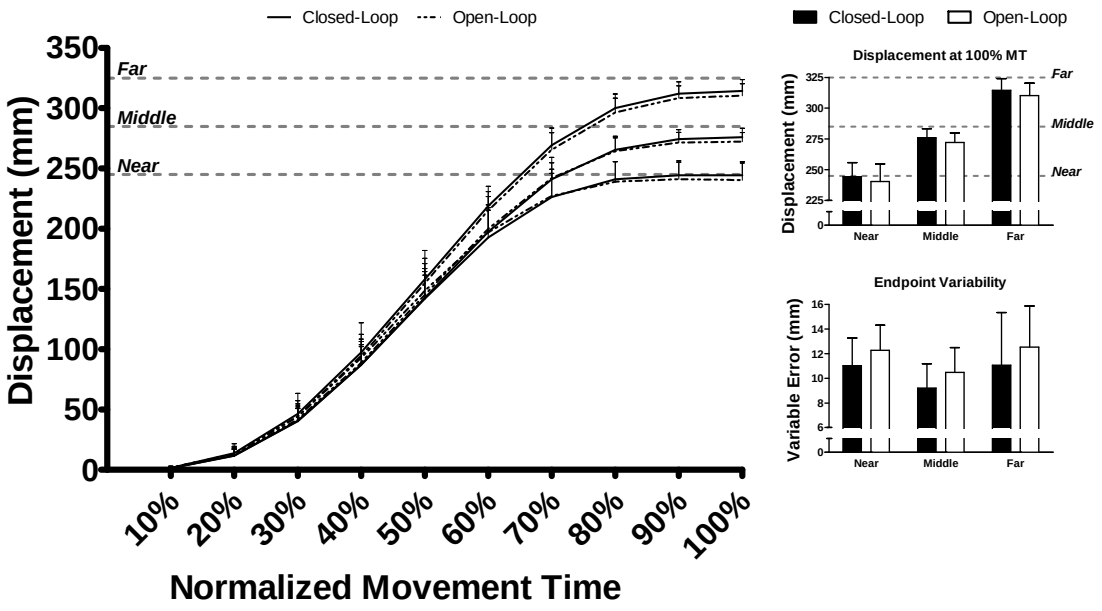

Figure 3: Displacement of the reaching limb from 10-100% of normalized movement time to the near, middle and far target locations across closed- and open-loop reaches (*left panel*). Mean values for reach displacement at 100% of movement time (*top right panel*) and endpoint variability (*bottom right panel*) as a function of visual condition and target eccentricity. Error bars represent between participant standard deviations.

Table 1: Means and between participant standard deviations (in parentheses) for movement time (MT), variable error (VE), and the horizontal displacement of the limb at normalized deciles of movement time (50-100%) as a function of the reported main effects of visual condition (V) target eccentricity (T) and their interaction (VxT). Visual condition by target eccentricity interactions were decomposed via a between condition contrast of slopes relating spatial displacement to target eccentricity. The far right column shows the regression equations for visual conditions that exhibited a reliable linear effect of T. Note: No reliable effects of V or T or their interaction were noted from 10-40% of normalized MT.

