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Effects of Motion Pattern Characteristics on the Perception of Visual Acceleration

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

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Effects of Motion Pattern Characteristics on the Perception of Visual Acceleration
(Thesis format: Monograph)

by

Alexandra S. Mueller

Graduate Program in Psychology

A thesis submitted in partial fulfillment
of the requirements for the degree of
PhD in Psychology, Behavioural and Cognitive Neuroscience

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The University of Western Ontario
London, Ontario, Canada

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Abstract

The ability to perceive visual motion is one that we use every day to perform goal-directed activities, such as intercepting or avoiding objects. As objects and observers rarely move at constant velocities, it is important to be able to detect changes in velocity. However, little attention has been paid to how we perceive visual acceleration in the literature. This thesis explored the influence of real world-relevant motion pattern characteristics on visual acceleration perception. Observers rarely see object motion with an unlimited field of view, and therefore we first examined how physically constraining the horizontal distance over which a stimulus can move affects the ability to detect and pursue horizontal acceleration and deceleration at different average velocities. Results indicated that detection improves and smooth pursuit worsens as average velocity increases. Moreover, both improve as the horizontal aperture size increases. Given our asymmetrical experience with the frequency and relevance of upward compared to downward events due to gravity, we then investigated whether acceleration and deceleration detection vary as a function of vertical direction. We also tested whether the effects of aperture size on detection and pursuit persist on the vertical axis. Our data suggested that detection is better for downward than upward motion, and both detection and smooth pursuit improve as the vertical aperture size increases. Considering that we tend to see translation as well as more complex motion patterns outside the laboratory, we subsequently explored whether acceleration and deceleration detection vary between horizontal translation and radial optic flow, which is similar to the motion we see when moving forward or backward while looking straight ahead. We found that detection is better for radial than horizontal motion, although direction within each pattern type has no effect. Finally, we verified that sensitivity to the presence of acceleration is uniform across the optic flow field, regardless of radial direction. In summary, although we detect acceleration and deceleration similarly across a wide range of conditions, overall perception appears to be affected by the unique characteristics of the motion pattern.

Keywords: psychophysics, visual motion perception, acceleration perception, deceleration perception, smooth pursuit, motion display.

Co-authorship Statement

One manuscript has been published (Mueller & Timney, 2014a) with my co-author and PhD advisor, Dr. Brian Timney. Dr. Timney assisted with designing the experiments, analyzing and interpreting the data, and preparing all of the manuscripts for publication. All of the psychophysical experiments of this thesis were conducted in Dr. Timney's laboratory at the University of Western Ontario, London, Ontario. Another manuscript has also been accepted pending revision for publication and two more are in preparation. Dr. Timney is a co-author on all of those manuscripts. Two of those manuscripts have three other co-authors: Drs. Esther G. González, Martin J. Steinbach, and Chris McNorgan. Dr. González helped design and conduct the eye movement experiments. She was also instrumental for analyzing and interpreting the psychophysical and eye movement data and she provided valuable insight on the manuscripts. The eye movement data were collected in Dr. Steinbach's laboratory in the Vision Science Research Program at the Toronto Western Hospital, Toronto, Ontario. In addition to providing the resources for running those studies, Dr. Steinbach also gave constructive input on the two manuscripts. During the early stages of analysis, Dr. González and I worked with Dr. McNorgan to design MATLAB programs to extract certain variables from the eye movement datasets. Although those variables were not included in this thesis, his programming efforts were important for understanding the eye movement data and led to the analyses that were ultimately reported in the papers and in this thesis. Dr. McNorgan also gave feedback on the manuscripts.

In addition, three abstracts have also been published (Mueller & Timney, 2014b, 2014c; Mueller, González, McNorgan, Steinbach, & Timney, 2014). The contributions of my co-authors for these abstracts are the same for the manuscripts as described above. As stated in the Acknowledgements, we are extremely grateful to Hans Mueller for his invaluable technical assistance with experimental design and analysis, Runjie Shi for programming the MATLAB scripts that were used to calculate the peak eye velocity data, and Peter April for his help in programming all of the visual motion stimuli.

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Chapter 1

1 Introduction

The ability to detect changes in luminance is a fundamental property of any visual system. These signals that characterize the light distribution across the retina are generally well organized and thus serve as the basis for describing changes in object position in the retinal image (Lettvin, Maturana, McCulloch, & Pitts, 1959). Moreover, the first derivative of change in position with respect to time (i.e., velocity) is an invaluable source of information for the observer to know where he or she is relative to objects in the environment. For example, motion information gives the observer the ability to accomplish goal-direct activities, such as when walking or catching a falling ball. Mechanisms that have evolved to process visual motion information range from very simple systems in insects, such as Reichardt detectors (Reichardt, 1961, 1987; Reichardt & Poggio, 1979), to very complex, multiple levels of processing in humans. In primates, the first specialized motion sensitive neurons are found in the primary visual cortex (V1), where local components of motion (i.e., temporal and spatial frequencies) are processed by neurons (i.e., complex cells) with small receptive fields (Hubel & Wiesel, 1968; Priebe, Lisberger, & Movshon, 2006; Singh, Smith, & Greenlee, 2000). In addition, there are numerous areas beyond V1 that are also involved in motion processing, including but not limited to: V2, V3, V3A, V4, V5/middle temporal area (MT), the medial superior temporal area (MST), the fundus of superior temporal sulcus (FST), lateral intraparietal area (LIP), the ventral intraparietal area (VIP; Orban et al., 2003; Tolias, Smirnakis, Augath, Trinath, & Logothetis, 2001; Vanduffel et al., 2001), and the anterior superior temporal polysensory area (STPa; Anderson & Siegel, 1999). Furthermore, there are also several subcortical areas that have been implicated in motion processing, such as the pulvinar (Vanduffel et al., 2001), nucleus of the optic tract, and dorsal terminal nucleus of the accessory optic tract (Hoffmann & Distler, 1989).

With so many areas involved, it is generally accepted that there is a functional motion processing hierarchy in the primate visual system, as simpler aspects of motion are processed relatively earlier than more complex features (Andersen, 1997; Andersen,

Snowden, Treue, & Graziano, 1990; Maunsell & Van Essen, 1983; Van Essen & Gallant, 1994). In particular, although motion detectors are found in areas as early as V1, further along the visual pathway the receptive fields of these neurons increase in size and complexity, and thereby enable us to process more complex and integrated aspects of motion (e.g., form, surface, depth, and heading) in a wide range of contexts. Even so, there are parallel horizontal, feedforward, and feedback pathways that interact throughout the visual system to provide a rich perception of the world (for a review see Lamme, Supèr, & Spekreijse, 1998) and also allow for attentional modulation to enhance the perception of task-related aspects of motion in the visual image (Treue & Maunsell, 1999).

It is a complex task for the visual system to process changes in position or velocity with respect to time in the retinal image. Part of the challenge lies in the fact that the visual system must extract motion-related information from a two-dimensional retinal image of a three-dimensional world. Nevertheless, this process happens quickly (e.g., velocity discrimination performance asymptotes with stimulus presentations as brief as 150 to 200 ms, De Bruyn & Orban, 1988; Snowden & Braddick, 1991), and consequently humans are remarkably adept at perceiving visual motion. However, despite the breadth of the literature on motion perception, most studies have focused on how we perceive constant velocity and not acceleration. This is a critical gap in the literature, given that objects and observers outside the laboratory rarely move at constant velocities. For instance, when moving through the environment, people constantly speed up or slow down and make turns, automobiles regularly change their velocity, and gravity affects the motion of any object. With such variability in speed and direction, it is important to be able to detect changes to visual motion in order to accomplish voluntary goal-directed tasks, such as navigating and intercepting or avoiding objects (Braun, Schütz, & Gegenfurtner, 2010).

1.1 Acceleration Perception

The neural coding of visual acceleration may present a more complicated physiological challenge than the coding for constant velocity, because any neural mechanism involved must process progressive changes in velocity rather than a single velocity, either through

the rate of acceleration directly or through comparisons of velocity over time. Prior to physiological studies on how the primate visual system processes acceleration, a number of psychophysical studies were conducted to explore how humans perceive acceleration. The ‘direct’ hypothesis holds that there are cortical neurons in the visual system that are tuned to specific rates of acceleration in the retinal image, just as there are cortical neurons that are sensitive to specific ranges of constant velocity. The ‘indirect’ hypothesis, in contrast, proposes that humans and other primates do not have cortical neurons tuned to specific acceleration rates and, instead, velocity-sensitive neurons are recruited to signal changes in velocity over time. Hypothetically, there ought to be a mechanism that uses the population responses of those neurons to detect, integrate, and evaluate velocity variations in order to detect the presence of acceleration.

We note, however, that this nomenclature of ‘direct’ and ‘indirect’ mechanisms may be misleading, given that visual motion processing does not begin immediately at the retina in primates, but further along the visual pathway in areas such as V1 and onward. Therefore, even constant velocity is technically encoded indirectly at a cortical level because it is based on information about position-related changes from the retina. Nevertheless, the indirect hypothesis does not refer to this aspect of general motion perception. Rather, it argues that, even though constant velocity is coded explicitly at some point in the visual pathway, there may not be a mechanism that similarly codes acceleration *rate* in the same way. If this is the case, one may wonder how we are able to perceive acceleration at all if we do not have neurons that are sensitive to acceleration rate directly. The indirect hypothesis proposes that we have a mechanism responsible for signaling the presence of acceleration that somehow detects and integrates changes in velocity over time, but not the rate of change *per se*.

In general, the literature supports the indirect hypothesis. For example, Timney, Kearney, and Asa (2012) found that the ability to detect the presence of acceleration (i.e., to distinguish an accelerating stimulus from a constant velocity stimulus) does not rely on the stimulus’ rate of acceleration, but rather on the difference between its initial and final velocities. To demonstrate this, they manipulated acceleration rate by altering the middle of the motion profile. Halfway between the initial and final velocities of the accelerating

stimulus' presentation, they introduced a sudden constant velocity plateau, different acceleration rate, or deceleration rate. Hypothetically, if humans have neurons that are directly sensitive to the rate of acceleration, performance would have varied as a function of the modification of the motion profile. However, the authors found that performance was similar across conditions when the data were plotted as a function of the difference between the initial and final velocities. This suggests that an indirect mechanism is responsible for acceleration perception, and that it 'infers' the presence of acceleration (although this does not imply cognition) through changes in velocity over time.

Similarly, if we perceive acceleration through the rate of change in velocity directly, the duration of a stimulus' presentation should have little effect on detection performance (Gottsdanker, Frick, & Lockard, 1961). For instance, constant velocity discrimination performance has been reported to be relatively stable after 150 to 200 ms across a wide range of base velocities (De Bruyn & Orban, 1988; Snowden & Braddick, 1991). However, if we perceive acceleration indirectly through a mechanism that relies on detecting and integrating changes in velocity over time, a longer presentation should make it easier to detect acceleration. In other words, a faster rate of acceleration should be needed for shorter presentations in order for the difference between the initial and final velocities of the stimulus to reach the threshold of an indirect mechanism that signals the presence of acceleration. In support of the latter hypothesis, Brouwer, Brenner, and Smeets (2002), Gottsdanker et al. (1961), and Timney, Solti, and Fernando (2010) demonstrated that acceleration detection improves with longer presentations (i.e., slower acceleration rates are needed for longer durations to detect acceleration reliably). Furthermore, these authors showed that the effect of duration disappears or greatly diminishes when performance is re-plotted as a function of the relative difference between the initial and final velocities of the accelerating stimulus. These findings suggest that observers rely on the difference between the initial and final velocities to detect the presence of acceleration (at least for the brief durations tested), and we do not appear sensitive to the rate of acceleration itself.

Another compelling line of evidence supporting the indirect hypothesis comes from the abrupt velocity change detection and contiguous velocity discrimination literature. These

paradigms are useful tools for investigating the mechanisms that underlie acceleration perception because acceleration is progressive changes in velocity over time. However, instead of testing a large number of contiguously presented velocities in a single stimulus presentation, these paradigms typically test only a few distinct velocities. By using fewer but discrete velocities, the researcher can manipulate the response of different groups of neurons tuned to specific velocities. For example, in many abrupt velocity change detection paradigms (e.g., Braun et al., 2010; Hohnsbein & Mateeff, 2002), a trial typically begins with a stimulus moving at a certain constant velocity and after a specified time the stimulus abruptly increases or decreases its velocity and moves at that new velocity for a brief period, after which it returns back to its original velocity. Similar contiguous velocity presentations in velocity discrimination paradigms involve distinct velocities presented for equal durations one after the other without a temporal separation (e.g., Mateeff et al., 2000; Snowden & Braddick, 1991); in other words, the two velocities appear sequentially within the same stimulus moving in a single direction. In comparison, most constant velocity discrimination paradigms present different velocities one after the other with a temporal separation (i.e., appearing in separate intervals).

Hypothetically, the velocities tested should elicit different responses from distinct sets of neurons tuned to ranges that overlap with those speeds and directions, regardless of whether there is a temporal separation. However, performance tends to be poorer when discriminating between contiguously presented velocities than between temporally separated velocities (Snowden & Braddick, 1991; Werkhoven, Snippe, & Toet, 1992). This suggests that the visual system may use different mechanisms to identify changes in velocity depending on whether there is a temporal separation between the distinct velocities. In particular, the visual system may use a mechanism that infers a difference when the velocities are presented contiguously in a manner that is similar to that which has been suggested for how acceleration may be processed. This is because without the temporal separation the visual system has to rely on the combined population response of velocity detectors that varies with respect to time. Moreover, consistent with the above discussion on the effect of presentation duration on acceleration sensitivity, Gegenfurtner, Xing, Scott, and Hawken (2003) reported that contiguous velocity discrimination performance is better for longer (1000 ms) than shorter presentations (200 ms) of the

second velocity to which the stimulus suddenly increases or decreases from base velocity. Although Mateeff et al. (2000) found little difference in performance between contiguously and temporally separately presented velocity discrimination tasks for presentations longer than 500 ms and mean velocities above 8 deg/s, this most likely reflects the fact that constant acceleration is more difficult to perceive than two contiguously presented velocities, regardless of their presentation durations (Gottsdanker et al., 1961).

The difference in how we perceive constant and variable velocity is highlighted by the general disparity in threshold performance. Weber fractions of constant velocity discrimination thresholds tend to be extremely low, between 4 and 7 % of base velocities ranging between 4 and 64 deg/s, across a wide range of stimulus parameters (De Bruyn & Orban, 1988; Clifford, Beardsley, & Vaina, 1999; Mateeff et al, 2000; McKee, 1981; McKee & Nakayama, 1984; Orban, De Wolf, & Maes, 1984; Orban, Van Calenbergh, De Bruyn, & Maes, 1985). In comparison, Weber fractions of acceleration and abrupt velocity change detection thresholds as well as of contiguous velocity discrimination thresholds tend to be much higher (e.g., Gottsdanker et al., 1961; Hohnsbein & Mateeff, 2002; Snowden & Braddick, 1991; Werkhoven et al., 1992). For instance, Brouwer et al. (2002) reported that a minimum 25 % difference between the initial and final velocities is necessary for observers to reliably detect the presence of acceleration, although other studies have reported Weber fractions that are much larger for acceleration detection (e.g., between 40 and 80 % in Calderone & Kaiser, 1989). Moreover, Watamaniuk and Heinen (2003) showed that, when using the same accelerating stimuli, observers perform better when asked to judge which stimulus is faster than when judging which stimulus is accelerating faster. The authors suggested that one of the reasons why the mechanism underlying acceleration perception is less sensitive than the one responsible for constant velocity perception is because it must smooth or average over local variations in the responses of the velocity detectors, which should adversely affect the visual system's ability to register the stimulus' acceleration rate (or even to detect that a change in velocity has occurred).

The physiological non-human primate evidence also supports the indirect hypothesis of

acceleration perception. Despite having cortical neurons that are sensitive to velocity, the primate visual system does not appear to have neurons that are sensitive to acceleration rate in areas that process visual motion, such as MT (Lisberger & Movshon, 1999; Price, Ono, Mustari, & Ibbotson, 2005; Schlack, Kregelberg, & Albright, 2007). Instead, the findings of these neurophysiological studies suggest that velocity tuned neurons are recruited to process changes in velocity over time. For example, a velocity detector's response (i.e., firing rate) will increase progressively, then peak as the accelerating stimulus' velocity passes through that neuron's preferred velocity range, after which its response will begin to wane as the stimulus' velocity continues beyond the preferred range—Price et al. described a typical MT neuron's response to acceleration as inverted U-shaped. Although the signals of individual neurons do not code acceleration rate directly, their pooled population response to velocity changes over time, which is derived from their transient and sustained velocity tuning and adaptation, appears to constitute a mechanism to perceive acceleration indirectly.

In summary, the literature on acceleration perception has been largely devoted to establishing whether the underlying mechanism is direct or indirect, and the evidence is overwhelmingly in favour of an indirect mechanism. However, there are a number of other aspects of acceleration perception that have not been considered in any systematic way. One of these aspects is how the motion pattern characteristics of a stimulus affect how humans perceive visual acceleration, which was the purpose of this thesis.

1.2 Ecological Influences on Acceleration Perception

There are physical constraints on how we perceive motion in a natural environment. We do not see motion through a limitless expanse, but rather through spaces, such as windows, spectacle frames, computer monitors, and gaps between objects. A question that arises from this is whether the physical constraints of the visual field (i.e., the aperture, or the space through which we view a moving object) influence our sensitivity to the presence of acceleration. The size of an aperture determines the distance over which an object can travel and also for how long it remains visible. Given that presentation duration has been shown to affect acceleration perception (Brouwer et al.,

2002; Gottsdanker et al., 1961; Timney et al., 2010), the longer a stimulus is able to travel uninterrupted the better the observer should be at discerning its motion profile (i.e., that the stimulus is accelerating).

Most studies that have explored the effect of aperture size on motion perception, either with respect to abrupt velocity change detection or constant velocity discrimination, have done so under fixation (e.g., De Bruyn & Orban, 1988; Hohnsbein & Mateeff, 2002; Mateeff et al., 2000). However, the length of an aperture along the axis of motion may affect an observer's ability to track an accelerating stimulus: hypothetically, the smaller the aperture size is the more difficult it should be to track an accelerating stimulus. Moreover, it is possible that the ability to track acceleration may influence how well we can detect the presence of acceleration.

The purpose of smooth pursuit eye movements is to align the fovea with the moving target in order to reduce the amount of retinal slip in the visual image, which may provide the observer with a cleaner signal to identify progressive changes in velocity. However, there is a delay in the ocular motor feedback that is needed to correct the velocity of the eye's rotation to match the target's velocity, which changes as the target speeds up or slows down. Haarmeier and Thier (2006) have argued that this retinal slip during pursuit may in fact provide the visual system with cues that the target has changed its velocity. They tested patients with neurological disorders who tracked using saccadic pursuit and found that the patients tended to misinterpret stimuli moving at constant velocity as accelerating when tracking, but not when viewing under fixation. A consequence of tracking with saccadic pursuit is that the target continuously falls out of the foveal region and thus produces more retinal slip as compared to when tracking with smooth pursuit. As a result, Haarmeier and Thier suggested that the retinal slip during saccadic pursuit signals to the visual system that changes in velocity are occurring even when the stimulus is moving at constant velocity. Although patients tended to misperceive constant velocity as accelerating, they also showed a systematic bias in their sensitivity to positively changing velocity at the cost of being comparatively insensitive to negatively changing velocity. (However, there was no difference in sensitivity to either type of velocity change under fixation.) This was attributed to the fact that, when tracking, the target

remains on the same side of the fovea as it speeds up whereas the target will move to the other side of the fovea as it slows down. Consequently, when tracking using saccadic pursuit, larger negative velocity changes are necessary to move the target far enough to the other side of the fovea in order to create adequate retinal slip to signal that velocity is changing¹. Crucially, moreover, this difference between velocity increase and decrease detection did not appear in the psychophysical performance of observers with normal smooth pursuit. In addition, performance improved with normal smooth pursuit as compared to under fixation. Similarly, several other studies (with normal observers) have also reported that smooth pursuit improves motion sensitivity as compared to under fixation (Braun et al., 2008, Braun et al., 2010; Spering, Schütz, Braun, & Gegenfurtner, 2011; Werkhoven et al., 1992).

Although Haarmeier and Thier's (2006) data suggest that the visual system may use retinal slip to detect changes in target velocity, their findings also indicate that there may be an optimal amount of retinal slip that is necessary for detecting velocity changes reliably. (Otherwise, systematic biases emerge that produce inaccurate motion percepts, as shown in their patient data). Therefore, it might be reasonable to expect that the size of the aperture through which the observer is able to view a stimulus accelerate should not only influence how well observers are able to track that stimulus, but also how well he or she is able to detect the presence of acceleration.

Despite the fact that this method of manipulating aperture size on the axis of motion has not been investigated with respect to acceleration perception, as mentioned above several earlier studies have examined the effects of aperture size, but they have produced mixed results. Some studies report that aperture size has little effect on velocity discrimination, except at faster velocities (256 deg/s in De Bruyn & Orban, 1988, and 32 deg/s in Mateeff et al., 2000). In comparison, other studies have reported an effect of aperture size across a wider range of velocities. For instance, Hohnsbein and Mateeff (2002) presented

¹Haarmeier and Thier (2006) acknowledged that their data cannot explain whether target position relative to the fovea (i.e., ahead or behind) during pursuit informs the visual system of the sign of acceleration. Rather, their data only support the notion that it is retinal slip and not eye velocity that predominantly contributes to the perception of changing velocity during pursuit. (They found that the ability to detect velocity changes does not vary proportionally with the amount of retinal image velocity when tracking.)

random dot arrays at base velocities between 8 and 32 deg/s through a rectangular aperture orientated at 0 ° or 90 °, so that the distance that the dots traveled varied depending on whether the longer or shorter sides of the aperture lay on the axis of motion. They found that abrupt velocity change detection improved when the aperture was rotated to increase stimulus distance travelled, especially for velocity increases (the effect was only moderate on velocity decrease detection, although the asymmetry may have been due to differences in velocity range for each condition, as discussed in the section *Acceleration vs. Deceleration* below). Unfortunately for our purposes, Mateeff et al. and Hohnsbein and Mateeff presented their stimuli peripherally and under fixation, and De Bruyn and Orban presented their stimuli with durations that fell within the latency of smooth pursuit, and thus the effects observed in those studies cannot be attributed to differences in eye movements. On the other hand, Heinen and Watamaniuk (1998) found that aperture size affects smooth pursuit when tracking constant velocities, as eye acceleration increases and latency decreases as the aperture size increases for base velocities of 4 to 8 deg/s. However, the authors manipulated the vertical height of the aperture while presenting horizontally translating stimuli, and consequently the effect of aperture size was primarily attributed to differences in the number of dots in the array (i.e., more dots in larger areas) as opposed to the area *per se* restricting or encouraging pursuit.

It is therefore still an open question whether the distance over which a stimulus is able to travel influences acceleration sensitivity. Although there may be a relationship between the ability to perceive and pursue acceleration depending on distance travelled, a functional dissociation between the ocular motor and visual perceptual systems has been reported in earlier studies (e.g., Gegenfurtner et al., 2003; González, Lillakas, Greenwald, Gallie, & Steinbach, 2014; Spering & Gegenfurtner, 2007; Spering, Pomplun, & Carrasco, 2011; Tavassoli & Ringach, 2010). For the purpose of this thesis, the relevance of a functional dissociation concerns the fact that there are reports that the velocity of a stimulus has opposite effects on motion sensitivity and smooth pursuit. Specifically, sensitivity to abrupt changes in velocity tends to improve at higher velocities (Hohnsbein & Mateeff, 2002), whereas smooth pursuit worsens as velocity increases (Ke, Lam, Pai, & Spering, 2013; Meyer, Lasker, & Robinson, 1985; Schütz, Braun, Movshon, &

Gegenfurtner, 2010; Tychsen & Lisberger, 1986). To further complicate the matter, there are mixed reports on whether constant acceleration perception is affected by average velocity (e.g., Brouwer et al., 2002; Calderone & Kaiser, 1989; Gottsdanker et al., 1961; Timney et al., 2010; Watamaniuk & Heinen, 2003).