	Post Hoc Contrasts	**Target Amplitude**			**Regression Equations**
		245mm	**285mm**	**325mm**	
MT					
T: p<0.02	-	391 (26)	389 (30)	405 (32)	
VxT: p<0.01					
CL	Linear: p<0.01	386 (27)	389 (32)	407 (32)	y= 318 +0.27x, R^2=0.87
OL	p=ns	396 (28)	389 (28)	402 (32)	y= 374 +0.08x, R^2=0.24
VE					
V: p<0.01					
T: p<0.02	Quadratic: p<0.01	11.7 (2.0)	9.9 (1.9)	11.8 (3.8)	
50%					
T: p<0.01	-	145.4 (28.6)	144.0 (18.7)	156.5 (16.9)	-
VxT: p<0.05					
CL	Linear: p<0.01	142.2 (24.9)	142.8 (18.8)	158.1 (17.5)	y= 91.0 +0.20x, R^2=0.78
OL	p=ns	148.5 (33.5)	145.2 (19.4)	154.8 (16.5)	-
60%					
T: p<0.01	-	194.9 (26.9)	198.8 (18.5)	217.0 (16.0)	y= 124.8 +0.28x, R^2=0.88
VxT: p<0.03					
CL	Linear: p<0.01	192.8 (24.6)	197.7 (17.8)	218.9 (16.4)	y= 110.1 +0.33x, R^2=0.89
OL	Linear: p<0.01	197.0 (29.7)	200.0 (20.0)	215.2 (15.8)	y= 139.3 +0.23x, R^2=0.87
70%					
T: p<0.01	-	226.7 (21.0)	241.5 (15.4)	267.4 (14.2)	y= 100.4 +0.51x, R^2=0.98
VxT: p<0.02					
CL	Linear: p<0.01	226.3 (19.8)	241.0 (13.9)	269.3 (14.3)	y= 92.5 +0.54x, R^2=0.97
OL	Linear: p<0.01	227.2 (22.3)	242.1 (17.3)	265.5 (14.2)	y= 108.2 +0.48x, R^2=0.98
80%					
V: p<0.01					
T: p<0.01	Linear: p<0.01	240.0 (15.5)	265.0 (11.1)	298.3 (11.8)	y= 60.2 +0.73x, R^2=0.99
90%					
V: p<0.01					
T: p<0.01	Linear: p<0.01	242.7 (13.0)	272.9 (8.1)	310.3 (9.9)	y= 34.7 +0.84x, R^2=0.99
100%					
V: p<0.01					
T: p<0.01	Linear: p<0.01	242.3 (12.7)	274.1 (7.5)	312.4 (9.6)	y= 26.6 +0.88x, R^2=0.99

The spatial displacement data in the primary movement direction revealed a number of main effects and interactions (see Table 1 for details) and produced a highest-order interaction involving time by vision by target eccentricity, $F(18,198) = 2.40$, $p < 0.03$. In decomposing this interaction, the effect of visual condition and target eccentricity was examined at each decile of MT. Figure 3 shows that no significant effects of visual condition or target eccentricity (or their interaction) were observed from 10% through 40% of MT (ps = ns). At 50% of MT, CL trials demonstrated a linear increase in amplitude as a function of increasing target eccentricity ($p < 0.001$) whereas OL trials did not (p = ns). In other words, CL trajectories reflected the characteristic of the target that was visible following movement onset (i.e., the near, middle and far targets) whereas OL trajectories elicited scaling to the target that was presented prior to movement onset (i.e., the middle target). Later in the response (i.e., 60% through 100% of MT) both CL and OL amplitudes scaled linearly to target eccentricity (ps < 0.001); however, the slopes relating displacement to target eccentricity were greater in CL as compared to OL trials (see Table 1 for details). Additionally, Figure 3 demonstrates that endpoints (i.e., 100% of MT) for CL trials were more accurate than their OL counterparts. Further, analysis of the spatial distribution of endpoints at 100% of MT (i.e., variable error) indicated that CL trials were less variable than OL ones, $F(1,11) = 28.37$, $p < 0.001$, and that variability was influenced by target eccentricity, $F(2,22) = 4.98$, $p < 0.02$. In particular, endpoints for the perturbed targets (near and far) were more variable than the unperturbed middle target (ps < 0.01) (see Table 1 for details).

ERP response to presentation of visual condition.

The electroencephalograhic data revealed that the cuing of experimental condition (CL or OL) impacted the focus of visuospatial attention. Specifically, we observed an enhanced N1 component (180-280ms) for CL as opposed to OL reaches with maximal differences observed at an electrode site contralateral to the reaching limb being used, $t(11) = -3.71$, $p<0.01$ (electrode PO7: CL: -1.43μV SD=3.49, OL -0.54μV SD=3.97) (see Figure 4). In other words, the N1 component, typically associated with the focusing of visuospatial attention during the performance of goal-directed reaching (Krigolson,

Holroyd, Van Gyn, & Heath, 2008), was more negative for CL as compared to OL reaches at a posterior electrode site contralateral to the reaching limb.

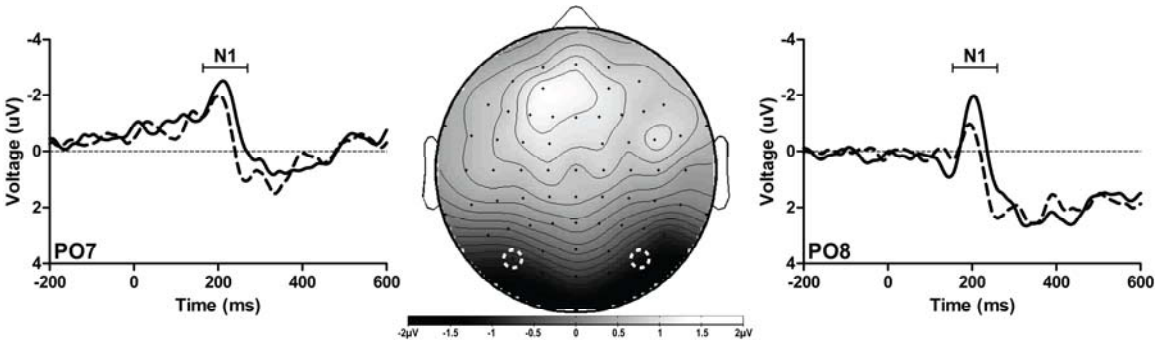

Figure 4: Grand-averaged ERP waveforms time-locked to the cuing of visual condition between closed- and open-loop reaches (CL=solid line, OL=dashed line). Waveforms measured at the left hemisphere electrode (PO7: *left panel*), and right hemisphere electrode (PO8: *right panel*) are displayed above, along with the associated difference-wave scalp topography (*middle panel)*. Electrodes of interest on the scalp topography are outlined with a white dashed circle. Negative voltages are plotted up by convention.

Additionally, an enhanced frontal component showing a bilateral topography in the P2 time range (210-310ms; $t(11) = 5.36$, $p<0.01$) was found to be maximal at electrode AF3. In particular, a larger P2 amplitude was associated with CL as compared to OL reaches (CL = 1.87µV SD=4.52, OL = 0.36µV SD=5.32) (see Figure 5). In other words, the P2 component demonstrated a topography with localized activation in pre-frontal cortical areas with greater positivity for the planning of CL reaches.

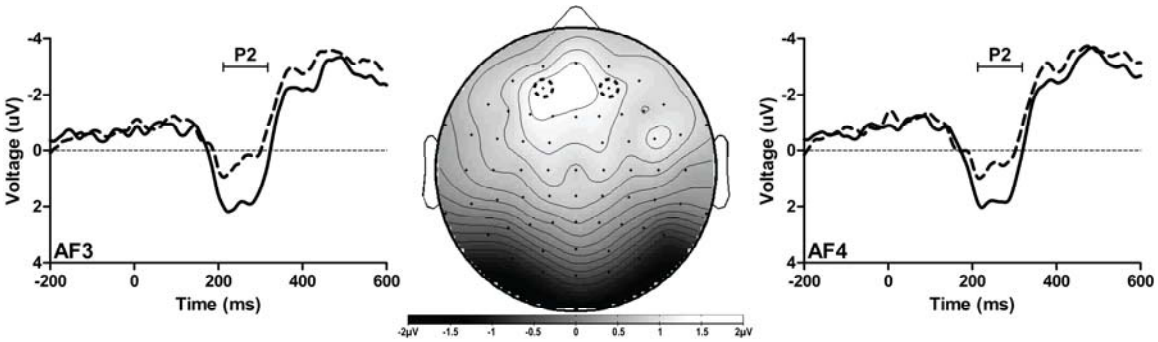

Figure 5: Grand-averaged ERP waveforms time-locked to the cuing of visual condition between closed- and open-loop reaches (CL=solid line, OL=dashed line). Waveforms measured at the left hemisphere electrode (AF3: *left panel*), and right hemisphere electrode (AF4: *right panel*) are displayed above, along with the associated difference-wave scalp topography (*middle panel)*. Electrodes of interest on the scalp topography are outlined with a black dashed circle. Negative voltages are plotted up by convention.