The effect of average velocity on acceleration detection may vary depending on the distance over which a stimulus is able to travel. For example, motion viewed through smaller apertures appears faster than when viewed through larger apertures (Ryan & Zanker, 2001; Snowden, 1999). This effect of aperture size on apparent speed has also been shown in the Ebbinghaus–Titchener illusion (where the size of surrounding stimuli influences the perceived size of the central object). When a dot moves in a circular aperture that is surrounded by circular objects of either larger or smaller diameters, its velocity appears faster when the perceived size of the aperture is smaller (in other words, when it is surrounded by larger objects; Pavlova & Sokolov, 2000). Therefore, if the average velocity of an accelerating stimulus affects how well an observer is able to detect the presence of acceleration, it is possible that its effect on detection may vary depending on the size of the aperture.

1.3 Vertical Acceleration Perception

Many of the aforementioned studies on motion perception have used horizontal translation, however the direction of movement within the visual image may affect acceleration sensitivity because certain directions may be more behaviourally relevant than others. Due to the energy required to overcome earth's gravitational pull, objects tend to move downward more often than they move upward in the natural world; for example, fruit growing on a tree will fall more often than it will rise into the air. Furthermore, downward motion may be more salient to the observer than upward motion, because we tend to intercept or avoid descending objects more frequently than those traveling upward. Given our asymmetrical experience with vertical motion as a result of our daily experience with gravity, it is unclear whether we have similar anisotropies in our ability to perceive vertical acceleration.

Due to the effects of gravity, when an object is thrown upward it decelerates while

moving upward until it reaches a vertical speed of zero, and then it accelerates downward at a constant rate. Similarly, motion duration discrimination has been reported to be more precise for downward than upward acceleration when consistent with the influence of gravity (Moscatelli & Lacquaniti, 2011). Moreover, Indovina et al. (2005) reported that the vestibular network selectively activates when the observer views acceleration that is consistent with the effects of gravity during a motion interception task (i.e., estimating when a falling object will hit a target). They suggested that this selective activation may reflect an internal model of gravity represented in the vestibular network that the visual system can recruit to help process input relating to visual acceleration. Expectations about the way gravity affects the vertical acceleration and deceleration of objects manifest early in life (Kim & Spelke, 1992), and the downward bias in positive acceleration sensitivity has been attributed to an experience-based adaptation in the human visual system (Moscatelli & Lacquaniti, 2011). However, it remains to be demonstrated whether we have a bias to perceive deceleration in the opposite direction.

Alternatively, Hecht, Kaiser, and Banks (1996) reported that observers rely on average velocity, as opposed to acceleration rate, to judge the distance traveled of objects in free fall. Similarly, Senot, Prévost, and McIntyre (2003) found that observers use online information about velocity, and not acceleration rate, to estimate time-to-contact for intercepting accelerating objects. Consequently, if we are relatively insensitive to acceleration on the vertical axis, perhaps vertical direction affects acceleration and deceleration detection similarly. Therefore, one might expect a general downward bias in acceleration and deceleration perception. Furthermore, if the area over which one can track improves sensitivity, there may be an interaction between vertical direction and aperture size on acceleration and deceleration detection. In other words, a difference in acceleration and deceleration sensitivity (if one exists) as a function of vertical direction may change depending on the size of the aperture.

1.4 Acceleration Perception in Optic Flow

A criticism that most psychophysical studies face is that they typically use stimuli moving linearly on the horizontal or vertical axes (i.e., translation in the fronto-parallel

plane, where all of the dots in the array move leftward or rightward) instead of more visually complex motion patterns. Although we do experience translation when we move our heads laterally or when tracking objects moving across our visual field, we also tend to see more complex forms of motion when we move through the environment because we live in a three-dimensional world. In consideration of Gibson's (1979) ecological approach to understanding visual perception, we may be 'wired' in some fashion to perceive motion better in certain kinds of stimuli than in others. Specifically, the more visually complex and realistic stimuli are, the more representative psychophysical performance should be in a laboratory setting. One type of motion pattern that meets these criteria is radial optic flow because as we move through the environment, or when objects move relative to us, we typically see visual patterns of radial optic flow. Moreover, radial optic flow is more visually complex than translation because there is simultaneous cardinal and oblique motion throughout the display. Nevertheless, it remains to be shown whether there is a difference in how we detect the presence of acceleration in radial optic flow patterns as compared to in horizontal translation patterns. Studies that have investigated the effect of motion pattern type on motion perception in general (although not with respect to visual acceleration perception) have produced conflicting results (e.g., Bex & Makous, 1997; Bex, Metha, & Makous, 1998; Edwards & Badcock, 1993; Edwards & Ibbotson, 2007; Freeman & Harris, 1992; Lee & Lu, 2010).

Another aspect of radial optic flow that may influence acceleration perception is direction because it is associated with visual heading. Specifically, when moving forward we tend to see radial expansion (i.e., features moving away from the centre of the visual field toward the periphery) and when traveling backward we see radial contraction (i.e., features moving from the periphery toward the centre of the visual field). Interestingly, both expanding and contracting optic flow can elicit impressions of self-motion even in the absence of vestibular or proprioceptive input (Brandt, Dichgans & Koenig, 1973; Palmisano, Allison, & Pekin, 2008). Although there are mixed reports as to whether there is a difference in sensitivity to expanding and contracting motion (e.g., Beardsley & Vaina, 2005; Bex et al., 1998; Edwards & Badcock, 1993; Edwards & Ibbotson, 2007; Geesaman & Qian, 1998; Meese & Anderson, 2002; Shirai, Kanazawa, & Yamaguchi, 2006), a radial anisotropy in acceleration sensitivity has not been reported.

Even though direction of optic flow informs the observer about his or her motion relative to the environment, a critical point of information about heading comes from the focus of optic flow. In particular, heading discrimination has been reported to be better when optic flow is presented in the centre of the visual field than in the periphery as well as when the focus of optic flow is near the fovea (Warren & Kurtz, 1992). Similarly, although Crowell and Banks (1993) observed that heading sensitivity is more affected by the eccentricity of the focus of optic flow than where the optic flow field is located on the retina, they too reported that sensitivity is higher when the focus of optic flow is near the fovea. This in turn raises the question of whether observers rely more on the centre of the optic flow field than the periphery to detect the presence of acceleration.

1.5 Acceleration Versus Deceleration

A feature of acceleration is that it can be positive or negative. Although one might assume that there should be little difference in how we perceive positively and negatively changing velocity, the evidence is inconsistent (e.g., Gottsdanker, 1961; Gottsdanker et al., 1961; Hick, 1950; Hohnsbein & Mateeff, 2002; Laldin, Wilcox, Hylton, & Allison, 2012; Schlack, Kregelberg, & Albright, 2008; Träschütz, Zinke, & Wegenger, 2012; Trehwella, Edwards, & Ibbotson, 2003). To test whether there is a difference in how we perceive acceleration and deceleration, we used an acceleration detection paradigm in this thesis that is similar to the paradigms used by Brouwer et al., (2002), Calderone and Kaiser (1989), and Gottsdanker et al. (1961), which controls for the possibility that acceleration and deceleration detection might differ because the velocity ranges for each condition are not the same (Figure 1). Specifically, we held the average velocity constant between the acceleration and deceleration conditions (see Figure 1C and *Equation 1* in Chapter 2: *General Psychophysical Method*). In every trial participants viewed a stimulus moving at constant velocity and another stimulus that was accelerating/decelerating, and they had to indicate which of the two was accelerating/decelerating. This is a well-established method of assessing acceleration perception.

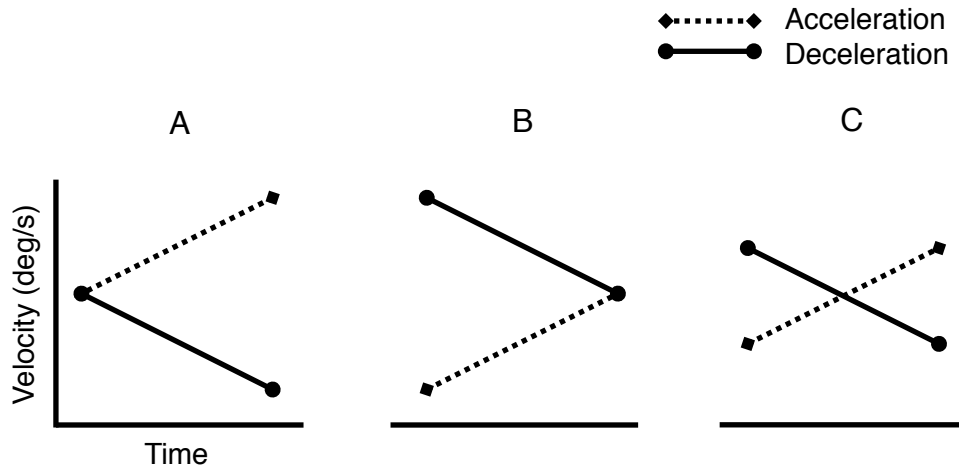


Figure 1. Schematic examples of some methods of presenting accelerating and decelerating stimuli by holding initial (A) or final (B) velocities constant or average velocity constant (C). Note that the sizes of these acceleration and deceleration rates are exaggerated for ease of visual comparison.

1.6 Summary of Experiments

One of the goals of this thesis was to explore how the ability to detect the presence of acceleration is affected by physically constraining the distance over which a random dot stimulus can travel. We did this by manipulating the size of the aperture on the axis of the stimulus' motion. In particular, we varied the aperture's horizontal distance for horizontally accelerating and decelerating stimuli in Experiment 1 and its vertical height for vertically accelerating and decelerating stimuli in Experiment 3. We hypothesized that larger apertures would encourage smooth pursuit and improve acceleration and deceleration detection, whereas smaller fields would restrict smooth pursuit and worsen detection. To test whether the size of the aperture does affect the ability to track, we conducted control experiments in which we measured the effects of aperture size on smooth pursuit on the horizontal and vertical axes in Experiments 2 and 4, respectively.

Due to the mixed reports of an effect of average velocity on acceleration sensitivity, we had no hypotheses as to whether acceleration and deceleration sensitivity would improve as average velocity increases, although we anticipated that smooth pursuit should worsen

as average velocity increases. Nevertheless, we expected that sensitivity and smooth pursuit should improve as the size of the aperture increases, regardless of average velocity. Using horizontal translation, in Experiments 1 and 2 we manipulated the average velocity of the acceleration and deceleration conditions for various horizontal aperture distances. Experiment 1 measured acceleration and deceleration detection accuracy, and Experiment 2 was a control experiment designed to determine whether the aperture size manipulation varies how observers pursue acceleration and deceleration as a function of average velocity.

In Experiment 3, using vertically translating random dot stimuli, we tested two alternative hypotheses with respect to the effects of vertical direction and sign of acceleration on acceleration detection as a function of vertical aperture height. First, it is possible that the visual system is sensitive to the effects of gravity and thereby also to the sign of acceleration as a function of vertical direction. If this is the case, we should detect downward acceleration and upward deceleration better than upward acceleration and downward deceleration. On the other hand, such a degree of sensitivity needed to distinguish between vertical acceleration and deceleration may be an inefficient use of resources, considering that we do not appear to be particularly sensitive to the rate of acceleration in the first place. The second hypothesis holds that the downward bias in detection persists regardless of the sign of acceleration. Both hypotheses are consistent with the idea of an experience-based adaptation and each would predict acceleration and deceleration detection to improve as the area over which one is able to pursue the moving stimuli increases. If the ability to detect acceleration and deceleration is better over larger than smaller areas, the effect of aperture size may alter the strength of the asymmetry (if it exists) between the acceleration and deceleration conditions as a function of vertical direction. Experiment 3 measured the effects of vertical direction, aperture size, and sign of acceleration on acceleration detection accuracy. Experiment 4 was a control experiment to test whether the height of the vertical aperture varies smooth pursuit of vertical acceleration and deceleration.

Although Experiments 1 and 3 tested the influence of aperture size, average velocity, and translational direction on acceleration and deceleration perception, another question was

whether our sensitivity to acceleration varies as a function of the type of motion pattern viewed. Several earlier studies on optic flow perception used radially moving random dot stimuli that were designed to mimic a three-dimensional experience in order to increase the ecological validity of the task (e.g., Figure 2). In other words, those stimuli tended to contain dot speed, size, and density gradients (i.e., the speed, size, and density of the dots change as a function of eccentricity from the centre of the visual field). However, dots in translating stimuli do not contain gradients in these dot parameters as a function of location within the display. The problem with designing optic flow stimuli in this way when comparing sensitivity to radial and horizontal motion is that there are mixed reports that stimulus size, velocity, and density may affect motion sensitivity in general (e.g., De Bruyn & Orban, 1988; Edwards, Badcock, & Smith, 1998; Edwards & Ibbotson, 2007; Giaschi, Zwicker, Young, & Bjornson, 2007; Gray & Regan, 1999; Habak, Casanova, & Faubert, 2002; Khuu & Badcock, 2002; Hohnsbein & Mateeff, 2002; Whitaker, McGraw, & Pearson, 1999). Consequently, in Experiment 5, we held the parameters relating to dot size, motion profile, and average density constant across the visual field in our horizontal and radial motion displays to investigate the effect of motion pattern type on acceleration and deceleration detection. Although this level of control came at an expense of the realism of our optic flow stimuli, it was necessary in order to establish whether the motion pattern itself affects acceleration perception. Moreover, an advantage of holding dot size and average density constant is that the observer cannot distinguish which stimulus belongs to which condition based on a single frame.

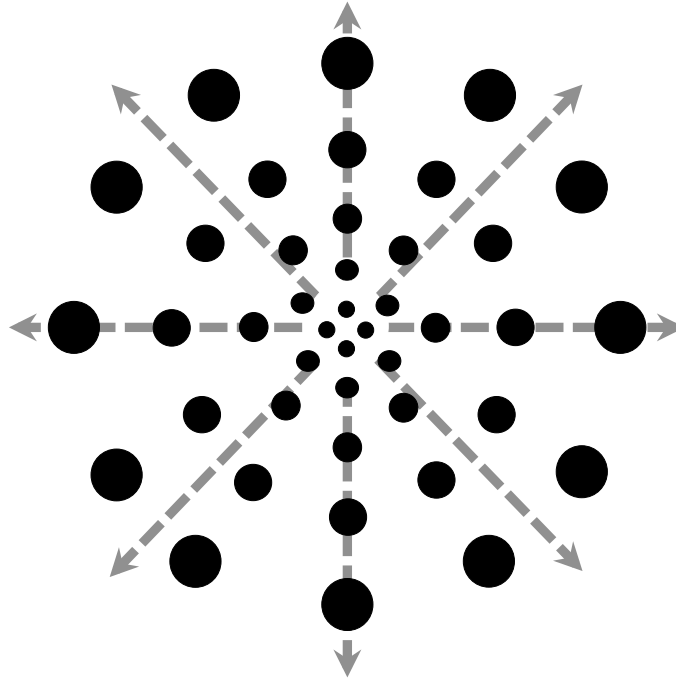


Figure 2. Schematic example of radial optic flow with dot size and density varying as a function of eccentricity from the focus of expansion. Grey dashed lines signify direction of motion.

As radial anisotropies have yet to be reported for acceleration or deceleration detection, in Experiment 5 we also manipulated the direction of the radial and horizontal motion patterns to see whether the effect of pattern type is modulated by the effect of motion direction. Although we did not anticipate a difference between leftward and rightward motion, we tested horizontal direction as a methodological control. In Experiment 6 we varied the location (i.e., eccentricity) of the optic flow field while participants fixated the middle of the display so that the optic flow pattern fell either on the central or peripheral area of the retina. We used this manipulation to determine whether sensitivity to the presence of acceleration in radially expanding and contracting motion is uniform across the visual field. In addition, we held dot size, motion profile, and average density constant throughout the visual field in Experiment 6 in consideration of the possible confounding effects of each factor as discussed above.

Chapter 2

2 General Methods

There are two types of studies reported in this thesis: psychophysical and eye tracking. The experiments within each category used the same general methodology. In this chapter, the general psychophysical methodology is outlined first, followed by the general eye tracking methodology. Each of the subsequent chapters that describe an individual experiment includes a Method section with the methodological particulars.

2.1 General Psychophysical Method

Experiments 1, 3, 5, and 6 (in Chapters 3, 4, 5, and 6 respectively) tested acceleration detection accuracy with a two-interval forced choice (2IFC) task using the psychophysical method of constant stimuli. These experiments were conducted at the University of Western Ontario, London, Ontario, in accordance with the guidelines and regulations of the university's Research Ethics Board. Participants volunteered or were reimbursed up to \$40 for travel expenses in Experiments 1 and 3, and they were paid \$20 in Experiment 5 and \$10 in Experiment 6.

2.1.1 Participants

All participants had normal or corrected-to-normal visual acuity and stereoacuity with no known visual or ocular motor disorders (e.g., strabismus or amblyopia) and no history of eye muscle surgery or patching. Visual acuity and stereoacuity were measured using a Master Ortho-Rater (Bausch and Lomb, Rochester, NY), and stereoacuity was further assessed using the Randot® StereoTest (Stereo Optical Co., Inc., Chicago, IL).

Participants wore their normal optical correction if necessary.

2.1.2 Stimuli and Apparatus

Stimuli were created and presented using VPixx software (version 2.87 in Experiments 1 and 3, and version 3.14 in Experiments 5 and 6; VPixx Technologies Inc., Saint-Bruno, Quebec, Canada) on a 51.5 cm LaCie electron22blue II CRT monitor (Mitsubishi Electric Corporation, Japan) with a 120-Hz refresh rate and a resolution of 1024 x 768 pixels (one

pixel was 0.001°). The stimuli were continuously (and 100 % coherently) moving random dot arrays of white dots (96.7 cd/m^2) on a black background (0.06 cd/m^2) through a simulated, invisible stationary aperture (i.e., the border of the aperture was not visibly defined and dots disappeared when they left the aperture area). Dot position was updated every frame and dot lifetime was unlimited. Dot size, average density, and velocity/acceleration/deceleration were constant across the aperture in every condition within an experiment, although the dot parameters varied between experiments. Every aperture through which the random dot arrays were presented was centered in the middle of the screen. Aperture size and shape were specific to each experiment.

Two types of motion patterns (on a 2-D surface) were tested in this thesis: translation (horizontal and vertical) and radial optic flow (expansion and contraction). At the start of every stimulus' presentation, a set of dots was generated and placed at (average) uniformly distributed random positions in the frame. Within each subsequent frame, the dots were displaced by the same amount, which corresponded to the stimulus' speed divided by the frame rate. For the horizontally (Experiments 1, 2, and 5) or vertically moving stimuli (Experiments 3 and 4), all of the dots moved in the same direction. For the expanding or contracting stimuli, the direction of displacement depended on the dot location in the stimulus; specifically, dots were displaced in a direction along the vector from the centre (or periphery) of the stimulus to their current position. This resulted in all of the dots streaming outward (for expansion) or inward (for contraction) from the centre of the display; however, there were no spatial speed or density gradients in the arrays. Every dot's speed increased or decreased over the course of the presentation according to the acceleration rate for that particular trial.

For the experiments using horizontal or vertical translation, dots were replaced in random locations along the border of the aperture opposite to the direction of motion when they disappeared outside the visible area. In other words, the horizontally and vertically translating random dot arrays moved in a 'wrap around' fashion from behind the stationary apertures to present continuous motion while holding average dot density constant. For the experiments testing radial motion, when a dot reached the boundary (or centre) of the aperture, it was replaced in an area of the display that contained the lowest

dot density in order to keep average dot density uniform in every frame. Specifically, the VPixx program partitioned the optic flow field into eight uniformly spaced eccentricities and eight uniformly spaced meridians (resulting in 45 ° intervals). This produced 64 truncated annuli that were centred on the focus of expansion/contraction, which was located in the centre of the display. For a given frame, VPixx calculated the instantaneous dot density within each of these annuli and then calculated a low-pass filtered time-averaged density that was equal to half of the instantaneous density plus half of the previous frame’s time-averaged density. Whenever a dot reached the border of the aperture, it was replaced by a new one at a random location within the truncated annulus that had the lowest time-averaged density. Several earlier studies have used similar radial motion stimuli (e.g., Morrone et al., 2000; Smith, Wall, Williams, & Singh, 2006; Wall & Smith, 2008). These methods of presenting radial and horizontal motion meant that each individual frame was indistinguishable between the horizontal and radial motion stimuli.

Every experiment (including the eye movement experiments) presented both acceleration and deceleration, with the exception of Experiment 6, which only presented acceleration. Regardless of the sign of acceleration presented, the motion profile of every dot was calculated using the following formula:

$$velocity = v_{middle} + a * \left(t - \left(t_{duration}/2 \right) \right), \quad (1)$$

where v_{middle} represents the middle velocity (i.e., the midpoint velocity between the initial and final velocities of every stimulus, which defined the velocity range), a is the positive or negative acceleration rate, t refers to time, and $t_{duration}$ is the total stimulus presentation duration (which was constant for every experiment at 750 ms). The average velocity of the stimuli was the same as the middle velocity in *Equation 1*. As these experiments measured acceleration and deceleration detection accuracy, in every trial there was always a standard stimulus that moved at constant velocity, which was defined by the average velocity of a given condition. Another consideration for our method of holding average velocity constant between the standard and comparison stimuli is that both stimuli traveled the same distance for the acceleration and deceleration rates and average velocities tested in this thesis. Therefore, participants could not judge which stimulus was

accelerating or decelerating based on the distance travelled within each trial, which was essential for our manipulation of aperture size. In addition, the initial and final velocities of an array were constant for a given rate of acceleration across aperture sizes within each velocity range tested.

2.1.3 Procedure

Every psychophysical experiment used a 2IFC task with the method of constant stimuli, in which there were 7 rates of acceleration and deceleration for the comparison stimuli for each condition (with the exception of Experiment 6, which only tested positive acceleration). A standard stimulus (constant velocity) and a comparison stimulus (acceleration/deceleration) were presented in random order in every trial. The task was to detect which stimulus was accelerating/decelerating.

Participants were always tested in the dark and viewed the screen binocularly from a distance of 60 cm, using a chin rest to minimize head movements. At the beginning of every trial a red fixation target with the shape of a 0.5° diameter crosshair against a black background was presented for 500 ms. We chose this fixation target shape because Thaler, Schütz, Goodale, and Gegenfurtner (2013) reported it to be the most effective in producing stable fixation. To control initial eye position participants were told to fixate the crosshair target at the beginning of every trial until the random dot stimuli were presented (during which they were free to move their eyes), with the exception of Experiment 6 where participants were told to keep fixating the centre of the screen even after the fixation target had disappeared. The fixation target then disappeared and was followed immediately by either the standard or comparison stimulus for 750 ms, followed by a black screen for 500 ms, and then the standard or comparison stimulus for another 750 ms. Participants were asked to identify whether the first or the second display accelerated (or decelerated) and they indicated their decision by pressing a key on a keyboard. Trials were self-paced, initiated by pressing the spacebar. An audible beep followed all key and spacebar presses.

In Experiments 1 and 3, acceleration and deceleration trials were always presented in separate blocked conditions. Within each acceleration and deceleration condition, trial

runs were blocked further according to experimental condition. The order of the acceleration and deceleration blocks was counterbalanced across participants. In Experiment 5, acceleration and deceleration were randomly interlaced across trials. Experiment 6 only presented accelerating stimuli. The order of the conditions and the stimulus values within each condition were always randomized in every experiment. In Experiments 1 and 3, direction within each condition (aperture size by average velocity in Experiment 1, and aperture size in Experiment 3) was randomized. In Experiments 5 and 6, direction was blocked into separate conditions. Direction was analyzed in Experiments 3, 5, and 6, but not in Experiment 1. Participants always completed one condition at a time.

Participants were given practice trials prior to beginning the experimental task, and the minimum number of practice trials varied between experiments. Every psychophysical experiment had a minimum number of 20 experimental trials per stimulus value per condition (with the exception of Experiment A2 in Appendix A which had a minimum of 10 trials). However, the maximum number of experimental trials per stimulus value included for each condition varied because it was based on the number of trial runs needed to obtain psychometric functions with non-significant Pearson Chi-square coefficients of goodness of fit per participant, as described below. The only exception to this was Experiment 5. All observers reported that the task in Experiment 5 with acceleration and deceleration randomly interlaced was quite difficult. Most individuals said that they tended to expect either acceleration or deceleration, but not both—even though the task instructions indicated that both would be presented at random throughout the experiment. Nonetheless, with enough practice participants began to perform reliably. Consequently, due to performance variability, in Experiment 5 we included only the last two runs (total of 20 trials per stimulus value per condition) for the analysis that, when combined, met the inclusion criterion of goodness of fit. Participants were not given feedback during the experimental task.

2.1.4 Analysis

SPSS Statistics software (IBM Corporation, Armonk, NY) was used to analyze the data. The number of correct responses for each stimulus value within each condition was plotted in terms of proportion correct as a function of acceleration or deceleration rate. Probit regression was used to get psychometric functions with non-significant Pearson coefficients of goodness of fit (as determined through Chi-square analyses) and to interpolate the 75 % correct threshold acceleration/deceleration rate for each condition.

In order to compare performance in the psychophysical experiments of this thesis to that of earlier studies, the absolute 75 % correct detection threshold rates were transformed into values that were functionally equivalent to Weber fractions. We could not transform the thresholds using the acceleration rates directly because the standard stimulus was always a pattern moving at constant velocity and therefore with an acceleration rate of zero. Using the standard equation to calculate the Weber fraction ($\Delta A/A$) would result in a denominator of zero and so the fraction could not be calculated. Instead, we performed a linear transformation to express the acceleration threshold rate in terms of the difference between the minimum and the maximum velocities (v_{\min} and v_{\max}) divided by the velocity of the standard stimulus (i.e., the average velocity of the accelerating or decelerating stimulus). In other words, the transformed thresholds represent the threshold percent difference between the maximum and minimum velocities of the comparison stimulus relative to the velocity of the standard stimulus needed to detect the presence of acceleration or deceleration. This method of transforming acceleration detection thresholds has been reported before (e.g., Brouwer et al., 2002; Calderone & Kaiser, 1989; Gottsdanker et al., 1961). We used the following equation:

$$\text{transformed threshold} = \left(\frac{(v_{\max} - v_{\min})}{((v_{\max} + v_{\min})/2)} \right) 100. \quad (2)$$

The transformed threshold data were analyzed using repeated-measures ANOVAs. In the event that the data were non-spherical, the Greenhouse-Geisser correction was used. All pairwise comparisons were performed using the Holms-Bonferroni correction with α at

0.05. Although the transformed thresholds were of primary interest, in every psychophysical experiment the mean absolute 75 % correct acceleration and deceleration detection threshold rates are presented in tables. We note that statistical analyses revealed the same results for the absolute and transformed threshold datasets because the transformation was linear. The only exception to this was Experiment 1, which tested different average velocities and therefore large differences in absolute thresholds were to be expected (as discussed in Chapter 3).

2.2 General Eye Tracking Method

The purpose of the eye tracking experiments in this thesis was to serve as a control to test whether the ability to pursue an accelerating or decelerating random dot array varies depending on the aperture size on the horizontal and vertical axes. Experiments 2 and 4 investigated smooth pursuit using a single stimulus presentation method. Both experiments were conducted at the Toronto Western Hospital, Toronto, Ontario, in accordance with the guidelines and regulations of the University of Western Ontario and the University Health Network's Research Ethics Boards. The data from Experiments 2 and 4 were collected during the same testing session. The order of experiments was counterbalanced across participants. Participants were reimbursed for travel expenses up to \$40.

2.2.1 Participants

Five volunteers (including author ASM) participated in both Experiments 2 (horizontal eye movements) and 4 (vertical eye movements), having also previously participated in the psychophysical Experiments 1 (horizontal motion) and 3 (vertical motion). These five individuals had an average age of 25.6 years ($SD = 1.52$) and four were female.

2.2.2 Stimuli and Apparatus

The random dot stimuli and conditions were the same between each psychophysical and corresponding eye tracking experiment. The luminance of the white dots was 88.3 cd/m^2 and the black background was 3.1 cd/m^2 . As with the psychophysical experiments, the stimuli for Experiments 2 and 4 were created and generated using the VPixx program

(version 2.87) on a 45 cm Samsung monitor (Sync Master 900 NF; Samsung, Seoul, South Korea), with a 120-Hz refresh rate and 1024 x 768 pixel resolution. The MacBook Pro laptop used to run the VPixx program was connected to a desktop remote video-based EyeLink 1000 eyetracker (SR Research Ltd., Mississauga, Ontario, Canada) through the eye tracker's host computer using a DATAPixx interface (VPixx Technologies Inc., Saint-Bruno, Quebec, Canada). The DATAPixx interface recorded time and stimulus condition information in the data files. Eye position was recorded with the eye tracker with a sampling rate of 250-Hz. The eye tracker was calibrated for every participant prior to the experimental task using its software's standard calibration and validation procedures.

2.2.3 Procedure

Participants were tested at a 60 cm viewing distance in an illuminated room, viewing binocularly, and sitting with their head (chin and forehead) resting against a headrest. A single motion stimulus was presented in every trial. Trials were initiated automatically and began with a red 0.5 ° diameter crosshair fixation target on a black background for 1000 ms, followed immediately by an accelerating or decelerating stimulus presented for 750 ms. Another trial followed immediately. The participants were instructed to fixate the crosshair target at the beginning of every trial and then to track the moving stimulus and try to determine if the motion was accelerating or decelerating (in order to keep participants focused on the task), however no verbal or key press responses were required. Acceleration and deceleration trials were randomly presented within each condition. Order of conditions (aperture size by average velocity in Experiment 2, and aperture size in Experiment 4) and direction within each condition was randomized. There were 10 trials for each stimulus value per condition. Participants completed one condition at a time.

The stimulus values used in Experiments 2 and 4 were based on the absolute 75 % correct detection threshold rates in Experiments 1 and 3, respectively. Three values were used for each condition in each eye movement experiment. The first stimulus value was the acceleration/deceleration rate that corresponded to the absolute 75 % correct detection

threshold rate obtained in the corresponding condition in the psychophysical experiment. The second and third rates were 50 % and 100 % greater than the 75 % correct detection threshold rate, respectively, in order to have a range of stimulus values to measure observers' smooth pursuit in response to acceleration and deceleration. The three stimulus values tested in every condition were unique to each participant. We note, moreover, that smooth pursuit performance was similar between the three rates tested within each condition for Experiments 2 and 4.

2.2.4 Smooth Pursuit Analysis

The eye movement data were analyzed offline, and saccades, fixations, and blinks were removed from the data prior to analysis of smooth pursuit. Saccades were identified using the standard EyeLink saccade detection algorithm, with a combined criterion of eye velocity > 22 deg/sec and eye acceleration > 4000 deg/sec² (saccades were analyzed separately from the smooth pursuit data). In the event of a blink, the data corresponding to 100 ms before and 100 ms after the initial occlusion of the pupil were removed (Aguilar & Castet, 2011).

We analyzed smooth pursuit in terms of peak eye velocity and eye position traces. The reason why we analyzed peak eye velocity, despite having presented continuously accelerating stimuli, is because data are lost through the filtering process used to calculate the second derivative (which is also susceptible to noise). Moreover, the aim of using the measure of peak velocity is to see whether it varies as a function of experimental condition, and a similar pattern would be expected to emerge for peak acceleration. Schwartz and Lisberger (1994) reported that brief speed perturbations are more effective in eliciting a matching response in eye velocity during pursuit on the axis of the stimulus' motion as compared to on the orthogonal axis, whereas they are minimally effective when viewing under fixation. Similarly, if the size of the aperture or the average velocity of the stimulus influences the ability to track acceleration or deceleration, the peak velocity of the eye should correspondingly be affected. Specifically, we expected higher peak velocities when participants could track easily (i.e., for larger apertures than for smaller apertures) and when viewing faster stimuli. The examination of the eye position

traces allowed us to understand the peak velocity data. An advantage with investigating eye position with respect to time is that, because the eye tracker records eye position over time, this method has no data loss. Furthermore, by plotting the traces of eye position against stimulus position, we obtained interesting results with respect to eye trajectory and location within the visual field, which would not have been evident if we had only analyzed peak eye velocity. Only eye movements (of the right eye) made in the direction of the stimulus motion are reported.

2.2.4.1 Peak eye velocity analysis. Peak velocity of the right eye during epochs of uninterrupted smooth pursuit was calculated using a custom MATLAB (MATLAB, Mathworks, Natick, MA) script that used a 5-point differentiator. The program approximated the first derivative of eye position with respect to time (i.e., eye velocity) through the 5-point stencil method (*Equation 3*, where x is eye position and h is the spacing between eye positions):

$$f'(x) = \frac{-f(x + 2h) + 8f(x + h) - 8f(x - h) + f(x - 2h)}{12h} \quad (3)$$

First we calculated the peak eye velocity for every uninterrupted epoch of smooth pursuit. Then, we created a weighted average of all of the peak velocities (taking into account the number of data points that contributed to each peak velocity value) that occurred for a particular stimulus value within an experimental condition. (Recall that there were three stimulus values, i.e., acceleration or deceleration rates, per condition.) Finally, we averaged those weighted average values in order to obtain a measure of mean weighted average peak eye velocity for each condition per participant. We submitted the mean weighted average peak eye velocities to repeated measures ANOVAs, using the Greenhouse-Geisser correction if necessary and the Holms-Bonferroni correction with α at 0.05 for all pairwise comparisons. As an aside, although one might wonder whether these data reflect the maximum velocities of the stimuli tested, the peak eye velocities reported in Experiments 2 and 4 are much higher than any of the peak stimulus velocities.

2.2.4.2 Analysis of eye and stimulus position traces. As random dot arrays were used in every experiment, it was not possible to determine which dot (if any) participants tracked.

Therefore, after obtaining the stimulus velocities for every time point using *Equation 1*, we calculated stimulus position using *Equation 4*²:

$$position_{i+1} = position_i + velocity_i (t_{i+1} - t_i). \quad (4)$$

We set the initial position of the stimulus to the initial position of the right eye at the beginning of every epoch of uninterrupted smooth pursuit, because all of the dots within the array accelerated or decelerated at the same rate across the visual field. For the cases in which the initial eye position occurred outside the area of the aperture, we set the stimulus' initial position at the boundary of the aperture closest to the initial eye position in order to keep the stimulus motion restricted to the aperture area. Whenever the stimulus reached the edge of the aperture in the direction of motion, it was reset to the opposite side of the aperture for the subsequent time point. This reset method for the instances in which smooth pursuit was interrupted by either a saccade or a blink avoids the issue of stimulus positions depending on the number and accuracy of saccades. Examples of this analysis are shown in Experiments 2 and 4.

2.2.5 Saccade Analysis

In addition to smooth pursuit eye movements, we also explored saccadic eye movements (of the right eye only). There were two types of saccades: regressive saccades (in the opposite direction of stimulus motion) and catch-up saccades (in the direction of stimulus motion). Prior to analysis, we removed all the saccades that occurred during the pre and post-100 ms of the initiation of a blink as well as during the first 200 ms of the stimulus presentation; that is, during initiation of pursuit from fixation (Krauzlis, 2004; Lisberger,

² The eye tracker sampled at 250-Hz whereas the CRT monitor refreshed at 120-Hz. Given that we calculated stimulus velocity and position values at 250-Hz in order to compare eye and stimulus position traces, we explored the error between the sampling rates in our estimation of stimulus position because it was calculated at a faster sampling rate than the actual monitor's refresh rate. We calculated the stimulus' final position for the largest acceleration/deceleration rates tested for each average velocity in Experiments 2 and 4 at sampling rates of 10,000, 1,000, 500, 250, 120, and 60-Hz. Hypothetically, if error was being introduced as a function of sampling rate we should see the impact of the error best in the final position (where it should be highest). Results indicate that the error was negligible; for example, the difference was less than 0.5 ° between 10,000 and 60-Hz. Therefore, we conclude that the difference between the sampling rates of 250 and 120-Hz has little impact on our method of calculating stimulus position.

Morris, & Tychsen, 1987; Westheimer, 1954). Due to the complexity of the experimental designs and the low number of saccades overall, it was not possible to conduct non-parametric statistical analyses. Therefore, we visually explored regressive and catch-up saccades in terms of number per trial and amplitude as a function of the experimental conditions.

Chapter 3

3 Effects of Aperture Size and Average Velocity

Experiment 1 was designed to investigate whether physically constraining the distance over which a stimulus can travel influences the ability to perceive acceleration. We anticipated that the distance traveled should also affect how well the observer is able to track the moving stimulus (Experiment 2), which in turn should be related to the effect of aperture size on psychophysical performance because there are reports that smooth pursuit can improve motion sensitivity (e.g., Braun et al., 2008; Braun et al. 2010; Haarmeier & Thier, 2006; Spering, Schütz, et al., 2011; Werkhoven et al., 1992). In the present series of experiments we manipulated distance traveled by varying the horizontal extent of the aperture through which we presented horizontally accelerating and decelerating random dot arrays, and we also explored the effect of average velocity on acceleration sensitivity. In Experiment 1 we measured acceleration and deceleration detection accuracy as a function of aperture size and average velocity. Experiment 2 was a control experiment to determine whether the size of the aperture varies how well observers can track accelerating and decelerating stimuli as a function of velocity.

We hypothesized that acceleration and deceleration detection would improve as the size of the aperture increases at both slower and faster average velocities in Experiment 1. Although Hohnsbein and Mateeff (2002) reported that abrupt velocity change detection improves as velocity increases, studies on constant acceleration perception, such as Brouwer et al. (2002), have reported mixed findings for the effect of velocity depending on the task and whether thresholds are reported as absolute or relative (i.e., $\Delta v_{\text{final-initial}}/v_{\text{average}}$). Although we expected large differences in absolute thresholds between the two velocity ranges as a simple consequence of Weber's Law, we had no hypotheses as to whether performance would change as a function of average velocity once the thresholds were transformed into values that were functionally equivalent to Weber fractions (see *Equation 2* in Chapter 2: *General Psychophysical Method*). Moreover, as we held average velocity constant between the acceleration and deceleration conditions, we predicted that observers should be equally sensitive to the presence of acceleration

and deceleration within each experimental condition. Finally, in Experiment 2, we anticipated that smooth pursuit should improve as aperture size increases but worsen as average velocity increases.

3.1 Experiment 1

3.1.1 Method

3.1.1.1 Participants. The sample comprised of nine volunteers (including author ASM) with an average age of 25 years ($SD = 2.35$). Two additional participants (not included in the sample N) were recruited but were unable to do the task reliably and therefore removed from the study.

3.1.1.2 Stimuli and apparatus. Horizontally moving random dot arrays (leftward and rightward) were presented in three conditions of horizontal aperture size subtending 1° , 14.3° , and 27.5° . The vertical height of the apertures was held constant at 1° to discourage vertical eye movements. Dot size ($0.15^\circ \times 0.15^\circ$) and average density (1.5 dots/deg²) were held constant across all conditions. Two middle/average velocities were tested using *Equation 1* (Chapter 2: *General Psychophysical Method*): 2.04 deg/s (slower) and 10.2 deg/s (faster). Horizontal direction was randomized across trials and not analyzed.

3.1.1.3 Procedure. There were seven rates of acceleration or deceleration in the comparison stimuli for each condition and the same range of rates was used for every participant. The acceleration rates were in steps of 0.66 deg/s² from 0.66 to 4.64 deg/s² in the slower velocity range and were in steps of 1.53 deg/s² from 1.53 to 10.71 deg/s² in the faster velocity range. Deceleration rates were the same except with a negative sign. The standard stimuli moved at constant velocity, which was set at the average velocity of a given condition (i.e., 2.04 deg/s for the slower condition and 10.2 deg/s for the faster condition).

Participants performed at least 360 practice trials prior to the beginning of the experiment. For each participant, there were between 20 and 80 experimental trials per stimulus value included in the analysis of each condition, depending on the combined

number of trial runs needed to obtain non-significant Pearson goodness of fit coefficients for the probit regression used to interpolate threshold rates. Stimulus conditions were defined by aperture size (small, medium, and large) and velocity range (slower and faster) for each block of acceleration and deceleration.

3.1.2 Results

Table 1 shows the mean absolute 75 % correct acceleration and deceleration detection threshold rates. We note that the same pattern of effects emerged in the absolute and transformed data, with the exception of the effect of average velocity. Absolute thresholds are higher for faster velocities than for slower velocities, however this is to be expected given Weber's law. The transformed threshold data (see Chapter 2: *General Psychophysical Method* for detail on the transformation method) were analyzed using a 3(aperture size) x 2(average velocity) x 2(sign of acceleration) repeated measures ANOVA.

Table 1

Mean absolute 75 % correct acceleration and deceleration detection threshold rates (deg/s²) as a function of aperture size and average velocity

		Acceleration rate	Deceleration rate
Average velocity	Aperture size	<i>Mean (SD)</i>	<i>Mean (SD)</i>
Slower	Small	2.04 (0.62)	2.06 (0.45)
	Medium	1.88 (0.60)	1.75 (0.41)
	Large	1.89 (0.75)	1.78 (0.50)
Faster	Small	6.25 (2.04)	6.62 (2.02)
	Medium	5.01 (2.00)	5.31 (1.53)
	Large	4.60 (1.76)	5.41 (1.64)

Results indicate that transformed thresholds decrease as aperture size and average velocity increase, although there is no difference between medium and large apertures in either velocity condition. There is no difference in performance between the acceleration and deceleration conditions. Statistical analysis confirmed that there is a main effect of aperture size, $F(1.96, 15.71) = 13.25, p < .001, \eta^2_p = 0.62$: thresholds for small apertures are higher than for medium, $t(8) = 4.42, p < 0.05$, Cohen's $d = 1.47$, and large apertures, $t(8) = 4.26, p < 0.05$, Cohen's $d = 1.42$, but there is no difference between medium and large apertures, $t(8) = 0.13, ns$. There is also a main effect of average velocity, $F(1, 8) = 102.11, p < .001, \eta^2_p = 0.93$, with thresholds decreasing as velocity increases.

Acceleration and deceleration detection thresholds are not different in any condition, $F(1, 8) = 0.02, p = 0.90$. In addition, there are no interactions between the experimental variables (Figure 3).

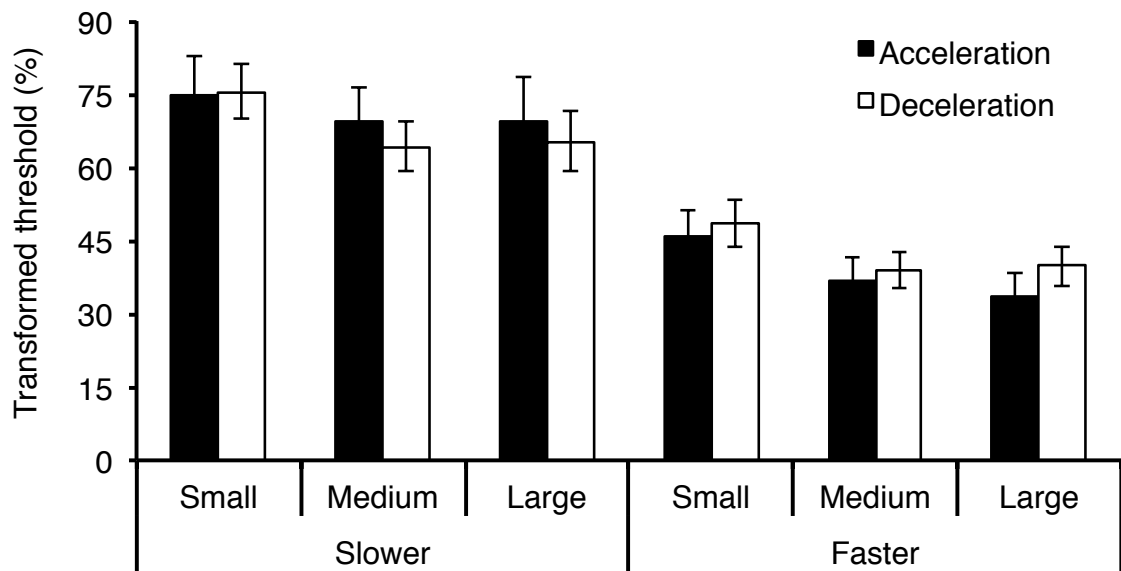


Figure 3. Mean transformed acceleration and deceleration detection thresholds (%) as a function of aperture size and average velocity. Error bars are $\pm 1 SE$.

3.2 Experiment 2

Experiment 1 showed that physically constraining the horizontal distance over which a stimulus can travel affects an observer's ability to detect acceleration and deceleration on the horizontal axis. Experiment 2 was conducted to determine whether the horizontal

extent of the aperture influences the ability to track horizontally accelerating and decelerating random dot arrays for different velocity ranges.

3.2.1 Method

3.2.1.1 Participants. Five individuals from Experiment 1 participated in this experiment.

3.2.1.2 Stimuli, apparatus, and procedure. The same random dot array stimuli and experimental conditions used in Experiment 1 were used in this experiment. See Chapter 2: *General Eye Tracking Method* for stimuli, apparatus, and procedural details of this experiment.

3.2.2 Results

3.2.2.1 Peak eye velocity. At slower velocities aperture size appears to have little influence on peak eye velocity, however the effect is considerable at faster velocities (although there is no difference between medium and large apertures). Moreover, peak eye velocity is generally higher at faster velocities than at slower velocities. Finally, there seems to be no difference in performance between the acceleration and deceleration conditions (Figure 4).

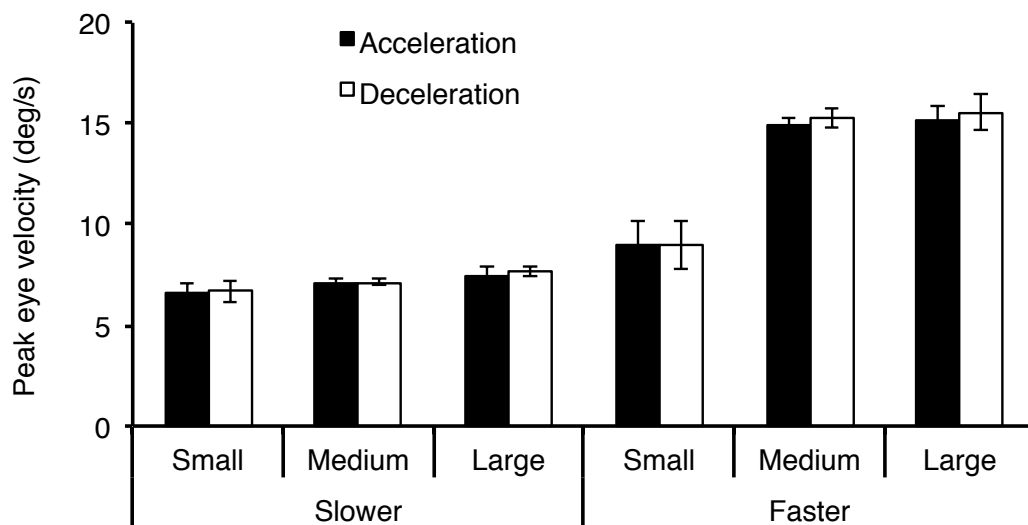


Figure 4. Mean weighted average peak eye velocity (deg/s) as a function of aperture size, average velocity, and sign of acceleration. Error bars are $\pm 1 SE$.