Discussion

The present investigation contrasted the behavioural and ERP components associated with CL and OL reaching movements. In particular, I focused on the ERP components associated with the planning of CL and OL reaches to test the competing predictions of the PAM and PMTA. Moreover, I used a target perturbation paradigm such that on 33% of trials a central target visible at response cuing remained stationary during the response whereas for the remaining trials the central target 'jumped' (near or far) following movement onset. The basis for using the target perturbation was to create a situation in which the target constraints present during movement planning were sometimes different from that associated with movement execution. In other words, I wanted to create a situation wherein participants would be unable to reliably predict the physical location of the to-be-reached target in advance of movement onset (Bridgeman et al., 1979; Elliott et al., 1999; Prablanc & Martin, 1992).

Behavioural results: Limb vision influences the efficiency and effectiveness of online trajectory amendments

CL and OL reaches elicited equivalent RTs and exhibited early trajectories with spatial parameters corresponding to the veridical properties of the target present during response planning. In particular, displacements for CL and OL reaches scaled to the middle target during the early stages of the response (i.e., 10 to 40% of MT). These results suggest that the initial kinematic parameterization of reaches in both conditions were structured in advance of movement onset via central planning mechanisms (e.g., Meyer, Abrams, Kornblum, Wright, & Keith Smith, 1988; see also Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 1979). Notably, however, examination of later trajectory kinematics indicated that CL reaches demonstrated an earlier scaling to veridical target locations than OL reaches; that is, CL trajectories adapted to the target perturbation earlier than OL reaches. Specifically, at 50% of MT the displacement of CL reaches scaled to veridical target eccentricity whereas a similar scaling for OL reaches was not observed until 60% of MT. Moreover, from 60% through to 70% of MT, the slopes relating displacement to target eccentricity were reliably steeper for CL compared to OL reaches. In addition, MT analyses indicated that CL reaches exhibited a linear increase in MT with increasing target eccentricity, whereas MTs for OL reaches corresponded to the initial (i.e., unperturbed) target location. Last, endpoints for CL reaches were more accurate and less variable then OL reaches: a finding that was consistent across perturbed and unperturbed target conditions.

Overall, my results are expected findings and demonstrate that adapting an ongoing reach trajectory to a physical change in target location occurs earlier and is implemented with greater efficiency and effectiveness when vision of the limb is available to the performer (Elliott et al., 1999; Prablanc & Martin, 1992; Reichenbach et al., 2009) and when the performer is provided advanced information that visual feedback will be available (Elliott & Allard, 1985; Jakobson & Goodale, 1991; Neely et al., 2008; Zelaznik et al., 1983). In particular, the effective scaling of CL reach trajectories to targets across perturbed and unperturbed trials indicates that online vision of the limb facilitates the evocation of error-nullifying trajectory amendments based on absolute limb and target comparisons (Elliott et al., 1999; Heath, 2005; Heath et al., 1998; Prablanc &

Martin, 1992; Reichenbach et al., 2009). In other words, CL reaches are able to engage the dedicated visuomotor networks of the dorsal visual pathway to support early and effective trajectory corrections. In contrast, the absence of online limb vision during OL reaches decreases the efficiency and effectiveness of trajectory amendments. Nevertheless, reaches in this condition are still able to implement (albeit less effectively) online corrections to perturbed target locations (Goodale et al., 1986; Pelisson, Prablanc, Goodale, & Jeannerod, 1986; Prablanc & Martin, 1992; Reichenbach et al., 2009; Sarlegna et al., 2003). As indicated by Sarlegna et al. (2003), OL reaches may implement trajectory corrections via the integration of target-related visual information and online limb proprioceptive feedback (Sarlegna et al., 2004). In summary, my behavioural results are consistent with previous work indicating that CL reaches show more efficient and effective online trajectory modifications than their OL counterparts (Carlton, 1979; Elliott et al., 1991; Heath, 2005; Heath et al., 2004).

ERP results: N1 and P2 differences in CL and OL reaches

Recall that a visual cue provided 1,000 ms prior to target onset indicated the nature (i.e., CL vs. OL trial) of a to-be-performed reaching response. Thus, I was interested in determining whether the onset of this instructional cue was associated with a difference in the central planning of CL and OL reaches. In particular, I wanted to investigate if advanced knowledge related to the availability of online visual feedback influences premovement visuospatial processing.