A 3(aperture size) x 2(average velocity) x 2(sign of acceleration) repeated measures ANOVA confirmed these observations. There is a main effect of aperture size, $F(1.19, 4.74) = 20.54, p = 0.01, \eta^2_p = 0.84$. Peak velocity is higher in the medium, $t(4) = 4.68, p < .05$, Cohen's $d = 2.09$, and large aperture conditions, $t(4) = 4.66, p < .05$, Cohen's $d = 2.08$, than in the small aperture condition, however there is no difference between the medium and large aperture conditions, $t(4) = -1.25, ns$. In addition, there is also a main effect of average velocity, $F(1, 4) = 49.82, p = 0.002, \eta^2_p = 0.93$, as peak eye velocity is higher at faster velocities than at slower velocities. There is no main effect of sign of acceleration, $F(1, 4) = 7.73, p = 0.05$. However, the first two main effects should be interpreted cautiously, given that there is an interaction between aperture size and average velocity, $F(1.65, 6.59) = 23.99, p = 0.001, \eta^2_p = 0.86$. There are no differences between the aperture sizes in the slower velocity condition, however in the faster velocity condition peak eye velocity is higher in the medium, $t(4) = 5.39, p < .05$, Cohen's $d = 2.41$, and large aperture conditions, $t(4) = 4.86, p < .05$, Cohen's $d = 2.17$, than in the small aperture condition, although there is no difference between the medium and large aperture conditions, $t(4) = -0.39, ns$. There are no other interactions between the experimental variables.

3.2.2.2 Eye and stimulus position traces. Observers are worse at tracking through small apertures than larger apertures. Even though participants make more regressive saccades for small apertures than for the larger apertures (see below), they do not consistently produce saccades every time the dot leaves the boundary of the small aperture, especially at faster velocities (Figure 5). Furthermore, the trajectory of the eye does not always change after the dot disappears from view in the small aperture conditions, particularly at faster velocities. These findings are to be expected given that it is easier to track at slower velocities, regardless of aperture size. Moreover, there is an inevitable delay between the stimulus' disappearance and the registration of its disappearance by the visual system, after which there is a further delay during which a signal must be sent to the ocular motor system to change the trajectory of the eye to keep following the stimulus' motion. Considering that the dots in the small aperture are replaced more often than in the larger apertures, this would explain why there are fewer changes in the eye's trajectory for the

small aperture conditions, especially at faster velocities.

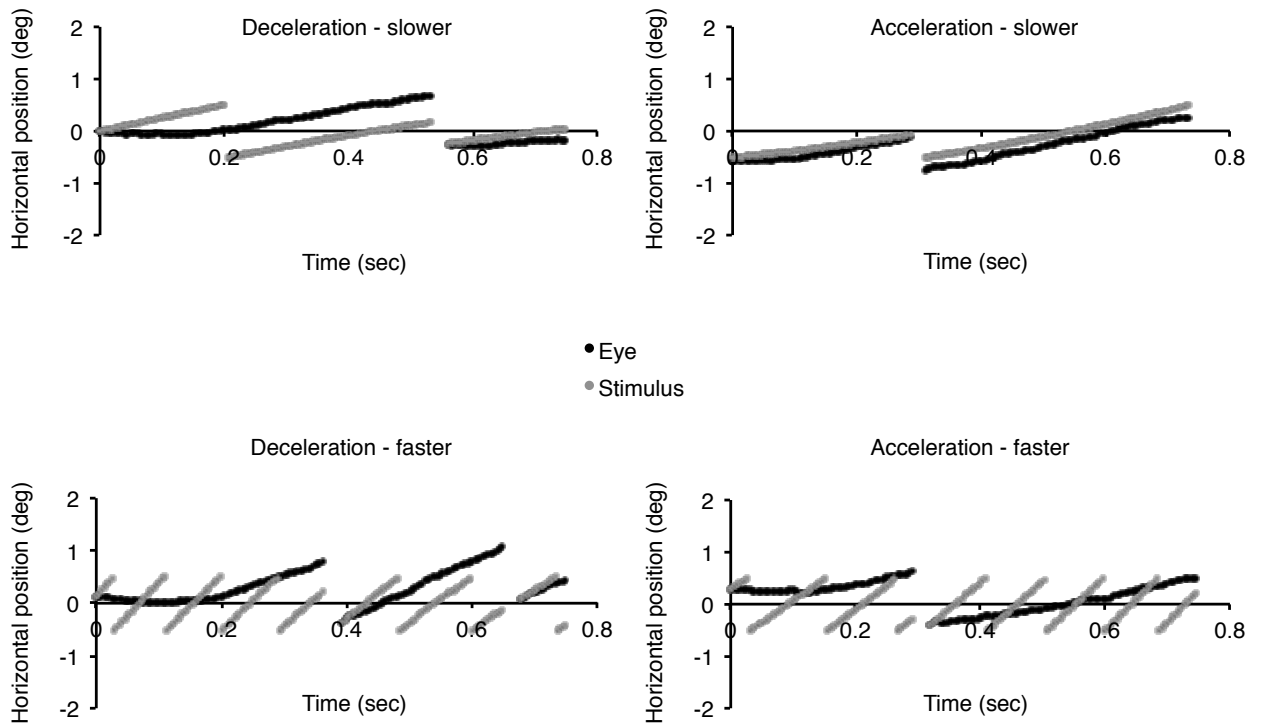


Figure 5. Example eye traces of one participant for trials belonging to the acceleration and deceleration slower and faster small aperture conditions. (Stimulus traces belong to threshold acceleration and deceleration rates, rightward motion only.)

In comparison, eye positions tend to better match the predicted stimulus positions over time across velocities in the medium and large aperture conditions (Figure 6). Although observers generally pursue motion similarly between the medium and large apertures, occasionally, the eye's trajectory does not change when the dot reaches the edge of the medium aperture in the faster velocity condition (on average, in 16 % of trials). This always happens toward the end of the trial within the last 250 ms, and most often occurring within the last 100 ms. Nonetheless, the tendency to not change trajectory occurs far more often and also throughout the trial in the small aperture conditions (on average, in 77.33 % and 100 % of trials for the slower and faster conditions, respectively). This never occurs in the slower medium aperture condition or in the slower and faster large aperture conditions.

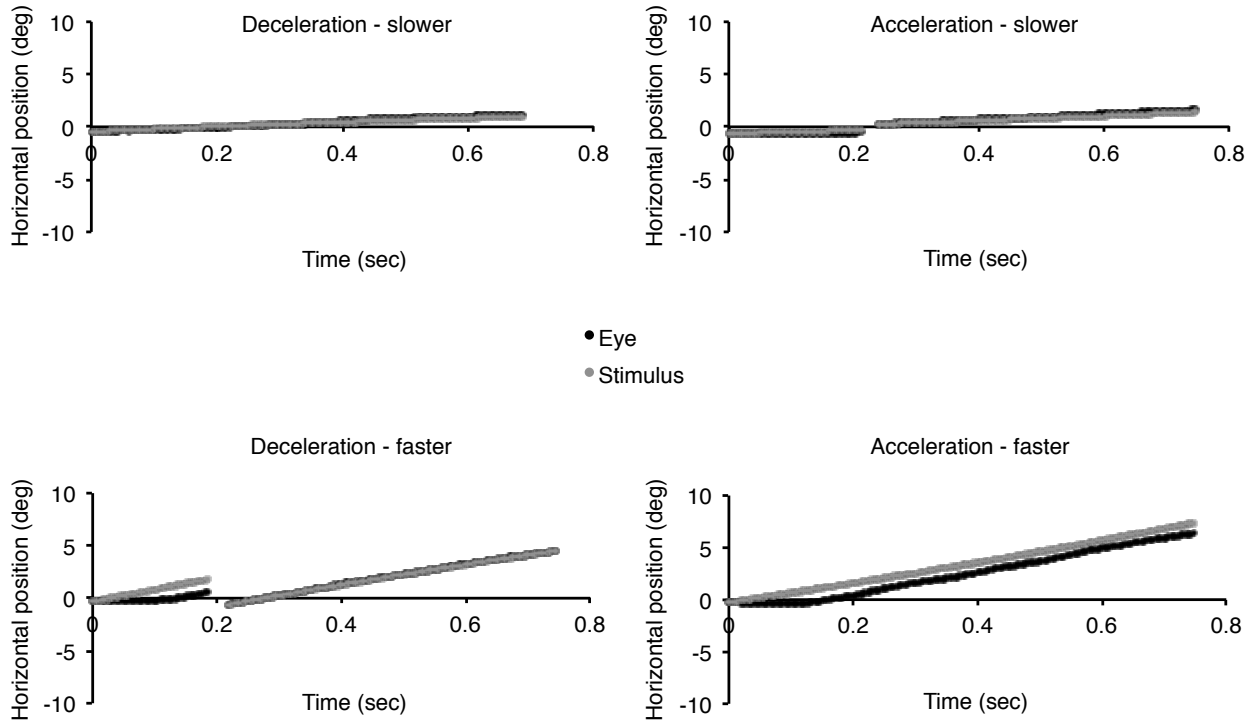


Figure 6. Example eye traces of the same participant in Figure 5 for trials belonging to the acceleration and deceleration slower and faster large aperture conditions. (Stimulus traces belong to threshold acceleration and deceleration rates, rightward motion only.)

Interestingly, observers do not always track foveally in the small aperture conditions, as eye positions often go beyond the boundaries of the stimulus (on average, in 85.67 % of trials in the small aperture conditions), and all observers do this in the small aperture conditions. This may reflect a principle of least effort for eye movements, especially when viewing a random dot array through a small aperture, in which it is difficult to track the individual elements. Eye positions fall outside the stimulus area in only one trial for one participant in the medium aperture condition and never outside the large aperture area.

3.2.2.3 Saccades. Observers make more regressive saccades than catch-up saccades.

There are also more regressive saccades and fewer catch-up saccades for the small apertures than for the larger ones, which is consistent with the hypothesis that the size of the aperture affects the ability to track. However, with so few saccades overall, it is unclear how meaningful the differences between the slower and faster velocity conditions

are for either saccade type, although there is little difference in the number of regressive and catch-up saccades between the medium and large apertures within each average velocity condition. There is also no evidence of an asymmetry in the number of either type of saccade between the acceleration and deceleration conditions (Figure 7).

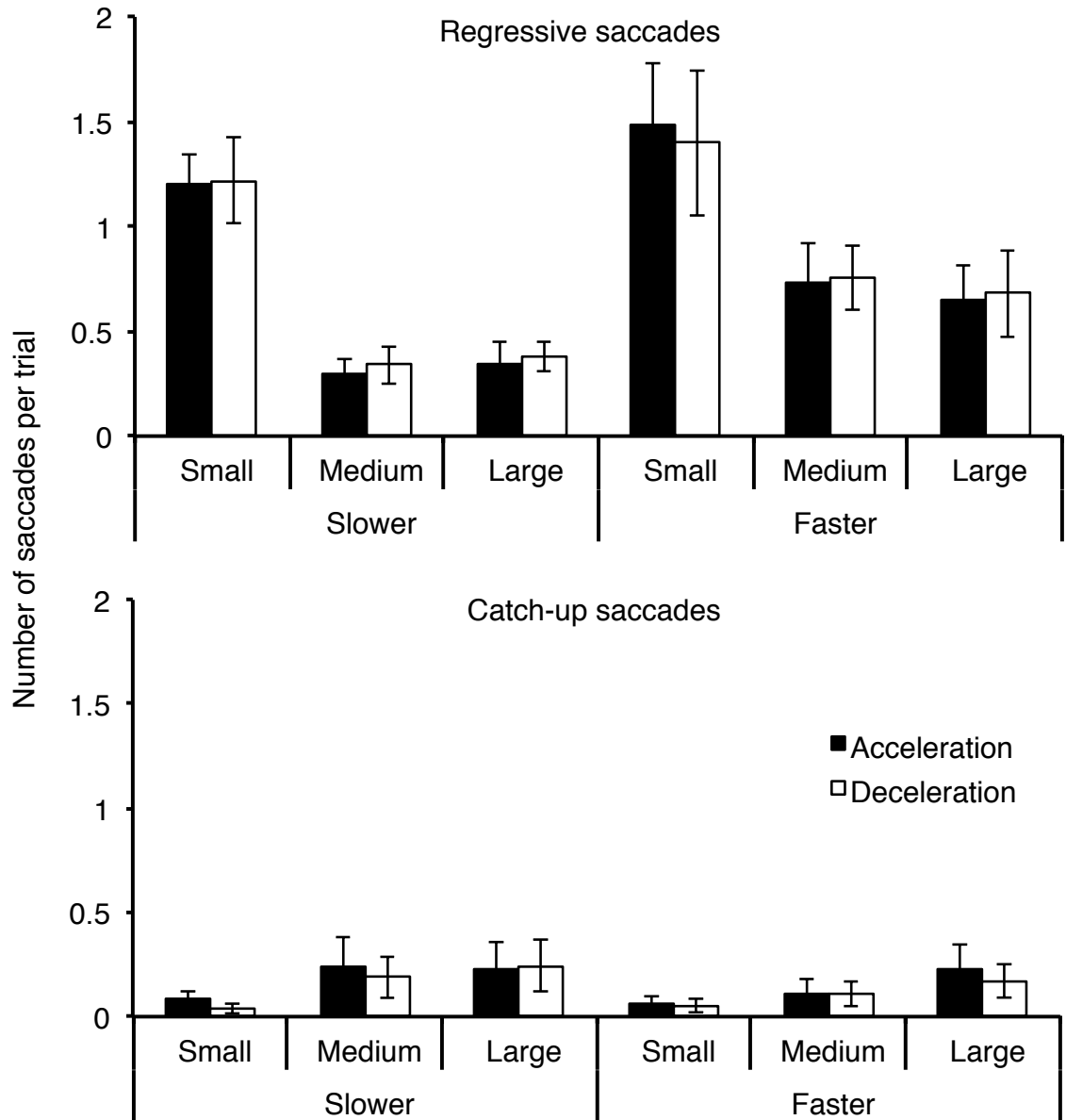


Figure 7. Mean number of regressive and catch-up saccades per trial as a function of aperture size, average velocity, and sign of acceleration. Error bars are $\pm 1 SE$.

The amplitude of the regressive saccades is affected by aperture size and velocity (predominantly for the medium and large aperture conditions), whereas the amplitude of the catch-up saccades seems to only vary as a function of aperture size. Even though there appears to be little difference in the amplitude of the regressive saccades between the medium and large aperture conditions in each velocity range, the amplitude of the catch-up saccades appears to be moderately affected by all aperture sizes. Nevertheless, it is unclear how important these differences are, given the small number of saccades overall. There is no difference in the amplitude of either type of saccade between the acceleration and deceleration conditions (Figure 8).

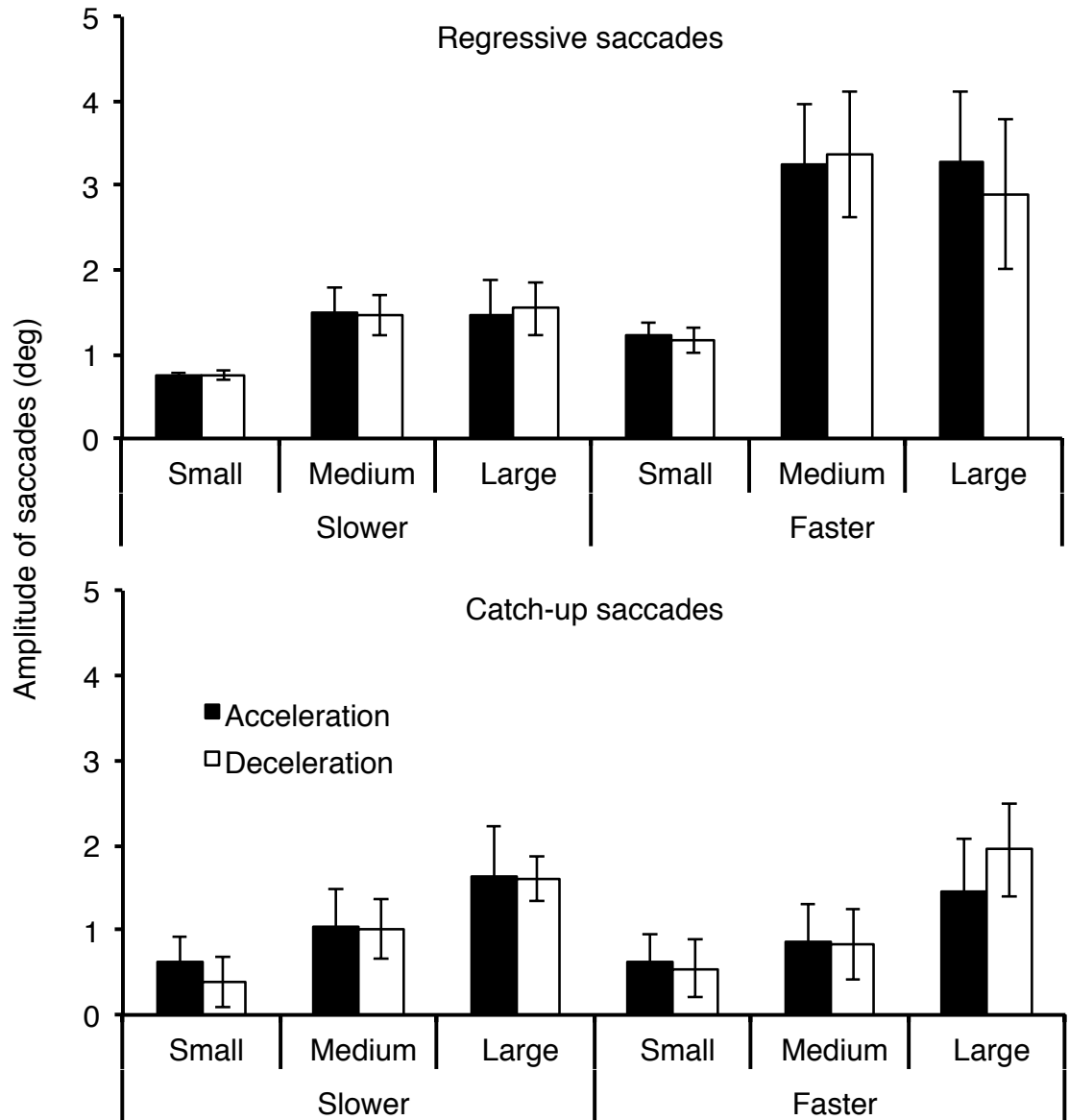


Figure 8. Mean amplitude of regressive and catch-up saccades (deg) as a function of aperture size, average velocity, and sign of acceleration. Error bars are $\pm 1 SE$.

3.3 Discussion

The findings of Experiment 1 showed that the ability to detect acceleration and deceleration improves as aperture size and average velocity increase. Moreover, there is little difference in detection performance between the acceleration and deceleration

condition within each velocity range across aperture sizes. The data from Experiment 2 confirm that the distance over which a stimulus can travel affects how observers track acceleration and deceleration. However, although the eye position traces revealed differences in how observers track through small and larger apertures across velocities, peak eye velocity only varies between small and larger apertures at faster velocities. This is most likely because the measure detects periods of rapid smooth pursuit, even if brief, which may not necessarily reflect the overall pattern of performance for the whole trial. Although the mean weighted average of peak eye velocity is approximately 7 deg/s for the slower velocity condition, which is faster than the average velocity of that condition (2.04 deg/s) or the maximum velocities of any of the conditions tested in the slower velocity range (on average, 3.4 deg/s), it does not reflect velocities during saccadic eye movements as they would be substantially faster. For example, peak velocities of saccades have been reported to be well over 100 deg/s for a wide range of amplitudes (Henriksson, Pyykkö, Schalén, & Wennmo, 1980). Even so, peak eye velocity does not appear to be sensitive enough to differentiate performance between the aperture size conditions at slower velocities, which may be related to the fact that observers generally track better at slower velocities across aperture sizes. Nevertheless, the saccade data further support our findings that the size of the aperture affects smooth pursuit performance across velocities, as more regressive and fewer catch-up saccades are made for small apertures than for larger apertures and saccade amplitude increases as aperture size increases. Together, these findings suggest that the distance over which a stimulus can travel affects the ability to detect and visually pursue acceleration and deceleration.

Although the ability to detect acceleration and deceleration improves as average velocity increases in all apertures, smooth pursuit appears to be more strongly affected by average velocity in the medium and large apertures than in the small apertures. These findings point to a dissociation between the perceptual and ocular motor systems, which has been reported before (e.g., Gegenfurtner et al., 2003; González et al., 2014; Spering & Gegenfurtner, 2007; Tavassoli & Ringach, 2010). Furthermore, the inverse effects of velocity on perception and tracking may be explained by how the visual system seems to use retinal slip to identify the presence of visual acceleration. Haarmeier and Thier (2006) argued that it may be too computationally expensive and noisy for the visual system to

calculate the second-order derivative of position with respect to time directly from retinal and ocular motor information, especially in light of the fact that we do not appear to have cortical neurons that are sensitive to acceleration rate directly (Lisberger & Movshon, 1999; Price et al., 2005; Schlack et al., 2007). Instead, as discussed in Chapter 1, the authors suggested that the visual system might determine when changes in velocity are taking place by using the displacement of the target's retinal image relative to the fovea (i.e., retinal slip). The retinal slip is caused by the delay in the ocular motor feedback needed to correct the velocity of the eye's rotation to match the target's velocity, which, in our study, constantly changed as stimuli accelerated or decelerated through the apertures.

Within each aperture condition, we found that the ability to detect acceleration and deceleration is worse at slower velocities than at faster velocities, which suggests that the task is more difficult in the slower velocity condition, even though tracking is more accurate. The relatively higher accuracy of smooth pursuit at slower velocities might mean that greater rates of acceleration and deceleration, in proportion to the velocity of the standard stimulus, are needed for the retinal slip to rise above a threshold in order for the visual system to correctly identify the presence of acceleration and deceleration in the comparison stimulus. In contrast, pursuit is worse and detection is better at faster velocities. With less accurate smooth pursuit, smaller rates of acceleration and deceleration (relative to the velocity of the standard stimulus) may be needed to detect the presence of acceleration and deceleration at faster velocities.

In Experiment 1 we demonstrated that humans appear similarly sensitive to the presence of acceleration and deceleration (within the same average velocity range) in horizontal translation. Nevertheless, it is possible that vertical direction may have an influence that produces an asymmetry in the ability to detect acceleration and deceleration, which does not appear on the horizontal axis. Specifically, objects thrown upward in the natural environment tend to accelerate downward and decelerate upward due to the effects of gravity, and our asymmetrical experience may produce anisotropies in our sensitivity to the presence of vertical acceleration and deceleration. As Experiment 1 demonstrated that the size of the aperture influences detection, it is appropriate to ask whether aperture size

affects the perception of acceleration and deceleration in the vertical plane. These questions were addressed in Experiment 3, and Experiment 4 was designed to test whether the vertical size of the aperture affects how observers track accelerating and decelerating stimuli as a function of vertical direction.

Chapter 4

4 Effects of Vertical Direction and Aperture Size

Experiment 1 demonstrated that the distance over which a stimulus can travel affects an observer's ability to detect acceleration on the horizontal axis, and Experiment 2 showed that the size of the aperture influences the ability to track an accelerating stimulus as a function of average velocity. Furthermore, Experiment 1 also showed that although average velocity affects acceleration perception, in that detection is better at faster velocities than at slower velocities, there is no difference between acceleration and deceleration detection within the same velocity range. In Experiment 3 we explored whether physically constraining the distance over which a stimulus can travel affects our ability to detect acceleration on the vertical axis. We did this because although there is little reason to expect anisotropies in detection on the horizontal plane (and we confirmed this in Experiment 5), upward and downward motion are categorically different. In nature, downward motion is more frequent than upward motion; for example, fruit tends to fall off the branches of trees instead of rising into the air. In addition, downward motion may also be more behaviourally relevant to goal-directed activities, such as when intercepting or avoiding falling objects. Consequently, in Experiment 3 we manipulated vertical direction as well as vertical aperture height. Moscatelli and Lacquaniti (2011) reported that motion duration discrimination is more precise for downward acceleration when it is consistent with the effects of gravity, which they attributed to an experience-based adaptation. Therefore, we anticipated that sensitivity to the presence of acceleration would be higher for downward motion than for upward motion. Nevertheless, it still remains to be seen whether deceleration perception is similarly affected by vertical direction.

On the one hand, it is possible that we are more sensitive to upward deceleration than downward deceleration because of the way objects naturally decelerate vertically in the world when thrown upward. On the other hand, we may be more sensitive to downward motion regardless of the sign of acceleration. The reason why the downward bias may persist across acceleration and deceleration detection is because it may be a more

efficient use of resources for the visual system to be more sensitive to downward motion overall because it may be more behaviourally relevant than upward motion.

If a vertical asymmetry exists in our detection of acceleration and deceleration, either as an interaction between vertical direction and sign of acceleration or as a general downward bias, the size of the aperture may influence the strength of that asymmetry. However, we had no hypotheses as to whether the strength of the difference would increase or decrease with aperture size. As Experiment 1 revealed that there is little difference in detection between medium and large apertures, we tested only the small and large aperture sizes in Experiments 3 and 4 on the vertical axis. In addition, as Experiment 2 had demonstrated that the effect of aperture size with respect to peak eye velocity is greater at faster velocities than at slower velocities, in Experiments 3 and 4 we tested only the faster average velocity range.

4.1 Experiment 3

4.1.1 Method

4.1.1.1 Participants. Ten volunteers (including author ASM), with an average age of 24.4 years ($SD = 2.07$), participated in this experiment and seven were female. Two additional participants were unable to do the task reliably and were not included.

4.1.1.2 Stimuli and apparatus. Dot size was $0.15^\circ \times 0.15^\circ$ and average density was 1.5 dots/degree². There were two aperture size conditions with the vertical distance subtending 1° (small) and 27° (large). The horizontal distance was held constant at 1° . Middle/average velocity was constant at 10 deg/s using *Equation 1* (Chapter 2).

4.1.1.3 Procedure. The comparison stimuli had seven rates of acceleration and deceleration, ranging from ± 1.5 to 10.5 deg/s^2 in steps of $\pm 1.5 \text{ deg/s}^2$. The standard stimuli moved at a constant velocity of 10 deg/s. Vertical direction was the same for the comparison and standard stimuli within each trial.

Participants completed at least 240 practice trials prior to the experimental task. There were a minimum of 20 and a maximum of 60 experimental trials per stimulus value for

each condition per participant included for analysis, depending on the number of runs (each containing 10 trials per stimulus value per condition) needed to obtain non-significant goodness of fit measures for the probit regression analyses. Stimulus conditions were defined by aperture size (small and large) for each block of acceleration and deceleration, and vertical direction was randomized within each condition.

4.1.2 Results

Table 2 shows the mean 75 % correct acceleration and deceleration detection threshold rates as absolute values. Transformed thresholds (see *Equation 2* in Chapter 2) were submitted to a 2(vertical direction) x 2(sign of acceleration) x 2(aperture size) repeated measures ANOVA. The data were spherical and therefore no correction was used.

Table 2

Mean absolute 75 % correct acceleration and deceleration detection threshold rates (deg/s²) as a function of vertical direction and aperture size

		Acceleration rate	Deceleration rate
Vertical direction	Aperture size	Mean (SD)	Mean (SD)
Upward	Small	6.72 (1.90)	7.43 (2.08)
	Large	5.31 (2.03)	6.52 (2.37)
Downward	Small	6.40 (1.86)	6.39 (2.19)
	Large	5.46 (1.83)	6.07 (2.19)

Consistent with our hypothesis for a general predisposition to be more sensitive to downward acceleration and deceleration, detection tends to be more accurate for downward motion than upward motion, $F(1, 9) = 7.21, p = 0.03, \eta^2_p = 0.45$, and there are no differences between the acceleration and deceleration conditions, $F(1, 9) = 1.82, p = 0.21$. Furthermore, the distance over which a stimulus can travel appears to affect vertical acceleration and deceleration detection, because thresholds are lower for large apertures

than for small apertures, $F(1, 9) = 9.74, p = 0.01, \eta^2_p = 0.52$ (Figure 9). There are no interactions between the experimental variables.

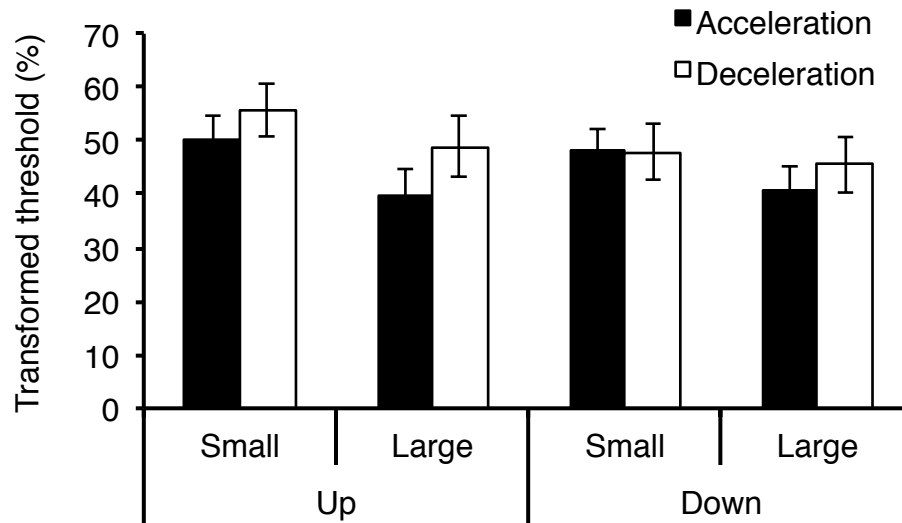


Figure 9. Mean transformed acceleration and deceleration detection thresholds (%) as a function of vertical direction and aperture size. Error bars are $\pm 1 SE$.

4.2 Experiment 4

Experiment 3 demonstrated that physically constraining the vertical distance over which a stimulus can travel affects the ability to detect the presence of vertical acceleration and deceleration. Experiment 4 was designed to establish whether the vertical height of the aperture alters how observers pursue vertically accelerating and decelerating random dot arrays.

4.2.1 Method

4.2.1.1 Participants. Five volunteers from the first experiment participated in this experiment.

4.2.1.2 Stimuli, apparatus, and procedure. This experiment used the same random dot stimuli and conditions as those used in Experiment 3. However, unlike Experiment 3, the large aperture height in this experiment was 23° (a pilot test revealed that there is a

negligible difference in psychophysical performance between 23 ° and 27 ° aperture sizes). The stimulus, apparatus, and procedure details for this experiment are described in Chapter 2.

4.2.2 Results

4.2.2.1 Peak eye velocity. Although there are no main effects of vertical direction, $F(1, 4) = 2.11, p = 0.22$, or sign of acceleration, $F(1, 4) = 1.41, p = 0.30$, as hypothesized, peak eye velocity is higher for the large apertures than for the small ones, $F(1, 4) = 51.23, p = 0.002, \eta^2_p = 0.93$. Moreover, there is an interaction between vertical direction and aperture size, $F(1, 4) = 8.50, p = 0.04, \eta^2_p = 0.68$. The overall difference between the large and small aperture conditions is somewhat greater in the upward condition than in the downward condition, $t(4) = 2.92, p = 0.04$, Cohen's $d = 1.30$, as a result of peak velocity being slightly higher for downward motion than for upward motion in the small aperture condition, but similar between the two directions in the large aperture condition. There is also an interaction between sign of acceleration and aperture size, $F(1, 4) = 10.85, p = 0.03, \eta^2_p = 0.73$, as the difference between the large and small aperture conditions tends to be slightly greater for the deceleration condition than for the acceleration condition, $t(4) = 3.29, p = 0.03$, Cohen's $d = 1.47$; however, this small difference in means appears to be negligible, as shown in Figure 10.

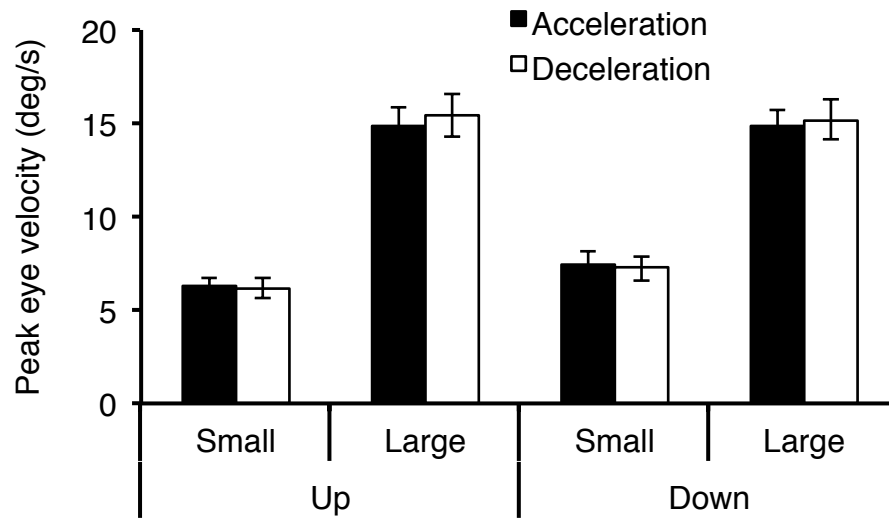


Figure 10. Mean weighted average peak eye velocity (deg/s) as a function of vertical direction, sign of acceleration, and aperture size. Error bars are $\pm 1 SE$.

4.2.2.2 Eye and stimulus position traces. Observers do not track well in the small aperture conditions (Figure 11). In many trials the eye tends to hover over the stimulus area with little movement in the direction of the stimulus, often without saccade interruption. For the trials in which the eye follows the stimulus' motion, observers do not appear to track an individual dot but rather the global motion of the stimulus. The trajectory of the eye does not consistently change when the dot disappears from view and regressive saccades (in the opposite direction of the stimulus) are not regularly produced when the dot reaches the edge of the small aperture. Eye positions also frequently occur outside the area of the small aperture (on average, in 84.83 % of trials), which indicates that observers do not consistently track the stimulus foveally. This occurs for all participants and it may be related to the difficulty in tracking elements in the array when it is presented through a small aperture. In contrast, observers track better in the large aperture conditions (Figure 12). Eye positions never occur outside the area of the large aperture, although one participant's eye trajectory remains constant after the dot reaches the border of the large aperture in 7 out of 120 trials, but usually toward the end of the trial. Overall, these findings suggest that observers are economical with their eye movements, especially when the stimulus is difficult to track due to aperture size.

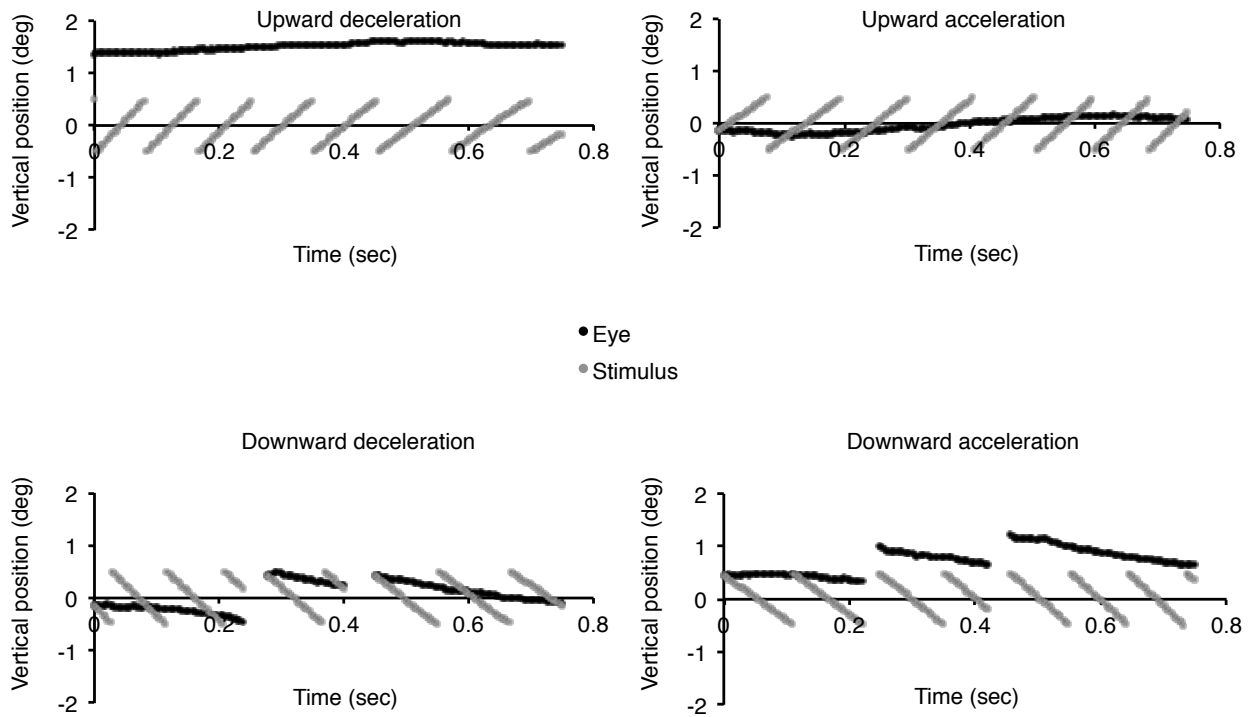


Figure 11. Example eye traces of one participant for trials belonging to the acceleration and deceleration upward and downward small aperture conditions. (Stimulus traces belong to threshold acceleration and deceleration rates.)

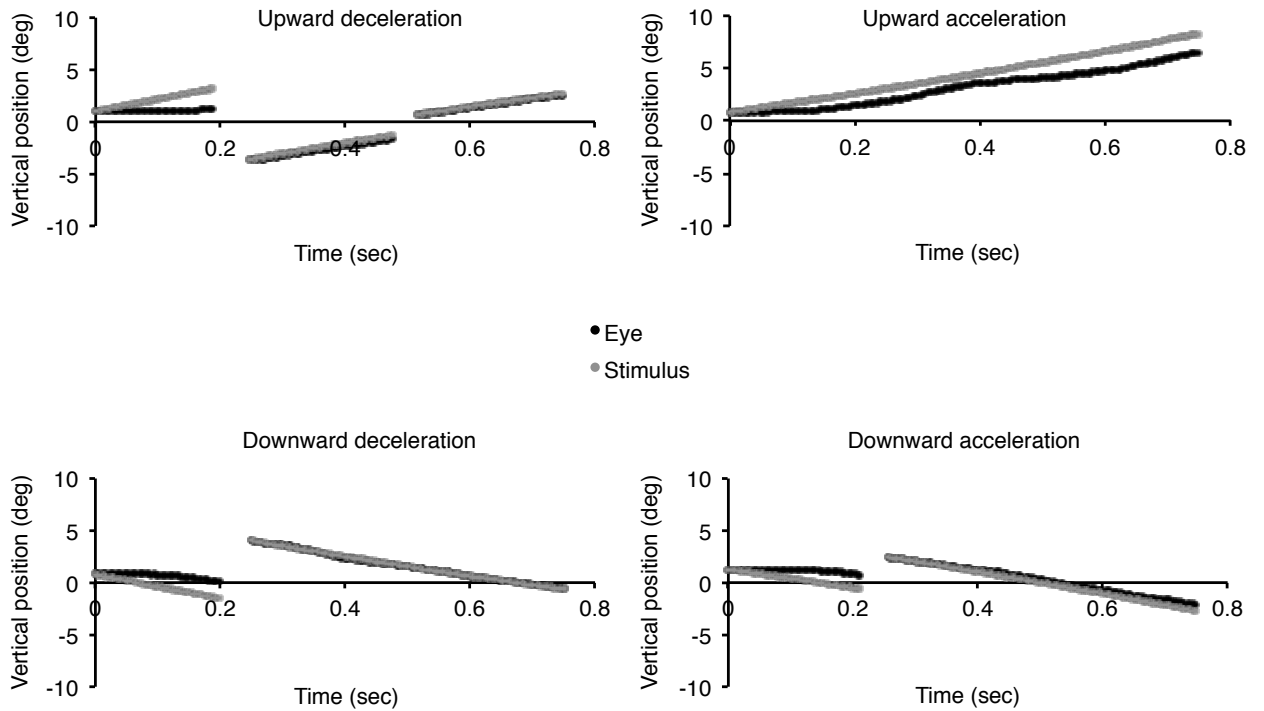


Figure 12. Example eye traces of the same participant in Figure 11 for trials belonging to the acceleration and deceleration upward and downward large aperture conditions. (Stimulus traces belong to threshold acceleration and deceleration rates.)

4.2.2.3 Saccades. There are more regressive than catch-up saccades in every condition (Figure 13). Although there are slightly more regressive saccades for the downward than upward conditions (there is little difference in the number of catch-up saccades), with so few saccades it is unclear how meaningful this asymmetry is. In comparison, observers tend to make regressive and catch-up saccades with greater amplitudes in the large aperture conditions than in the small aperture conditions, regardless of vertical direction (Figure 14). Finally, there is no evidence of differences in the number or amplitude of regressive and catch-up saccades between the acceleration and deceleration conditions.

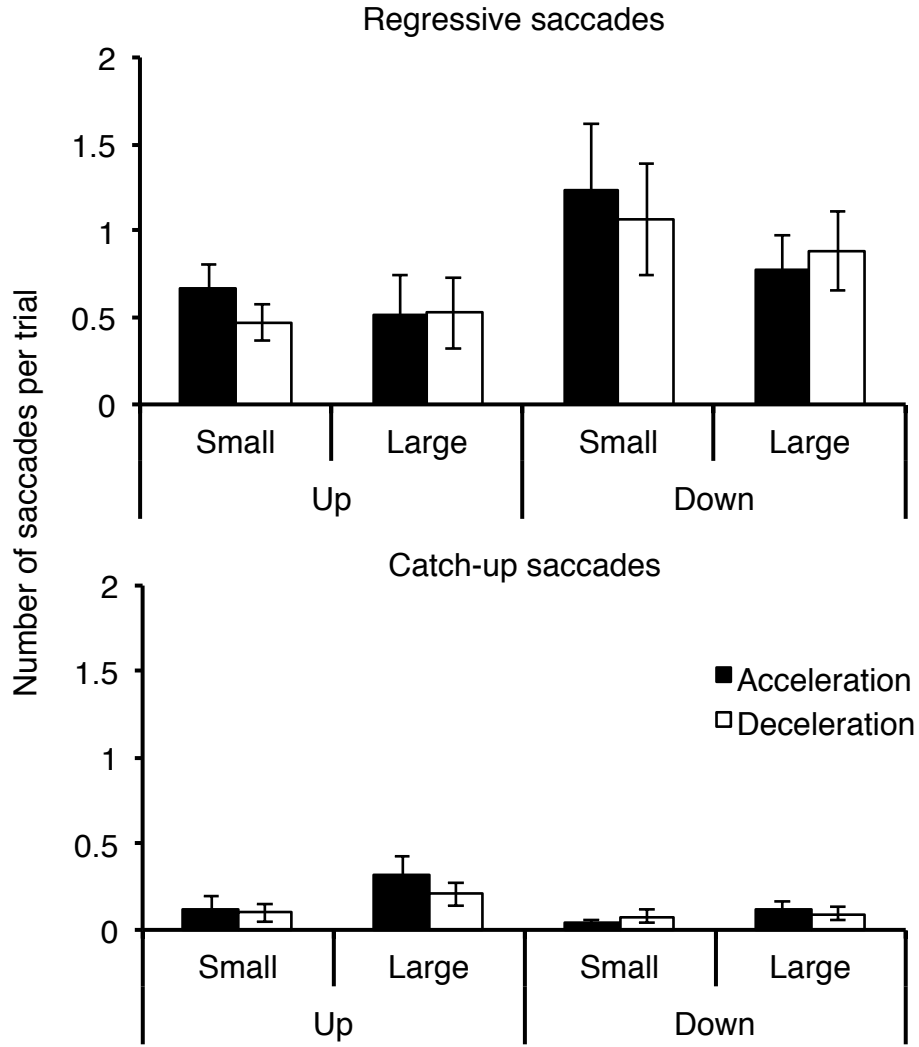


Figure 13. Mean number of regressive and catch-up saccades per trial as a function of vertical direction, sign of acceleration, and aperture size. Error bars are $\pm 1 SE$.

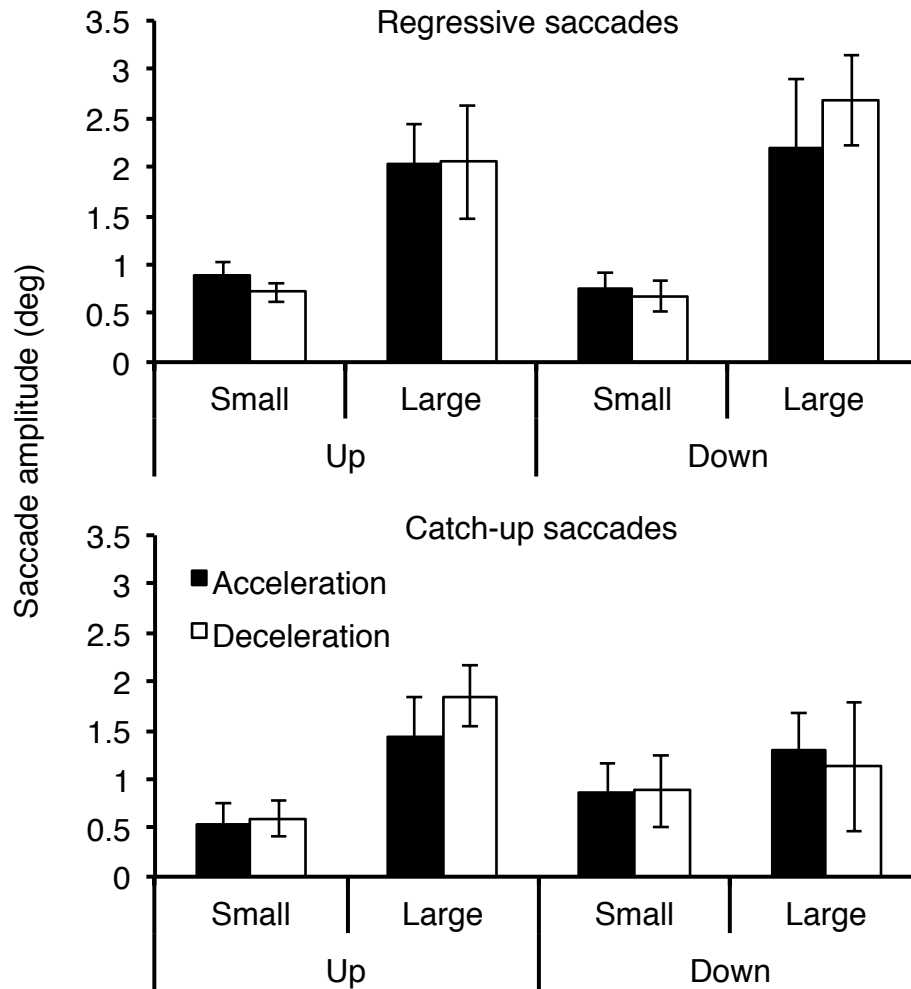


Figure 14. Mean amplitude of regressive and catch-up saccades (deg) as a function of vertical direction, sign of acceleration, and aperture size. Error bars are $\pm 1 SE$.