My results show that the N1 component (maximal over parietal-occipital electrode sites) reliably differed between CL and OL reaches. In particular, CL trials were associated with a larger N1 amplitude than OL trials. This results suggests an increased allocation of visuospatial attention occurred when participants were informed that limb vision would be available during the response (Hillyard et al., 1998; Mangun & Hillyard, 1987; Vogel & Luck, 2000; van Elk, van Schie, et al., 2010). Such a proposal is supported by a number of studies indicating that spatial attention (or visuospatial attention) shifts towards the responding hand during movement planning (Eimer et al., 2006; Eimer & van Velzen, 2006; Gherri & Eimer, 2010; van Elk, van Schie, et al., 2010). For example, Eimer, Forster, Van Velzen, and Prabhu (2005) found an enhanced

N1 during response planning for visual probes presented adjacent to a cued responding limb as compared to probes presented adjacent to an uncued (i.e., the opposite) limb. In other words, visuospatial attention (as indexed by the N1) is directed to the cued response hand during movement planning. Furthermore, Eimer and colleagues suggested that the observed shift in visuospatial attention to the responding limb reflects the selective amplification of sensory limb information during response planning (see also Hillyard et al., 1998). In terms of my results, the differences in the N1 suggest that enhanced attentional resources were devoted to the CL limb during reach planning. Recall that behaviourally, CL reaches demonstrated earlier and more effective trajectory modifications than their OL counterparts. Thus, in concert with my behavioural findings, I propose that the greater N1 in CL reaches evinces that advanced knowledge related to the availability of online limb vision amplifies the premovement processing of sensory-based limb information. Interestingly, although the N1 has been previously localized to areas in the ventral visual stream (Krigolson & Holroyd, 2007; Potts, 2004; van Elk, van Schie, et al., 2010), it is important to note that anatomical evidence has demonstrated the existence of extensive interconnections between ventral and dorsal stream visual areas (Merigan & Maunsell, 1993).

A reliable difference in the P2 component was also linked to the visual cue indicating the nature of the upcoming reach. Specifically, the P2 was found maximal over pre-frontal cortical areas (Makeig et al., 1999; Potts et al., 2004; van Elk, Crajé, et al., 2010; van Elk, van Schie, et al., 2010) with larger amplitudes for CL as compared to OL trials. This result suggests that when visual limb information was made available to participants during their reach, movement planning processes were linked the increased allocation of visuospatial attention to the reaching limb. In particular, I propose that the greater amplitude P2 reflects an action selection mechanism enabling the integration of visual limb information during the planning of CL reaches (Cisek, 2007; van Elk, Crajé, et al., 2010; van Elk, van Schie, et al., 2010). Certainly, such a finding is congruent with previous ERP studies showing increased P2 components for tasks completed in attentionally demanding environments and in those emphasizing visuomotor integration (Fritzsche et al., 2011; Kim et al., 2008; Koivisto & Revonsuo, 2010; Lenartowicz et al., 2010; Makeig et al., 1999; Potts, 2004; Potts et al., 2004; van Elk, Crajé, et al., 2010; van

Elk, van Schie, et al., 2010). For example, van Elk, van Schie et al. (2010) observed an increased N1 and P2 component for the planning of visually guided grasping as compared to reaching movements. van Elk and colleagues interpreted the between-task differences in the P2 as an index of processes related to visuomotor integration. In particular, modulations of the P2 were interpreted to reflect a selection for action mechanism whereby visual information relevant for the to-be-executed response was selectively amplified and integrated during movement planning. Moreover, the enhancement of the P2 was attributed to the greater number of visual features that required integration during grasp as compared to reach planning. Specifically, grasping movements were suggested to require the integration of visual features related to target size, orientation, and location, whereas reaching movements only required the integration of location related target properties. In terms of my study, the greater P2 for CL as compared to OL reaches suggests that reaches in the former condition integrated an enriched set of visual features during movement planning. In particular, I propose that the greater P2 reflects the additional integration of visual limb information during CL as compared to OL reach planning. Indeed, it may be the case that the increased premovement processing of visual limb information during CL reaches directly facilitated the use of visual limb feedback for online trajectory amendments during the response.