4.3 Discussion

The findings of Experiment 3 revealed that the downward bias in the ability to detect the presence of acceleration appears to persist regardless of the size of the aperture or sign of acceleration. This anisotropy is compatible with the idea that the visual system adaptively responds to the salience of upward and downward events in general, but it does not further distinguish between vertically accelerating and decelerating events. The absence of a vertical asymmetry in our sensitivity to acceleration and deceleration is not surprising, given that we are relatively insensitive to subtle differences in variable

velocity (Snowden & Braddick, 1991; Watamaniuk & Heinen, 2003; Werkhoven et al., 1992), which accounts for the fairly high acceleration and deceleration detection thresholds reported in Experiment 3 as well as every other experiment in this thesis. Nevertheless, Indovina et al. (2005) found that the vestibular network selectively activates when the visual system processes visual acceleration that is consistent with the effects of gravity. As discussed in Chapter 7: *General Discussion*, the vestibular network processes multimodal information related to self-motion and orientation with respect to gravity (Angelaki, Shaikh, Green, & Dickman, 2004; Merfeld, Zupan, & Peterka, 1999; Nishiike et al., 2002). Thus, Indovina et al. argued that the selective response of the vestibular network to gravity-consistent visual acceleration indicates that it stores an internal model of gravitational motion that can be used by the visual system. It is interesting that we found a downward bias in the absence of any contextual cues of gravity in our displays, but it is possible that having participants sitting upright was enough of an orientation cue. It has also been proposed that this internal representation of gravity is the result of experience and, because downward motion may be more behaviourally relevant than upward motion, this may help to explain the downward bias in visual acceleration and deceleration detection.

The implications for the downward bias in acceleration detection may be related to those that have been suggested to explain why motion sensitivity tends to be higher in the lower visual field than in the upper visual field (e.g., Edwards & Badcock, 1993). Although the effect of vertical direction on acceleration and deceleration perception is modest given the overall size of our sample's detection thresholds, these vertical asymmetries may still have consequences for how observers move around the environment safely. For example, it is advantageous to look downward when walking in order to avoid obstacles and maintaining one's balance (Marigold & Patla, 2008), and a downward bias in acceleration perception would be beneficial for catching falling objects accurately (Moscatelli & Lacquaniti, 2011; Senot, Zago, Lacquaniti, & McIntyre, 2005).

Our results also support the findings of Experiments 1 and 2, in that the vertical area over which a stimulus can travel influences the ability to detect and visually track vertical acceleration and deceleration, which indicates that the effect of aperture size is robust

across the horizontal and vertical axes. Both psychophysical performance (Experiment 3) and smooth pursuit (Experiment 4) are better for large vertical apertures than for small ones. Moreover, the peak eye velocity during smooth pursuit and the amplitude of saccades increase as the size of the aperture increases. Given that tracking is generally poor in the small aperture conditions, and at times hardly occurs at all, our data from Experiments 1 to 4 can be interpreted as suggesting that the visual system does not continuously incorporate information about eye movements into the motion perceptual signal.

Experiments 1 and 3 explored acceleration and deceleration perception on the horizontal and vertical axes using linear translation. However, in the natural environment our experience with visual motion can be decomposed into three types of motion: translational, rotational, and radial. Although we tend to see primarily radial optic flow when looking straight ahead while moving, radial optic flow fields containing rotational or spiral motion (i.e., curl) as well as translation are more common because our eyes are constantly moving as we move forward, backward, or sideways through the environment (Graziano, Andersen, & Snowden, 1994). Consequently, the motion patterns we tend to see outside the laboratory are quite complex and varied, but it is unclear whether the form of a motion pattern affects our sensitivity to visual acceleration. This was the subject of investigation of Experiment 5.

Chapter 5

5 Effects of Pattern Type and Direction

Experiment 3 demonstrated that we are better at detecting acceleration and deceleration in downward than upward motion, which is consistent with our asymmetrical experience with gravity and the behavioural relevance of downward motion. It has been suggested that the realism of a stimulus should affect psychophysical performance (Gibson, 1954; 1979), and Palmisano et al. (2008) found that optic flow displays containing random acceleration of self-motion (i.e., jittering or oscillating motion profiles on the horizontal and vertical axes) tend to elicit stronger impressions ofvection than those without. Their findings could be interpreted to indicate that acceleration may be an important aspect of the realism of optic flow. In general, radial motion is a simplified representation of the motion patterns we experience when moving forward or backward while looking straight ahead. Moreover, unlike horizontally moving random dot patterns where all of the dots move only leftward or rightward, radially moving patterns contain dots moving on all cardinal and oblique axes simultaneously across the visual field, making it a more visually complex stimulus. Correspondingly, perhaps we may be more sensitive to acceleration in radial optic flow than in horizontal translation.

Even though several earlier studies on the effects of pattern type on motion perception used rotational motion (Bex et al., 1998; Burr, Morrone, & Vaina, 1998; Clifford et al., 1999; Freeman & Harris, 1992; Geesaman & Qian, 1998; Lee & Lu, 2010), the current experiment did not test this type of optic flow. In order to prevent differences in dot parameters from confounding the effect of pattern type, dot size, average density, and motion profile were held constant throughout the display of every condition (see Chapter 2 for a description of the stimulus design). It is not possible to keep both the motion profile and synchrony constant across the display in rotational motion because dots travel shorter distances in the centre than in the periphery.

One might expect a radial anisotropy due to our familiarity with expansion over contraction because we move forward through the environment more often than we move backward. However, the psychophysical evidence is mixed in terms of whether an

asymmetry exists and, if so, whether it favours expansion or contraction (Beardsley & Vaina, 2005; Bex et al., 1998; Edwards & Badcock, 1993; Edwards & Ibbotson, 2007; Geesaman & Qian, 1998; Meese & Anderson, 2002; Shirai et al., 2006). As a radial anisotropy has yet to be reported for acceleration detection, we also manipulated radial direction as another experimental variable. Although we did not anticipate an asymmetry in horizontal acceleration detection, we varied horizontal direction as a methodological control as well. Additionally, we manipulated the sign of acceleration to determine whether we are similarly sensitive to acceleration and deceleration as a function of pattern type or direction.

5.1 Method

5.1.1 Participants

Seven individuals (including author ASM) with an average age of 26.3 years ($SD = 2.43$) comprised the sample, and five were female. Three additional participants (not included in the sample N) were recruited but two were unable to do the task and the third was removed due to performance variability.

5.1.2 Stimuli and Apparatus

Two types of random dot patterns were presented: horizontal translation and radial optic flow (see Chapter 2: *General Psychophysical Method* for stimulus descriptions). Direction was manipulated within each type of pattern (Figure 15) and there were four motion pattern conditions in total: leftward, rightward, expanding (i.e., dots moving from the centre of the display to the periphery), and contracting (i.e., dots moving from the periphery to the centre of the display). Dot size and average dot density were constant across the visual field at $0.1^\circ \times 0.1^\circ$ and 0.75 dots/deg^2 , respectively, and aperture size was constant at $37^\circ \times 27^\circ$ (width x height). The motion profile of each dot in all four patterns was centered on 10 deg/s using *Equation 1* (Chapter 2), and the standard (constant velocity) stimulus moved at 10 deg/s . There were seven comparison rates of acceleration and deceleration within each condition, drawn from a possible range of ± 1 to 10 deg/s^2 , in steps of $\pm 1 \text{ deg/s}^2$.

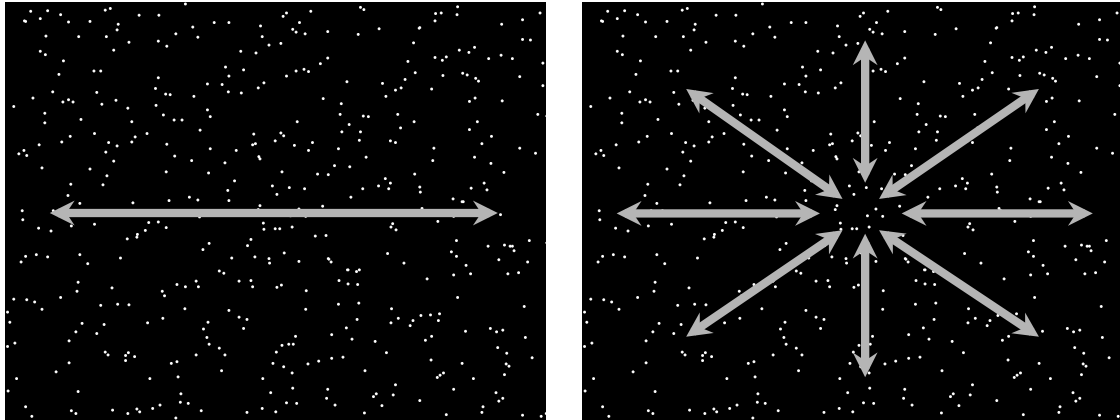


Figure 15. Schematic examples of random dot pattern directions for the horizontal (on left, showing leftward and rightward directions) and radial motion conditions (on right, showing expanding and contracting directions). Direction is signified by the grey lines.

5.1.3 Procedure

Accelerating and decelerating stimuli were randomly interlaced across trials within each motion direction condition. Participants completed one condition at a time. They were given at least 80 practice trials prior to the experimental task. Observers completed at least two experimental runs per condition, each containing 10 trials per stimulus value, for a total of 140 acceleration and 140 deceleration trials for each motion direction condition. Due to the difficult nature of the task and performance variability, only the last two usable runs that met the inclusion criterion of goodness of fit were included for analysis.

5.1.4 Analysis

To investigate the effect of pattern type on acceleration and deceleration detection, we performed a 2(pattern type: radial vs. horizontal) x 2(sign of acceleration) repeated measures ANOVA, thereby collapsing across direction within each pattern type. To test whether detection is influenced by horizontal or radial direction we performed a 2(direction) x 2(sign of acceleration) repeated measures ANOVA for the horizontal and radial motion conditions separately. We did not perform a 2(pattern type) x 2(direction) x 2(sign of acceleration) repeated measures omnibus ANOVA because direction within

each pattern type is not equivalent between pattern types, and therefore it is more appropriate to conduct separate ANOVAs for each research question, as opposed to having an overall variable called ‘direction’. The data did not violate the sphericity assumption and therefore no correction was necessary. Table 3 shows the mean absolute 75 % correct acceleration and deceleration detection threshold rates for each condition.

Table 3

Mean absolute 75 % correct acceleration and deceleration detection threshold rates (deg/s²) as a function of motion pattern direction

Condition	Acceleration Rate	Deceleration Rate
	<i>M (SD)</i>	<i>M (SD)</i>
Left	5.12 (1.13)	5.35 (2.32)
Right	5.36 (1.32)	5.52 (2.44)
Expansion	3.55 (0.87)	3.72 (1.12)
Contraction	3.40 (1.66)	3.98 (1.64)

5.2 Results

Pattern type appears to affect the ability to detect acceleration and deceleration because detection is better when viewing radial motion compared to horizontal motion. In addition, acceleration and deceleration are detected similarly, regardless of the pattern viewed. A 2(pattern type) x 2(sign of acceleration) repeated measures ANOVA confirmed these findings. There is a main effect of pattern type, $F(1, 6) = 22.98, p = 0.003, \eta^2_p = 0.79$, as detection thresholds are lower for radial motion than for horizontal motion. However, there is little difference in detection accuracy between the acceleration and deceleration conditions, $F(1, 6) = 0.39, p = 0.56$, and the sign of acceleration does not interact with pattern type, $F(1, 6) = 0.04, p = 0.86$.

Direction of motion does not seem to modulate the effect of pattern type on acceleration

and deceleration detection accuracy (Figure 16), which is supported by two separate 2(direction) x 2(sign of acceleration) repeated measures ANOVAs for the horizontal and radial motion conditions, respectively. There is no effect of horizontal, $F(1, 6) = 1.09, p = 0.34$, or radial direction, $F(1, 6) = 0.03, p = 0.87$, on detection thresholds. Moreover, acceleration and deceleration are detected with similar accuracy within the horizontal motion conditions, $F(1, 6) = 0.05, p = 0.83$, and within the radial motion conditions, $F(1, 6) = 0.84, p = 0.40$. Finally, neither horizontal, $F(1, 6) = 0.06, p = 0.82$, nor radial directions, $F(1, 6) = 1.02, p = 0.35$, interact with the sign of acceleration. We note that the transformed thresholds for the horizontal motion conditions are comparable to those reported in Experiment 1 for the large aperture condition at faster velocities, which is the same velocity range tested in this experiment.

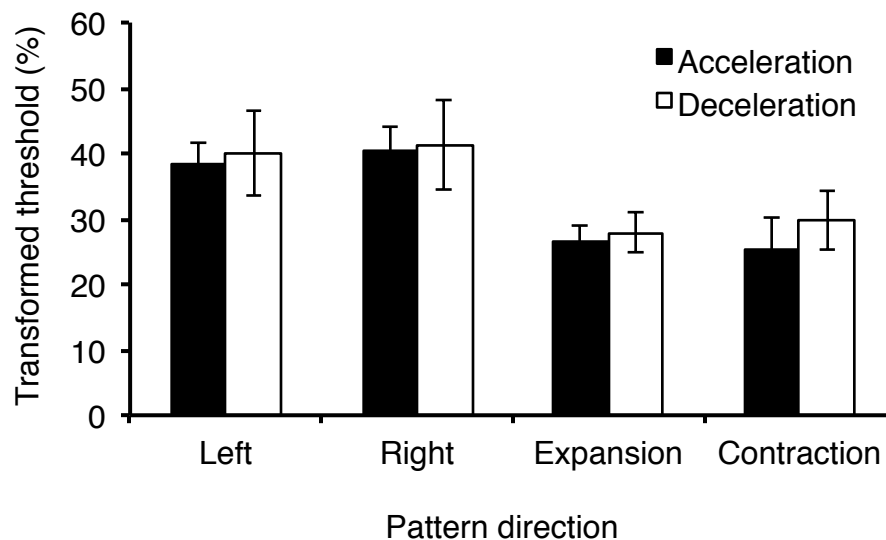


Figure 16. Transformed acceleration and deceleration detection thresholds (%) as a function of pattern direction. Error bars are $\pm 1 SE$.

5.3 Discussion

Our results show that we process radially and horizontally accelerating patterns differently, which suggests that the visual complexity of the motion pattern affects acceleration perception. Nevertheless, we found no effect of radial or horizontal direction

on acceleration or deceleration detection. Moreover, we appear equally sensitive to the presence of acceleration and deceleration, regardless of pattern type or direction, which is consistent with our findings from Experiments 1 and 3.

The absence of a radial anisotropy in sensitivity may be due to the fact that we held the dot parameters (i.e., size, average density, and motion profile) constant across all pattern conditions. This meant that individual frames of the random dot stimuli were indistinguishable between conditions, and therefore it was the global motion of the patterns that allowed participants to distinguish which stimuli belonged to which conditions. Due to this level of control, however, there were no depth cues in the optic flow displays to mimic the motion an observer would typically see when moving through a three-dimensional environment, such as looming or density and speed gradients. (Even though we used displays that had inherent acceleration or deceleration throughout the visual field, speed changes across space are not the same as speed changes with respect to time.) As a consequence of having no depth cues, our radial stimuli were not as realistic as the optic flow we tend to see when navigating the real world—although we note that several earlier studies on the effects of motion pattern type have also used stimuli that had similar departures in ecological validity in order to compare the motion pattern conditions directly (e.g., Aen-Stockdale, Ledgeway, & Hess, 2007; Bertone & Faubert, 2003; Bex et al., 1997; Geesaman & Qian, 1998; Lee & Lu, 2010). Nevertheless, most participants reported that our expanding and contracting optic flow stimuli gave the impression of forward and backward motion, respectively. This suggests that even our simplified motion patterns were compelling enough to elicitvection, which might indicate that our finding of a radial bias in acceleration detection may be consistent with Gibson's (1979) hypothesis that the realism of a stimulus should affect psychophysical performance.

Although beyond the scope of this thesis, it remains to be shown whether depth cues in optic flow displays reliably elicit a radial anisotropy in sensitivity. Several of the earlier studies that reported an asymmetry favouring radial contraction in motion coherence (e.g., Edwards & Badcock, 1993; Meese & Anderson, 2002; Shirai et al., 2006) and apparent speed perception (e.g., Clifford et al., 1999; Geesaman & Qian, 1998) used

radial optic flow stimuli that contained speed gradients. Moreover, Bubka, Bonato, and Palmisano (2008) reported shorter onset and greater magnitude of vection when viewing contracting optic flow than expanding optic flow using stimuli that contained speed gradients and looming. On the other hand, although Beardsley and Vaina (2005) found that direction discrimination thresholds increase when positive speed gradients are replaced with random speed gradients (i.e., the spatial distribution of dot velocity was random), Edwards and Ibbotson (2007) observed that motion coherence thresholds are lower when the speed gradient is removed entirely than when the optic flow stimuli contain positive, negative, or random speed gradients. Given the conflicting evidence, an alternative explanation for earlier reports of a radial anisotropy is that the asymmetry may manifest itself only in certain areas of the visual field, for example around the focus of expansion or contraction (i.e., the centre of optic flow). If this is the case, depending on the size of the stimulus, this difference in sensitivity as a function of eccentricity may drive a radial asymmetry in motion perception. We tested this hypothesis in the sixth experiment of this thesis.

As an aside, Bex and Makous (1997) and Bex et al. (1998) observed that, when using grating stimuli moving at constant velocities, radial motion appears overall faster compared to horizontal motion. We also observed this perceptual bias in the current study using random dot arrays, as did Geesaman and Qian (1998). However, it is unclear whether this may help to explain the asymmetry in acceleration detection, given that Bex et al. found no corresponding difference in velocity discrimination despite the faster apparent speed of radial patterns.

Chapter 6

6 Effects of Retinal Eccentricity and Radial Direction

Experiment 5 revealed that we do not appear to have a radial anisotropy in our sensitivity to visual acceleration and deceleration. Nevertheless, a question that was not addressed is whether sensitivity to the presence of acceleration is uniform across the optic flow field. Earlier studies on heading discrimination have reported that the focus of expansion in the central area of the optic flow field may contribute more strongly to heading perception than the periphery (Crowell & Banks, 1993; Warren & Kurt, 1992). Perhaps the focus of expansion or contraction may provide a more compact area over which the observer can assess the motion profile of the stimulus (i.e., to judge whether it is accelerating) as compared to the periphery. Furthermore, it remains to be demonstrated whether we detect acceleration differently between expanding and contracting optic flow as a function of the stimulus' eccentricity. If so, this may explain why some earlier studies found asymmetries in radial motion sensitivity whereas others did not, depending on the size of the stimuli (and perhaps whether observers fixated the middle of the display).

To answer these questions, we tested the effects of radial direction and retinal eccentricity of optic flow (while participants fixated the centre of the display) on the ability to detect acceleration. As in Experiment 5, we held dot size, average density, and motion profile constant throughout the display. However, we did not measure deceleration sensitivity in this experiment because the other psychophysical experiments demonstrated similar sensitivity to the presence of acceleration and deceleration, as long as the accelerating and decelerating stimuli move within the same velocity range (Experiment 1).

6.1 Method

6.1.1 Participants

We tested seven individuals who had a mean age of 26.6 years ($SD = 3.15$), and five were female.

6.1.2 Stimuli and Apparatus

Radial direction was the first independent variable, with two motion direction conditions: expansion and contraction. Stimulus retinal eccentricity was the second independent variable. Centrally presented stimuli occupied a circular area subtending 10° in diameter (Figure 17) located in the centre of the display. Peripheral stimuli were presented in an annular area with inner and outer diameters of 10° and 20° , respectively, with no dots inside the inner 10° circular area. Dot size ($0.1^\circ \times 0.1^\circ$) and average density (0.75 dots/deg²) were held constant in every condition. The average velocity of all stimuli was 8 deg/s (see *Equation 1*, Chapter 2), and the standard stimulus moved at a constant velocity of 8 deg/s. The comparison stimuli within each condition contained one of seven acceleration rates from a range of 0.75 to 5.25 (deg/s²) in steps of 0.75 deg/s².

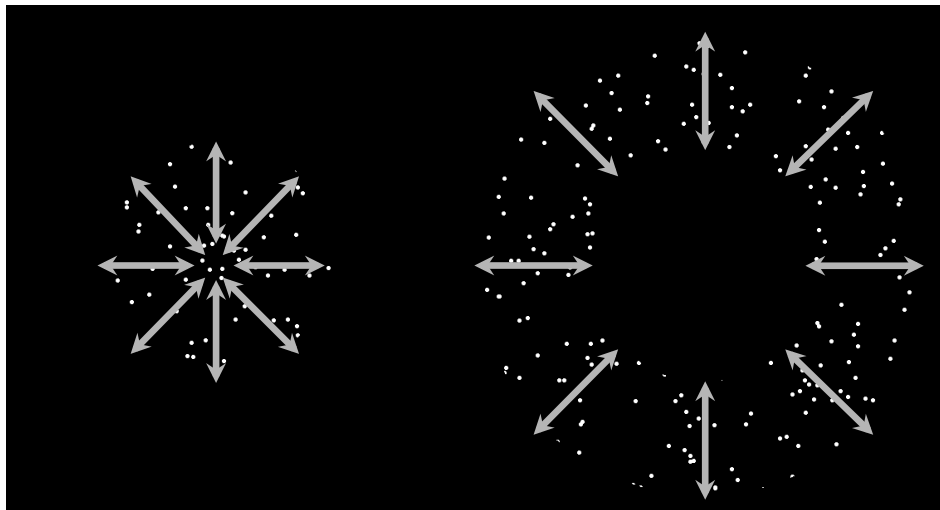


Figure 17. Schematic examples of centrally and peripherally presented random dot arrays. Grey lines signify direction for expanding and contracting motion.

6.1.3 Procedure

Observers were instructed to fixate the centre of the screen at all times. Participants completed at least 40 practice trials before performing the experimental task. They completed runs of 20 trials per acceleration rate per condition and, depending on their performance, between 20 and 40 trials per acceleration rate (i.e., one or two runs) per condition for each participant were included in the analysis.

6.1.4 Analysis

The transformed threshold data were submitted to a 2(radial direction) x 2(retinal eccentricity) repeated measures ANOVA. No correction for the violation of the sphericity assumption was necessary. Table 4 contains the mean absolute 75 % correct acceleration detection threshold rates.

Table 4

Mean absolute 75 % correct acceleration detection threshold rate (deg/s²) as a function of radial direction and retinal eccentricity

Condition		Acceleration Rate
		<i>M (SD)</i>
Expansion	Central	3.00 (0.81)
	Peripheral	2.94 (0.92)
Contraction	Central	3.25 (0.95)
	Peripheral	3.02 (1.15)

6.2 Results

There is no effect of radial direction, $F(1, 6) = 1.46, p = 0.27$, as acceleration detection thresholds are similar between the expansion and contraction conditions. In addition, there is no main effect of stimulus eccentricity on acceleration detection, $F(1, 6) = 0.21, p = 0.66$, as detection thresholds are similar between central and peripheral presentations. There is also no interaction between the experimental variables, $F(1, 6) = 0.07, p = 0.81$ (Figure 18). We also note that the transformed thresholds of the radial motion conditions between Experiment 5 and this experiment are very similar.

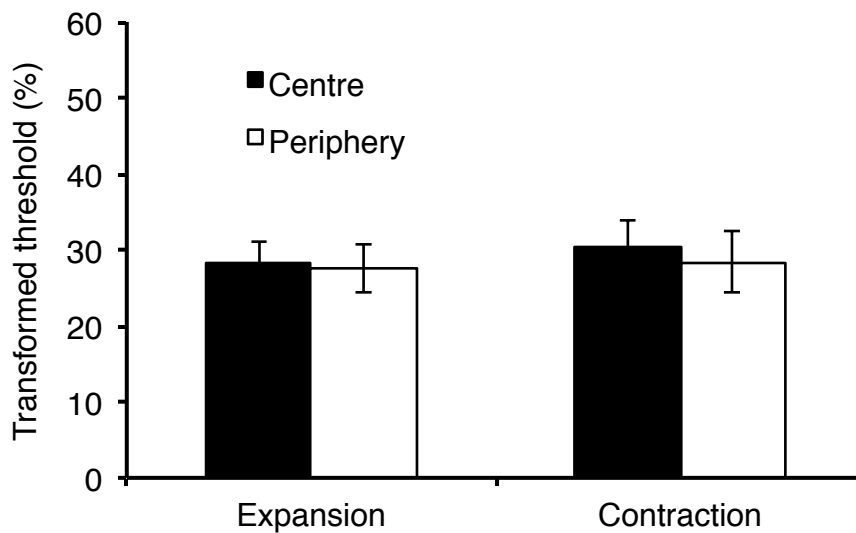


Figure 18. Mean transformed acceleration detection thresholds (%) as a function of radial direction and retinal eccentricity. Error bars are $\pm 1 SE$.

6.3 Discussion

These results demonstrate that the retinal eccentricity of optic flow has little effect on acceleration sensitivity. Our findings suggest that observers do not rely more on the foveal area to process radial acceleration as compared to more peripheral areas. This is consistent with the findings of earlier studies on vection and motion coherence, such as Nakamura and Shimojo (1998) and Habak et al. (2002), respectively, who reported that there is a relatively similar contribution from the central and peripheral areas of the visual field to the overall perception of optic flow. The discrepancy between our findings and those of earlier studies on heading discrimination may be due to differences in experimental task, as separate mechanisms probably underlie heading discrimination and acceleration detection. In addition, consistent with the findings of Experiment 5, we also did not observe an effect of radial direction on acceleration detection. As discussed in Chapter 5, previous reports of radial anisotropies may be due, in part, to differences in stimulus design.

Chapter 7

7 General Discussion

This thesis was designed to explore factors that might play a role in the ability to detect visual acceleration and deceleration. In particular, we asked whether the ‘ecological’ context, in the sense used by Gibson (1954; 1979), might modulate sensitivity to the presence of acceleration and deceleration. We did this by varying the characteristics of the visual display used for measuring acceleration and deceleration detection thresholds. We also examined the potential role of eye movements in acceleration and deceleration perception. Current evidence suggests that our visual system does not contain ‘acceleration detectors’ analogous to the velocity-sensitive neurons found in the visual cortex (Lisberger & Movshon, 1999; Price et al., 2005; Schlack et al., 2007). Instead, it is more likely that acceleration is detected indirectly through the comparison of different velocities over time, as opposed to by the rate of acceleration directly. However, little consideration has been given to the way in which real world-relevant characteristics of a motion pattern and smooth pursuit eye movements may contribute to acceleration sensitivity. To address these issues we conducted a series of six experiments.

Given that we do not always have an unlimited field of view to watch motion in the natural environment, in the first experiment we investigated how the horizontal distance over which a stimulus is visible affects the ability to detect horizontal acceleration and deceleration at different velocities. By varying the size of the aperture on the axis of motion through which the stimuli were viewed we also had an opportunity to determine how smooth pursuit eye movements are affected as a function of velocity in Experiment 2. In the third experiment, we explored how the ability to detect acceleration and deceleration changes on the vertical axis, given that downward motion tends to be more frequent due to the effects of gravity and may be more important for object interception and avoidance than upward motion. Moreover, in Experiment 3 we also explored how sensitivity to the presence of vertical acceleration and deceleration varies depending on the vertical distance over which a stimulus is able to travel. As in Experiment 2, in Experiment 4 we measured how vertical smooth pursuit is influenced by the size of the

vertical aperture in order to further explore how the ability to track is related to our ability to detect the presence of acceleration and deceleration.

Considering the potential roles of the ecological context and visual complexity of motion in acceleration perception, in the fifth experiment we investigated whether the ability to detect acceleration and deceleration changes depending on the type of motion pattern viewed using horizontal translation and radial optic flow. As the radial optic flow field contains information about self-motion and observers have been reported to rely on the focus of optic flow more heavily than the periphery to judge heading (Crowell & Banks, 1993; Warren & Kurt, 1992), in Experiment 6 we tested whether acceleration sensitivity is uniform across the radial optic flow field. We did this by manipulating the location (retinal eccentricity) of optic flow to place the stimulus in the centre or periphery of the observer's visual field.

7.1 Effect of the Extent of Field of View

The area over which an object can move in the natural environment affects many aspects of visual perception. For example, it is harder to discern an object's shape through smaller than larger spaces (hence the aperture problem, where motion vectors appear ambiguous when the observer is unable to see the edges of the stimulus to discern its direction). Similarly, the motion profile of a stimulus should be harder to judge when viewed through a small aperture than a large one, and this is consistent with what we observed in Experiments 1 and 3, in that the ability to detect acceleration and deceleration is better for larger apertures than for smaller ones. A consequence of the stimulus traveling farther distances is that we can track it longer without interruption, as revealed in Experiments 2 and 4. One may argue that this might give the visual system more integration time to register the presence of acceleration, which has been previously demonstrated to improve acceleration sensitivity (Brouwer et al., 2002; Gottsdanker et al., 1961; Timney et al., 2010). However, all of the stimuli were on screen for the same duration, regardless of aperture size. In addition, because we used random dot stimuli, the global motion was continuous in every aperture condition and the same maximum and minimum velocities were presented for a given velocity range across aperture conditions.

Moreover, longer integration time for larger apertures would not explain the findings of other studies, such as Braun et al. (2008), Braun et al. (2010), Haarmeier and Thier (2006), where motion perception tends to be better when pursuing the stimulus than when viewing the same stimulus under fixation. Therefore, it seems unlikely that integration time *per se* can account for the effect of aperture size on perception. Instead, our findings suggest that the important factor about aperture size appears to be the uninterrupted aspect (i.e., dots travel farther before reaching the edge of a larger aperture than a smaller one), which enables the observer to better track the moving stimulus. Consequently, our data indicate that the distance that the stimulus is able to travel changes how sensitive we are to the presence of acceleration.

Although stimulus distance travelled seems to be the most important variable, it is necessary to consider alternative possibilities. It might be argued, for example, that the effects of aperture size on perception and tracking may be due to differences in the number of dots. As a result of our stimulus design holding dot density constant there were more dots per frame in the larger apertures than in the small apertures: on average, there were 1.5 dots in the small apertures, 21.4 dots in the medium apertures, and between 40.5 (in Experiment 3, 34.5 in Experiment 4) to 41.3 (Experiment 1) dots in the large apertures. Even so, it is unclear whether dot number matters, given that the evidence is mixed for its effect on smooth pursuit and motion sensitivity. Heinen and Watamaniuk (1998) reported that dot number as a function of aperture size (on the axis orthogonal to motion) affects smooth pursuit, in that the acceleration of the eye increases and the latency of smooth pursuit decreases as the number of dots increase. However, the authors tested a sample of two participants and found mixed results for an effect of dot density on smooth pursuit, because latency was only affected in one observer. In comparison, Hutchinson, Ledgeway, and Allen (2014) found that motion coherence sensitivity improves as aperture size increases among young adults, regardless of whether dot number or density is held constant across aperture sizes.

We did not manipulate dot density and therefore cannot rule out that the differences in dot number may have a role in the effects of aperture size observed in the first four experiments of this thesis, but we argue that its effect is probably negligible. The

difference in dot number between the small and medium apertures was only half the difference between the small and large apertures, but the differences in dot number between the small and medium apertures and between medium and large apertures were the same. However, we found little difference in the psychophysical and eye movement data between the medium and large aperture conditions across average velocities in Experiments 1 and 2. Consequently, differences in dot number alone cannot account for the effects of aperture size. Rather, there may be a point at which acceleration detection becomes relatively stable once the aperture is large enough to encourage a minimum level of successful tracking, which depends on the stimulus' velocity range as discussed below.

Similarly, perhaps the latency of smooth pursuit can also help to account for our finding of an effect of aperture size on acceleration detection. In the small aperture faster velocity condition, the stimulus accelerated or decelerated so quickly that the dots that appeared initially on one side of the aperture had reached the opposite boundary within the latency of smooth pursuit. Smooth pursuit latency is approximately 150 ms (Carl & Gellman, 1987), which may partially explain why we saw little or very poor pursuit on the horizontal and vertical axes in those conditions, as the eye could not catch up (at least initially) with the accelerating and decelerating stimuli in the faster velocity range for the small aperture condition. In many cases where smooth pursuit was especially poor at faster average velocities, it appears as though participants simply looked at the background of the stimulus in a manner that is similar to fixation. In contrast, smooth pursuit was considerably better in the small aperture condition at slower average velocities, which is consistent with the notion that the eye was able to quickly catch up with the accelerating and decelerating stimuli. Given that several previous studies have reported that many aspects of motion perception are impaired under fixation compared to smooth pursuit (Braun et al., 2008, Braun et al., 2010; Haarmeier & Thier, 2006; Spering, Schütz, et al., 2011; Werkhoven et al., 1992), this would also partly explain why psychophysical performance was poorer in the small aperture conditions than in the larger aperture conditions in Experiments 1 and 3.

7.2 Relationship Between Smooth Pursuit and Acceleration Perception

The similar effects of aperture size on acceleration detection and smooth pursuit are consistent with the findings of earlier studies supporting a relationship (albeit indirect) between the ability to perceive and track visual acceleration (e.g., Braun et al., 2008; Braun et al. 2010; Haarmeier & Thier, 2006; Spering, Schütz et al., 2011). Moreover, we found little difference in smooth pursuit performance between the rates of acceleration and deceleration tested in Experiments 2 and 4 (even for rates that were twice the size of the threshold rates), which indicates that the pursuit system is relatively insensitive to constant acceleration. This insensitivity is similar to that of the perceptual system, as evidenced by the large detection thresholds reported in all of the psychophysical experiments of this thesis, and is consistent with earlier studies (e.g., Watamaniuk & Heinen, 2003).

Nevertheless, velocity range has been reported to have different effects on variable velocity (Hohnsbein & Mateeff, 2002) and constant acceleration perception (Brouwer et al., 2002; Gottsdanker et al., 1961; Timney et al., 2010; Watamaniuk & Heinen, 2003) and smooth pursuit (Ke et al., 2013; Meyer et al., 1985; Schütz et al., 2010; Tychsen & Lisberger, 1986). Our findings from Experiment 1 are consistent with these earlier reports of the different effects of velocity, which altogether point to a functional dissociation between the perceptual and ocular motor systems that has been reported before (Gegenfurtner et al., 2003; González et al., 2014; Spering & Gegenfurtner, 2007; Spering, Pomplun et al., 2011; Tavassoli & Ringach, 2010). Specifically, we appear to be similarly sensitive to the presence of acceleration and deceleration as long as the changes in velocity with respect to time occur within the same velocity range, because detection of both improves as average velocity increases (Experiment 1). In contrast, even though smooth pursuit is similar for accelerating and decelerating stimuli within a velocity range, it worsens as average velocity increases (Experiment 2).

At first glance, the inverse effects of average velocity on acceleration perception and smooth pursuit seem at odds with the fact that the ability to detect acceleration appears to improve with the ability to track. However, our results may be explained by how the

visual system might use the retinal slip produced during pursuit to detect the presence of acceleration and deceleration as a function of velocity, in light of the findings of Haarmeier and Thier (2006) as discussed in Chapters 1 and 3. In particular, as more retinal slip is generated at faster than slower velocities, observers seem to need relatively smaller differences between the initial and final velocities of the comparison stimuli relative to the standard stimuli to detect the presence of acceleration at faster velocities than at slower velocities. That said, as indicated by Haarmeier and Thier's patient data, there appears to be an optimal amount of retinal slip necessary and too much can result in systematic biases that lead to inaccurate perception. Our observation that the effect of aperture size on psychophysical performance and smooth pursuit is relatively constant across average velocities supports the notion that observers may require an optimal amount of retinal slip to gauge the presence of acceleration.

7.3 Ecological Influence of Vertical Direction

Vertical motion is essential for everyday goal-directed activities, however our experience with it tends to be asymmetrical due to the frequency and behavioural relevance of downward and upward events. Experiment 3 revealed that this vertical anisotropy is reflected in our sensitivity to vertical acceleration, in that we appear to detect downward acceleration better than upward acceleration. Our results also showed that the downward bias in detection persists for deceleration and that we are similarly sensitive to acceleration and deceleration within each direction. This downward bias may be related to a perceptual advantage for locomotion and interactions with objects, as discussed in Chapter 4. Specifically, having a higher sensitivity to downward acceleration may be beneficial for monitoring the observer's rate of motion relative to obstacles (which we elaborate upon below in *Radial Optic Flow Bias*) in order to avoid falling. This is similar to the interpretation made by Marigold and Patla (2008), who found that we have a predisposition to monitor the lower visual field when walking on varied terrain. In addition, the downward bias in acceleration detection would be advantageous for catching or avoiding falling objects accurately in most everyday situations (Moscatelli & Lacquaniti, 2011; Senot et al., 2005).

Although a higher sensitivity to downward acceleration has numerous behavioural advantages, we are still relatively insensitive to the presence of acceleration overall, as shown by the high thresholds found in Experiment 3. If the visual system does not have visual acceleration detectors, this might lead one to wonder how this asymmetry is possible, and the findings of Indovina et al. (2005) may help to explain how this occurs. As discussed in Chapter 4, the authors observed that the vestibular network activates when the visual system processes acceleration that is consistent with the effects of gravity. They suggested that its selective activation may be due to the visual system accessing a stored internal model of gravity in the vestibular network to process visual acceleration. Even though the visual system does not appear to contain neurons that are tuned to specific rates of acceleration, vestibular organs such as the semicircular canals are inherently sensitive to acceleration and deceleration, but insensitive to constant velocity and, in fact, register constant velocity in a similar manner to when stationary (Waespe & Henn, 1977). Studies onvection illustrate how sensitive the vestibular network is to visual information, given that sensations of self-motion can be induced solely with visual optic flow stimuli (Bubka et al., 2008; Palmisano et al., 2008). Therefore, according to Indovina et al., the vestibular network may provide a means for the visual system to adaptively respond to vertical changes in velocity with respect to time, which in turn may explain our findings for a general downward bias in acceleration and deceleration detection.

7.4 Radial Optic Flow Bias

Gibson (1954; 1979) suggested that psychophysical performance in a laboratory setting should be more representative of perception in the real world when observers are tested with more realistic stimuli. The downward bias in acceleration detection suggests that the ecological relevance of direction influences sensitivity. In a similar vein, outside the laboratory we generally see complex optic flow more often than pure translation (although we do still see lateral motion in the natural environment). Radial optic flow tends to occur whenever we move through the environment while looking straight ahead, although it is less commonly experienced than combinations of radial, translational, and rotational optic flow, which arise from changes in self-motion and object trajectory.

Nevertheless, for the purpose of Experiment 5, we used the simplest form of optic flow that human observers can experience outside the laboratory so that we could control the dot parameters and make direct comparisons of psychophysical performance between motion pattern types. Experiment 5 revealed that sensitivity to the presence of acceleration is higher for radial motion than for horizontal motion, and there is no difference between acceleration and deceleration detection overall. This suggests that the type of motion pattern viewed affects how well we can detect the presence of acceleration. Given that the rate of radial optic flow can help to inform the observer about his or her rate of movement through the environment (Prokop, Schubert, & Berger, 1997), having a higher sensitivity to radial acceleration may have important implications for navigating and interacting with objects.

The functional hierarchy of how motion is processed in the visual system may also help to explain the radial bias in acceleration perception. As discussed in Chapter 1, simpler aspects of motion such as local components (e.g., temporal and spatial frequencies) tend to be processed relatively earlier in the visual pathway, for example in areas as early as V1 (Hubel & Wiesel, 1968; Singh et al., 2000), than more complex features, such as form, depth, and heading (Andersen, 1997; Andersen et al., 1990; Maunsell & Van Essen, 1983; Van Essen & Gallant, 1994). In contrast, the coding of complex motion patterns occurs later on, in areas such as MST, by neurons that have larger receptive fields tuned to specific patterns, such as radial, translational, and rotational motion (Duffy & Wurtz, 1991a; Duffy & Wurtz, 1991b; Tanaka, Fukada, & Saito, 1989; Tanaka & Saito, 1989). Moreover, higher order areas, such as MST and VIP, are involved in processing heading information in optic flow (Bremmer, Duhamel, Ben Hamed, & Graf, 2002; Britten & van Wezel, 2002; Duffy & Wurtz, 1995; Zhang & Britten, 2011), and MST has been reported to show greater activation in response to radial optic flow than to translation (Smith et al., 2006). Therefore, it is possible that the self-motion cues in radial motion may induce the recruitment of those higher-order areas and, as a result, this greater processing power may be responsible for the difference in acceleration detection between horizontal and radial motion.

An interesting result arose when we compared the data from Experiments 5 and 6. In Experiment 5 participants were free to move their eyes around the visual field once the random dot stimuli were presented. In comparison, in Experiment 6 they were required to fixate the centre of the screen at all times. Despite differences in task instructions, dot parameters, and aperture size (the aperture size in Experiment 5 was more than twice as large as the two used in Experiment 6), acceleration detection thresholds are very similar between Experiments 5 and 6 (on average, 29 % and 28 %, respectively). It is unclear why performance is so consistent between these different experimental conditions. One might wonder whether observers attended more to the centre of the visual field than the periphery in Experiment 5, which would have resulted in limited tracking. Moreover, one might argue that it is more difficult to track radial motion than horizontal motion because dots move in all cardinal and oblique directions, which may also encourage observers to attend to certain areas, such as the centre, instead of the whole field. However, Experiment 6 revealed that there is no difference in acceleration sensitivity between the central and peripheral areas of optic flow. In addition, observers tend to make vergence eye movements (Busettini, Masson, & Miles, 1997), as well as optokinetic nystagmus and smooth pursuit (Niemann, Lappe, Büscher, & Hoffmann, 1999) in response to radial motion. Moreover, Niemann et al. found that observers can track individual dots in radial optic flow well when instructed to (OKN tends to be elicited when observers are instructed to attend to the whole field). Furthermore, a lack of tracking does not seem consistent with our findings that smooth pursuit improves motion sensitivity (Experiments 1 and 3), given that we demonstrated acceleration sensitivity is much higher for radial motion than horizontal motion in Experiment 5.

Another possibility is that participants may have not followed the instructions to maintain fixation in the centre of the display in Experiment 6, especially because we did not use a fixation cross during the random dot stimuli presentations in order to avoid relative motion cues. Consequently, as we did not record eye movements to ensure that participants fixated the centre of the screen, one might argue that the similarity in performance could actually be the result of tracking. However, this is unlikely because participants are generally able to maintain fixation when instructed to do so, especially if they are experienced observers (Braun et al., 2008), which most of the participants in

Experiment 6 were. Moreover, several participants reported that the task was difficult to do because of the instruction to maintain fixation, which indicates that they were adhering to the task instructions in Experiment 6. Therefore, instead, it is possible that radial acceleration perception is relatively insensitive to eye movements (and possibly aperture size) in general.

7.5 Future Directions

Even though we hypothesized that there may be a radial anisotropy in acceleration perception favouring expansion, as a result of our tendency to experience expansion more frequently than contraction because we move forward more often than backward, we did not observe an effect of radial direction on acceleration or deceleration detection. Perhaps the reason for this is because of our methodological control of dot parameters, as discussed in Chapter 5. It is possible that with looming cues and density gradients a radial anisotropy in acceleration and deceleration sensitivity may emerge in a manner that is consistent with our everyday experience. Given that it is to the observer's advantage to detect imminent collisions with approaching objects, one might expect a higher sensitivity to accelerating expansion than to decelerating expansion. This asymmetry might occur because it should be more important to detect when we are accelerating through the environment, or when objects are speeding up towards us, in order to avoid collisions (or to detect when we are falling, which would also result in accelerating expansion). There is support for this with respect to looming sensitivity for a single object stimulus (although not a radial optic flow field), as Trehwella et al. (2003) reported that observers are better at detecting an accelerating than decelerating rate of expansion of a black disc. However, an asymmetry between acceleration and deceleration detection may not exist for contracting optic flow, which is associated with backward self-motion or retreating object motion, and therefore there would be no time-to-contact cues in that direction.

A further consideration is how the realism of the motion stimulus influences the downward bias we observed in Experiment 3, which was relatively modest in comparison to the overall size of the sample's thresholds. Studies such as Moscatelli and Lacquaniti

(2011) used various stimuli to assess the role of contextual cues of gravity on the precision of motion duration discrimination. The authors found that, when using pictorial stimuli, duration discrimination was more precise for downward acceleration than upward, leftward, or rightward acceleration. However, when the authors tested non-pictorial stimuli containing abstract geometrical objects they found that those stimuli still elicited less precise judgments for upward motion, but downward and horizontal acceleration durations were judged with similar precision. In addition, using the abstract stimuli they also tested oblique motion (i.e., upward and downward motion containing horizontal components) and observed that the downward bias disappeared. Interestingly, moreover, when they tilted the monitor at a 45 ° angle using pictorial cues they reported that the downward bias remained but was weaker than when the monitor was upright. Therefore, the question remains as to whether the downward bias in the ability to detect the presence of acceleration and deceleration changes (perhaps it increases in strength) when using a pictorial stimulus.

There are three reasons why we did not use any of those types of stimuli in this thesis. First, it would not have been possible to control the dot parameters in order to make comparisons between Experiments 1 and 3 for the effect of aperture size on psychophysical performance (as well as to draw comparisons between Experiments 5 and 6) or between Experiments 2 and 4 for the effect of aperture size on smooth pursuit. Second, although pictorial stimuli have the advantage of presenting strong contextual cues of the effects of gravity, they also have relative motion cues throughout the display, which are unavoidable, but may confound any effects of vertical direction on acceleration and deceleration perception. Third, random dot stimuli allow for the continuous presentation of motion, regardless of aperture size or average velocity. This allowed us to test aperture sizes as small as 1 ° x 1 °.

7.6 Conclusions

This thesis has demonstrated that the ability to detect visual acceleration is affected by real world-relevant motion pattern characteristics. Results indicate that, although general detection improves as average velocity increases, there is little difference in our

sensitivity to the presence of acceleration and deceleration within each velocity range. As humans often see motion in the world through spaces between objects, we have shown that the extent over which a stimulus can travel uninterrupted changes our ability to detect acceleration. Specifically, the farther the stimulus is able to travel the better we are at tracking it and the more sensitive we are to the stimulus' acceleration. Similarly, and consistent with the observation that downward motion tends to be more frequent and relevant to voluntary tasks due to the influence of gravity, we also found that humans are better at detecting downward than upward acceleration and deceleration. Furthermore, we observed that humans are better at detecting acceleration in more complex patterns, in that we detect radial acceleration better than horizontal acceleration. In addition, sensitivity to radial acceleration appears to be relatively uniform across the visual field. The heightened sensitivity for radial acceleration may provide the observer with an advantage for safely navigating the environment and interacting with objects, which would be similar to the advantages of a downward bias in acceleration perception. In conclusion, even though observers detect the presence of acceleration and deceleration similarly across a wide range of conditions, overall acceleration perception appears to be affected by the unique characteristics of the motion pattern.

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Appendix A

Evaluating the Psychophysical Paradigm

As described in the Introduction (Chapter 1), there are discrepancies in the literature as to whether our sensitivity to acceleration and deceleration might be different. It is possible that some of these conflicting reports arose from the specific methodologies of individual experiments. In particular, the velocity ranges for velocity increase and decrease conditions were sometimes different because the investigators held constant the initial or final velocities of the stimuli (or both, e.g., Hohnsbein & Mateeff, 2002). In this thesis we took a different approach, holding the average velocity constant for both the acceleration and deceleration conditions in a given experiment and allowing the initial and final velocities to vary. This meant that there was an equivalent but opposite deceleration rate for each acceleration rate. In addition, because every psychophysical experiment used a 2IFC task, there was another benefit to this method of controlling velocity range for the average velocities tested in this thesis. That is, the dots in the standard and comparison stimuli traveled the same distance across the screen within each condition. Consequently, observers could not use dot distance traveled to make their judgments about which stimulus accelerated or decelerated in a given trial. Nevertheless, it was still possible that participants performed the psychophysical tasks in ways that may not have been expected.