Concerning the PAM and PMTA

Overall, my behavioural and ERP findings counter the PAM's assertion that the dorsal visuomotor networks are restrictively engaged in real-time movement planning. Indeed, if the PAMs real-time hypothesis were true then the advanced knowledge of the availability of limb vision should not have differentially influenced the ERP correlates of CL and OL reaches. Instead, my results indicate that advanced knowledge regarding the sensory information associated with a to-be-completed response influences central planning mechanisms. In particular, advanced knowledge related to the availability of online limb vision subserves an enhanced allocation of visuospatial attention to the reaching limb: a feature that I propose to facilitate online and error-nullifying trajectory amendments during the unfolding response. Such a finding is in line with the PMTA and the contention of a direct link between attention and action.

Chapter 2
Conclusions

In summary, my concurrent ERP and behavioural data provide evidence that advanced knowledge related to the availability of online limb vision influences early attentional and motor planning processes. Thus, my results support the notion that planning processes for CL and OL reaches are dissociable when participants are provided advanced knowledge related to the availability of online limb vision: a finding that provides convergent evidence for the PMTA's assertion of a direct link between attention and action.

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Appendix A

The University of Western Ontario Research Ethics Board of Approval notice

Western

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. Heath
Review Number: **17204S** **Review Level:** Full Board
Review Date: July 09, 2010 **Approved Local # of Participants:** 24
Protocol Title: The Effects of Limb Vision on the Voluntary Correction of Goal-Directed Reaching
Department and Institution: Kinesiology, University of Western Ontario
Sponsor: NSERC-Ref 191594
Ethics Approval Date: August 04, 2010 **Expiry Date:** August 31, 2011
Documents Reviewed and Approved: UWO protocol, Letter of Information and Consent, Oral Debriefing Script.
Documents Received for Information:

This is to notify you that The University of Western Ontario Research Ethics Board for Non-Medical Research Involving Human Subjects (NMREB) which is organized and operates according to the Tri-Council Policy Statement: Ethical Conduct of Research Involving Humans and the applicable laws and regulations of Ontario has granted approval to the above named research study on the approval date noted above.

This approval shall remain valid until the expiry date noted above assuming timely and acceptable responses to the NMREB's periodic requests for surveillance and monitoring information. If you require an updated approval notice prior to that time you must request it using the UWO Updated Approval Request Form.

During the course of the research, no deviations from, or changes to, the study or consent form may be initiated without prior written approval from the NMREB 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 monitor, telephone number). Expedited review of minor change(s) in ongoing studies will be considered. Subjects must receive a copy of the signed information/consent documentation.

Investigators must promptly also report to the NMREB:

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 this office for approval.

Members of the NMREB 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 NMREB.

Chair of NMREB: Dr. Riley Hinson
FDA Ref. #: IRB 00000941

Ethics Officer to Contact for Further Information			
☑ Grace Kelly (grace.kelly@uwo.ca)	☐ Janice Sutherland (jsutherl@uwo.ca)	☐ Elizabeth Wambolt (ewambolt@uwo.ca)	☐ Denise Grafton (dgrafton@uwo.ca)

This is an official document. Please retain the original in your files.

cc: ORE File

UWO NMREB Ethics Approval - Initial
V.2007-10-12 (rptApprovalNoticeNMREB_Initial) 17204S Page 1 of 1

Curriculum Vitae

Name: Ali-Asghar Mulla

Address: School of Kinesiology,
The University of Western Ontario,
London, Ontario, Canada

Post-Secondary Education and Degrees:

The University of Western Ontario, London, ON
Masters of Science Candidate, Kinesiology
2012

The University of Western Ontario, London, ON
B.A. Honors, Kinesiology and Physiology,
2009

Publications:

Weiler, J., Holmes, S.A., **Mulla, A.**, & Heath, M. (2011). Pro- and antisaccades: dissociating stimulus and response influences the online control of saccade trajectories. Journal of Motor Behavior, 43(5): 375-381.

Holmes, S.A., **Mulla, A.**, Binsted, G., & Heath, M. (2011). Visually and memory-guided grasping: aperture shaping exhibits a time-dependent scaling to Weber's Law. Vision Research, 51(17): 1941-1948.

Heath, M., **Mulla, A.**, Holmes, S.A., & Smuskowitz, L.R. (2011). The visual coding of grip aperture shows an early but not late adherence to Weber's law. Neuroscience Letters, 490(3): 200-204.

Nguyen, N., **Mulla, A.**, Nelson, A., & Wilson, T.D. (Submitted). Visuospatial anatomy comprehension: The role of spatial visualization ability and problem solving strategies.

Research presentations:

Nguyen, N**.**, **Mulla, A.**, Nelson, A.J., Wilson, T.D. (2012, April). Problem solving strategies and the relationship between visualization ability and spatial anatomy task performance [Abstract: Poster]. Annual meeting of the American Association of Anatomists: Experimental Biology 2012.

Mulla, A., Holmes, S.A., Binsted, G., Dhaliwal, P., & Heath, M. (2011, November). Visually derived and memory guided grasping elicit a temporally dependent adherence to Weber's law [Abstract: Poster]. Annual conference of the Society for Neuroscience: Neuroscience 2011.

Holmes, S.A., **Mulla, A.**, McDermid, A., Ethridge, E., Abes, A., & Heath, M. (2011, October). The variability of grip aperture shaping is determined by relative and absolute object properties [Abstract: Oral]. Annual conference of the Canadian Society of Psychomotor Learning and Sport Psychology: SCAPPS 2011.

Holmes, S.A., **Mulla, A.**, & Heath, M. (2011, May). Dynamic early adherence and late violation of Weber's law in goal-directed grasping [Abstract: Poster]. Vision Sciences Society 2011.

Weiler, J., Holmes, S.A., **Mulla, A.**, & Heath, M. (2011, May). Distinct response latencies do not influence pro- and antisaccade trajectories [Abstract: Poster]. Vision Sciences Society 2011.

Holmes, S.A., **Mulla, A.**, Smuskowitz, L.R., & Heath, M. (2011, January). Goal-directed grasping follows a process-dependent adherence to Weber's law [Abstract: Poster]. 2011 AGRS-FHS Symposium.

Mulla, A., Krigolson, O., De Grosbois, J., Binsted, G., & Heath, M. (2010, October). Distinct activation prior to movement onset indexes the recruitment of cortical areas responsible for the online control of discrete reaching movements [Abstract: Poster]. Annual conference of the Canadian Society of Psychomotor Learning and Sport Psychology: SCAPPS 2010.

Marriott, K., **Mulla, A.**, & Heath, M. (2010, October). A re-evaluation of Fitts (1954): veridical target width and effector precision influence the scaling of reach trajectories [Abstract: Poster]. Annual conference of the Canadian Society of Psychomotor Learning and Sport Psychology: SCAPPS 2010.

Weiler, J., **Mulla, A.**, Bingley, T., & Heath, M. (2010, May). Extrinsic manipulations of the mental number line do not impact SNARC-related influences on the planning and control of action [Abstract: Poster]. Vision Sciences Society 2010.

Awards and scholarships:

Mulla, A. (2011). Faculty of Health Sciences Graduate Student Conference Travel Award. Faculty of Health Sciences, The University of Western Ontario, $500.

Mulla, A. (2010). Kinesiology Travel Award. School of Kinesiology, Faculty of Health Sciences, The University of Western Ontario, $500.

Mulla, A. (2010). Faculty of Health Sciences Graduate Student Conference Travel Award. Faculty of Health Sciences, The University of Western Ontario, $400.

Mulla, A. (2010). Western Graduate Research Scholarship. School of Kinesiology, Faculty of Health Sciences, The University of Western Ontario.

Mulla, A. (2009). Kinesiology Travel Award. School of Kinesiology, Faculty of Health Sciences, The University of Western Ontario, $700.

Mulla, A. (2009). Western Graduate Research Scholarship. School of Kinesiology, Faculty of Health Sciences, The University of Western Ontario.

Teaching experience:

Graduate Teaching Assistant, September 2009 – April 2011
School of Kinesiology, The University of Western Ontario
Introduction to Sport Psychology
Introduction to Psychomotor Behavior

Professional associations:

Canadian Society for Psychomotor Learning and Sport Psychology
Society for Neuroscience
Vision Sciences Society