For every trial in each psychophysical experiment of this thesis, an accelerating or decelerating stimulus (i.e., a comparison stimulus) and a stimulus moving at constant velocity (i.e., a standard stimulus) were presented in random order. Early pilot testing revealed that the task of detecting changes in velocity was easier when the acceleration and deceleration conditions were blocked separately as compared to when the conditions were randomly interleaved across trials. This is probably because there is a higher cognitive load associated with the interleaved task, given that it requires participants to discriminate between constant and variable velocity while keeping in mind the sign of the acceleration. The blocked task, on the other hand, requires participants only to discriminate between acceleration (or deceleration) and constant velocity. It is possible

that the brevity of the stimulus likely makes the difference in cognitive load more important than it would be for tasks with longer stimulus presentations.

As a consequence of our velocity range control, accelerating stimuli always started slower whereas the decelerating stimuli started faster than the standard stimuli (the reverse was true for the final velocities). Hypothetically, given that we blocked the acceleration and deceleration conditions in Experiments 1 and 3 (and Experiment 6 only tested acceleration), it is possible that participants were comparing the initial or final velocities of the standard and comparison stimuli as their criterion for judging the presence of acceleration or deceleration, rather than detecting the continuous changes in velocity (or the difference between the initial and final velocity of a given stimulus) *per se*. To address this possibility, we conducted two control experiments to test whether participants were actually performing the tasks by detecting changes in velocity over time. It should be noted that because the average velocities in the standard and comparison stimuli were identical it would have been impossible to make discriminations on that basis.

We explored the possibility that observers may have used the initial or final velocity differences between the comparison and standard stimuli by changing the task so that they were not able to use this information. In Experiment 5, we presented accelerating and decelerating stimuli in random order across trials in a velocity change detection task, and consequently participants could not have relied on an initial or final velocity discrimination strategy to do that task. In the present experiment (Experiment A1), we separated the acceleration and deceleration stimuli into individual detection tasks using the same experimental conditions as Experiment 5.

As described in Chapter 1, variable velocity and acceleration detection thresholds tend to be much higher than constant velocity discrimination thresholds (Brouwer et al., 2002; Calderone & Kaiser, 1989; Snowden & Braddick, 1991; Watamaniuk & Heinen, 2003; Werkhoven et al., 1992). Therefore, if participants had been using a velocity change detection strategy to identify accelerating and decelerating stimuli in our experiments, performance should be very similar between Experiment 5 and Experiment A1. However,

if they had been using a velocity discrimination strategy based on either the initial or final velocities of the standard and comparison stimuli in the other experiments, then performance in Experiment A1 should be better than in Experiment 5.

A.1 Experiment A1

A.1.1 Method

A.1.1.1 Participants. Ten participants (including author ASM) with an average age of 26.9 years ($SD = 3.57$ years) comprised the sample, and six were female. Four of these individuals had also participated in Experiment 5. Five additional participants (not included in the sample N) were recruited but unable to do the task with the fixed acceleration and deceleration rates (described below) and were consequently removed.

A.1.1.2 Stimuli and apparatus. The same apparatus and stimuli used in Experiment 5 were used in this experiment, except the radial contracting stimuli. This is because we used version 2.87 of VPixx in Experiment A1 and as a result of a software error we discovered in that version of VPixx, which affected the presentation of acceleration and deceleration in radially contracting patterns, we had to remove the data belonging to the radial contraction condition. Nevertheless, Experiments 5 and 6 were conducted using version 3.14 (in which the software error had been corrected) and we were able to show in those experiments that there is no difference in acceleration and deceleration detection between radially expanding and contracting motion conditions. Therefore, in order to compare performance between Experiments 5 and A1 to determine the type of strategy observers were using to do the tasks, we will only present the data from the leftward, rightward, and expanding motion conditions here.

A.1.1.3 Procedure. This experiment used the same procedure described in Chapter 2: *General Psychophysical Method*, and acceleration and deceleration were blocked separately. There were seven rates of acceleration or deceleration in a range of ± 1 to 7 deg/s^2 in steps of $\pm 1 \text{ deg/s}^2$ for the comparison stimuli in each condition (the same range of stimulus values was used for every participant). The standard stimulus moved at a constant velocity of 10 deg/s . Participants were given at least 240 practice trials prior to

the experimental task. A minimum of 20 experimental trials per stimulus value was included per condition for analysis (the maximum number of trials included was 60).

A.1.2 Results

Both Experiments A1 and Experiment 5 show the same pattern of results for an effect of pattern type, in that acceleration and deceleration are detected similarly and overall detection is better for radial motion than for horizontal motion. In addition, performance for the radial expansion condition is comparable between both studies and similar to the performance observed for both radial motion conditions in Experiment 6. Table A1 show the mean absolute 75 % correct acceleration detection threshold rates for Experiment A1.

Table A1

Mean absolute 75 % correct acceleration and deceleration detection threshold rates (deg/s²) as a function of motion pattern direction in Experiment A1

Condition	Acceleration Rate	Deceleration Rate
	<i>M (SD)</i>	<i>M (SD)</i>
Left	4.68 (1.53)	4.41 (0.89)
Right	4.55 (1.48)	4.31 (0.92)
Expansion	3.39 (1.43)	3.48 (1.55)

Although thresholds are slightly higher in the horizontal motion conditions in Experiment 5 as compared to in this experiment (Figure A1), this is the result of the stimulus value range used in Experiment 5. Using the method of constant stimuli, Experiment 5 had a wider range of stimulus values, which enabled us to test participants who would have been unable to do the task with the range that we had used for Experiment A1. Likewise, the participants who needed the stimulus value range to be shifted up (i.e., to make the task easier) required a greater shift in the range for the horizontal motion conditions than for the radial motion conditions, which explains why performance for the radial

conditions is similar between experiments. This is because it is harder to detect acceleration and deceleration in horizontal motion than in radial motion, which reflects the purpose of Experiment 5.

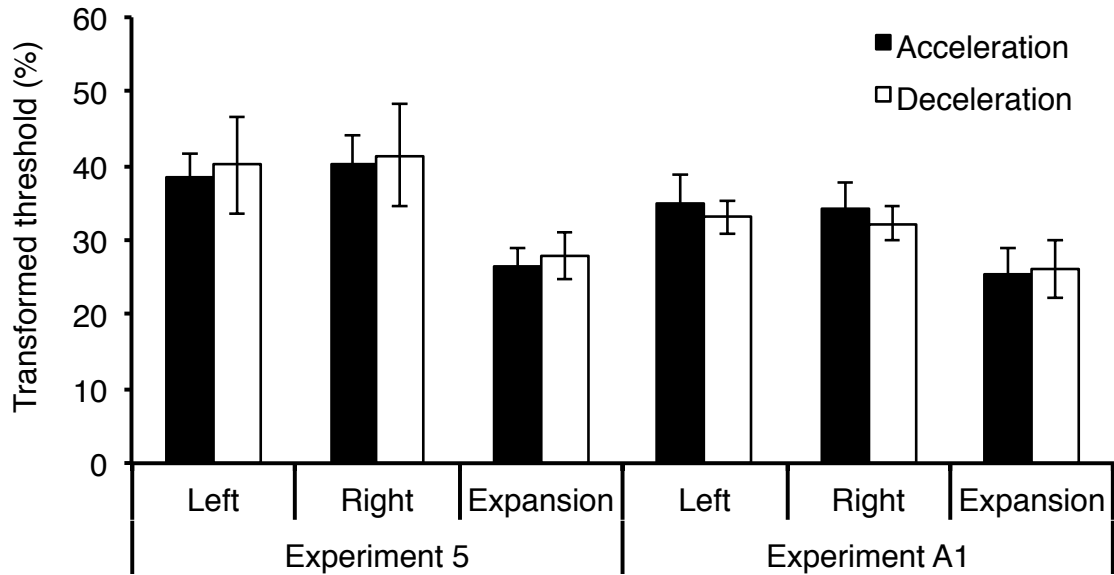


Figure A1. Mean transformed acceleration and deceleration detection thresholds (%) as a function of pattern direction (excluding radial contraction) for Experiments 5 and A1. Error bars are $\pm 1 SE$.

Nevertheless, in order to rule out the possibility that the differences in performance for the horizontal motion conditions between Experiments 5 and A1 were due to different strategies, we conducted another experiment (Experiment A2) using horizontal motion to compare against the data in Experiment A1. In Experiment A2, we restricted the stimulus values to fall between ± 1 and 7 deg/s^2 in steps of $\pm 1 \text{ deg/s}^2$, which is the same range used in Experiment A1, and randomly interlaced acceleration and deceleration using the same method as in Experiment 5. We tested only rightward motion in Experiment A2 because both Experiments 5 and A1 showed little difference in performance between the leftward and rightward conditions.

A.2 Experiment A2

A.2.1 Method

A.2.1.1 Participants. This sample was composed of six individuals (including author ASM) with an average age of 26.8 years ($SD = 2.56$), two of whom were female. Three of these individuals had also participated in Experiments 5 and A1. Two other individuals (not included in the sample N) were recruited to participate but could not do the experiment within the stimulus value range used and were therefore removed.

A.2.1.2 Stimuli and apparatus. The same apparatus and rightward motion stimuli used in Experiment A1 were used in this experiment.

A.2.1.3 Procedure. This experiment used the same procedure as Experiment 5, except all the usable runs that met the inclusion criteria were included for analysis. The same rates of acceleration and deceleration used in Experiment A1 were used in this experiment and the standard stimulus always moved at 10 deg/s. Participants performed a minimum of 8 practice trials prior to the experimental task. A minimum of 10 trials and a maximum of 40 trials per stimulus value for each condition were included for analysis.

A.2.2 Results

As anticipated, there is no difference in performance between the acceleration and deceleration conditions. Furthermore, the transformed thresholds between the acceleration and deceleration conditions in this experiment are very similar to those in the rightward condition in Experiment A1 (Figure A2). Therefore, the difference in detection thresholds in the horizontal conditions between Experiments 5 and A1 appears to be due to the range of stimulus values tested in the comparison stimuli. Specifically, by having a wider range in Experiment 5, we were able to test participants who could not have done the task in Experiment A1 with such a narrow range. In Experiment A2, the mean absolute 75 % correct detection threshold rate for the acceleration condition is 4.52 deg/s² ($SD = 1.32$) and for the deceleration condition is 4.98 deg/s² ($SD = 1.67$).

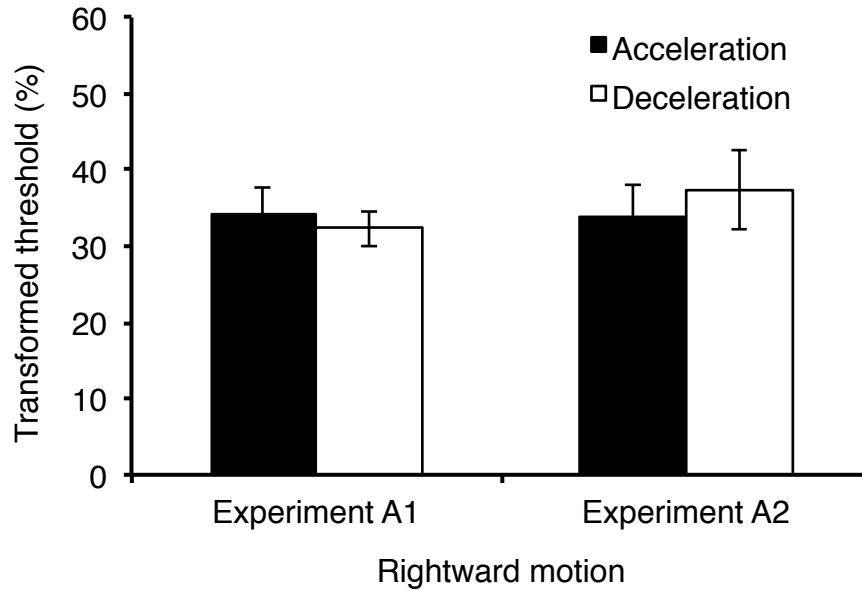


Figure A2. Mean transformed acceleration and deceleration detection thresholds (%) for Experiments A1 (rightward condition only) and A2. Error bars are $\pm 1 SE$.

Although the deceleration detection thresholds appear to be slightly higher in Experiment A2, this is due to performance variability. As explained in Chapter 2, the task with acceleration and deceleration randomly interlaced was more challenging than the task with acceleration and deceleration blocked separately. Nevertheless, participants began to perform reliably with enough practice, and therefore when we analyze only the last two usable runs that met the inclusion criteria for analysis (as we did in Experiment 5), the minor difference in Experiment A2 disappears.

A.3 Discussion

Similar results and thresholds were obtained within each comparable motion direction condition between Experiments 5, A1, and A2, which suggests that observers detected changes in velocity over time to do the tasks in our previous experiments, instead of using an initial or final velocity discrimination strategy. These findings indicate that holding the middle velocity (i.e., average velocity) of the stimuli constant is a useful way of investigating acceleration and deceleration detection within the same velocity range.

As discussed in Chapter 1, support for a difference between velocity discrimination and

acceleration detection/discrimination comes from the well documented observation that it is far more difficult for humans to discriminate between contiguously presented velocities than to discriminate between temporally separate velocities (e.g., Snowden & Braddick, 1991; Werkhoven et al., 1992). The transformed threshold values reported in every psychophysical experiment in this thesis are considerably larger than would be expected had participants been using a velocity discrimination strategy. In contrast, Weber fractions around 4 to 7 % have been reported throughout the literature for various studies on velocity discrimination using a wide range of stimulus parameters (e.g., De Bruyn & Orban, 1988; Clifford et al., 1999; Mateeff et al., 2000; McKee, 1981; McKee & Nakayama, 1984; Orban et al., 1984; Orban et al., 1985; Snowden & Braddick, 1991). However, our argument is not for the exact values of 4 to 7 %, but rather how small, relatively speaking, those Weber fractions are for velocity discrimination compared to those we obtained for our experiments. Moreover, motion integration has been reported to occur over periods as brief as 100 ms (e.g., Huff & Papenmeier, 2013; McKee & Welch, 1985; Snowden & Braddick, 1991; Werkhoven et al., 1992). Therefore, if observers had been performing the tasks in this thesis by comparing the initial or final velocities of the standard and comparison stimuli, which were temporally separated stimuli, we would have expected performance to be far better than we observed. In summary, given the size of the thresholds we have reported and our findings for similar performance between blocked and randomly interlaced detection tasks, we conclude that participants detected changing velocity in the comparison stimuli to do all of the psychophysical tasks reported in this thesis.

Appendix B

Ethics Approval



Western
Research

Research Ethics

Western University Health Science Research Ethics Board
NMREB Annual Continuing Ethics Approval Notice

Date: February 03, 2015
Principal Investigator: Prof. Brian Timney
Department & Institution: Social Science, Western University

NMREB File Number: 104931
Study Title: Perception of visual acceleration and deceleration in horizontal motion
Sponsor:

NMREB Renewal Due Date & NMREB Expiry Date:
Renewal Due -2016/01/31
Expiry Date -2016/02/13

The Western University Non-Medical Research Ethics Board (NMREB) has reviewed the Continuing Ethics Review (CER) form and is re-issuing approval for the above noted study.

The Western University NMREB operates in compliance with the Tri-Council Policy Statement Ethical Conduct for Research Involving Humans (TCPS2), Part 4 of the Natural Health Product Regulations, the Ontario Freedom of Information and Protection of Privacy Act (FIPPA, 1990), the Ontario Personal Health Information Protection Act (PHIPA, 2004), and the applicable laws and regulations of Ontario.

Members of the NMREB who are named as Investigators in research studies do not participate in discussions related to, nor vote on such studies when they are presented to the REB.

The NMREB is registered with the U.S. Department of Health & Human Services under the IRB registration number IRB 00000941.



Ethics Officer to Contact for Further Information

Erika Basile	Grace Kelly	Mina Mekhail	Vikki Tran
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Western University Health Science Research Ethics Board
HSREB Annual Continuing Ethics Approval Notice

Date: January 28, 2015
Principal Investigator: Prof. Brian Timney
Department & Institution: Social Science, Western University

HSREB File Number: 104343
Study Title: Perception of visual acceleration and deceleration in vertical motion
Sponsor:

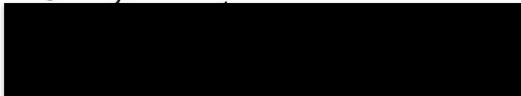
HSREB Renewal Due Date & HSREB Expiry Date:
Renewal Due -2016/01/31
Expiry Date -2016/02/13

The Western University Health Science Research Ethics Board (HSREB) has reviewed the Continuing Ethics Review (CER) Form and is re-issuing approval for the above noted study.

The Western University HSREB operates in compliance with the Tri-Council Policy Statement Ethical Conduct for Research Involving Humans (TCPS2), the International Conference on Harmonization of Technical Requirements for Registration of Pharmaceuticals for Human Use Guideline for Good Clinical Practice (ICH E6 R1), the Ontario Freedom of Information and Protection of Privacy Act (FIPPA, 1990), the Ontario Personal Health Information Protection Act (PHIPA, 2004), Part 4 of the Natural Health Product Regulations, Health Canada Medical Device Regulations and Part C, Division 5, of the Food and Drug Regulations of Health Canada.

Members of the HSREB who are named as Investigators in research studies do not participate in discussions related to, nor vote on such studies when they are presented to the REB.

The HSREB is registered with the U.S. Department of Health & Human Services under the IRB registration number IRB 00000940.



Ethics Officer to Contact for Further Information

Erika Basile	Grace Kelly	Mina Mekhail	Vikki Tran

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Western University Non-Medical Research Ethics Board
NMREB Amendment Approval Notice

Principal Investigator: Prof. Brian Timney
Department & Institution: Social Science, Western University

NMREB File Number: 104932
Study Title: Perception of visual acceleration and deceleration in radial motion
Sponsor:

NMREB Revision Approval Date: July 30, 2015
NMREB Expiry Date: February 13, 2016

Documents Approved and/or Received for Information:

Document Name	Comments	Version Date
Revised Letter of Information & Consent		2015/04/20
Other	Debriefing	2015/04/20
Revised Western University Protocol		2015/07/23

The Western University Non-Medical Science Research Ethics Board (NMREB) has reviewed and approved the amendment to the above named study, as of the NMREB Amendment Approval Date noted above.

NMREB approval for this study remains valid until the NMREB Expiry Date noted above, conditional to timely submission and acceptance of NMREB Continuing Ethics Review.

The Western University NMREB operates in compliance with the Tri-Council Policy Statement Ethical Conduct for Research Involving Humans (TCPS2), the Ontario Personal Health Information Protection Act (PHIPA, 2004), and the applicable laws and regulations of Ontario.

Members of the NMREB who are named as Investigators in research studies do not participate in discussions related to, nor vote on such studies when they are presented to the REB.

The NMREB is registered with the U.S. Department of Health & Human Services under the IRB registration number IRB 0000941.



Ethics Officer to Contact for Further Information

Erika Basile	Grace Kelly	Mina Mekhail	Vikki Tran
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University Health Network
Research Ethics Board



Notification of REB Continued Approval

Date: February 27th, 2015

To: Dr. Esther Gonzalez



Re: 13-5840-AE
Perception of Visual Acceleration and Deceleration

REB Review Type:	Expedited
REB Initial Approval Date:	March 11th, 2013
REB Annual Approval Date:	March 11th, 2015
REB Expiry Date:	March 11th, 2016

The UHN Research Ethics Board operates in compliance with the Tri-Council Policy Statement; ICH Guideline for Good Clinical Practice E6(R1); Ontario Personal Health Information Protection Act (2004); Part C Division 5 of the Food and Drug Regulations; Part 4 of the Natural Health Products Regulations and the Medical Devices Regulations of Health Canada. The approval and the views of the REB have been documented in writing.

Furthermore, members of the Research Ethics Board who are named as Investigators in research studies do not participate in discussions related to, nor vote on such studies when they are presented to the REB.

Best wishes on the successful completion of your project.

Sincerely,



Research Ethics Coordinator

For: Alan Barolet, MD PhD FRCPC
Co-Chair, University Health Network Research Ethics Board

Curriculum Vitae

Name: Alexandra S. Mueller

Post-secondary Education and Degrees: University of Guelph
Guelph, Ontario, Canada
2005 – 2009 B.A. Hons.

University of Guelph
Guelph, Ontario, Canada
2009 – 2011 M.A.

University of Western Ontario
London, Ontario, Canada
2011 – 2015 Ph.D.

Honours and Awards:

Entrance scholarship
University of Guelph
2005

Dean's Honours List for academic
excellence
University of Guelph
2005 – 2009

Ontario Textbook and Technology Grant
2009

College of Social and Applied Human
Sciences Dean's Scholarship
University of Guelph
2009 – 2010

Board of Graduate Studies Research
Scholarship
University of Guelph
2010

'Best in theme' poster award in the Council
for Automotive Human Resources
AUTO21 HQP Poster Competition
2011

Canadian Psychological Association
Certificate of Academic Excellence
2012

Honda Outstanding Student Paper Award
sponsored by Honda R&D Americas, Inc.
2013

Ontario Graduate Scholarship
2011 – 2015

Western Graduate Research Scholarship
University of Western Ontario
2011 – 2015

AGE-WELL Graduate Student and
Postdoctoral Award in Technology and
Aging
2015

AGE-WELL-NCE Conference and General
Meeting travel subsidy
2015

Related Work Experience:

Volunteer undergraduate research
internship
University of Guelph
2007

Volunteer undergraduate research assistant
University of Guelph
2007

Graduate Teaching Assistant
University of Guelph
2009 – 2011
The University of Western Ontario
2011 – 2015

Graduate Research Assistant
University of Guelph
2009 – 2011
University of Western Ontario
2011 – 2015

Journal Peer-Reviewer
Accident Analysis and Prevention,
Transportation; Research Part A: Policy

*and Practice; and Transportation Research
Part F: Traffic Psychology and Behaviour
2013 – 2015*

Postdoctoral fellowship
McMaster University
2015 – present

Publications:

- Mueller, A. S., & Timney, B. (2014). Effects of radial direction and eccentricity on acceleration perception. *Perception*, *43*, 805 – 810.
- Mueller, A. S., & Trick, L. M. (2013). Effect of driving experience on change detection based on target relevance and size. *Proceedings of the Seventh International Driving Symposium on Human Factors in Driving Assessment, Training, and Vehicle Design*, Bolton Lake, NY, 341 – 347.
- Mueller, A. S., & Trick, L. M. (2012). Driving in fog: The effects of driving experience and visibility on speed compensation and hazard avoidance. *Accident Analysis and Prevention*, *48*, 472 – 479.
- Mueller, A. S., González, E. G., McNorgan, C., Steinbach, M. J., & Timney, B. (2015). *Effects of vertical direction and aperture size on visual acceleration perception*. Manuscript accepted for publication pending revision in *Perception*.

Manuscripts in Preparation:

- Mueller, A. S., & Timney, B. (2015). *Visual acceleration perception for simple and complex motion*. Manuscript in preparation.
- Mueller, A. S., González, E. G., McNorgan, C., Steinbach, M. J., & Timney, B. (2015). *Effects of spatial and temporal constraints on the perception of visual acceleration*. Manuscript in preparation.

Abstract Publications:

- Mueller, A. S., González, E. G., McNorgan, C., Steinbach, M. J., & Timney, B. (2014). Perception and smooth pursuit of vertical acceleration and deceleration [Abstract]. Program No. 726.03. 2014 Neuroscience Meeting Planner. Washington, DC: Society for Neuroscience, 2014. Online.
- Mueller, A. S., & Timney, B. (2014). Perception of acceleration and deceleration as a function of pattern complexity and direction [Abstract]. *Canadian Journal of Experimental Psychology*, *68*, 304.
- Mueller, A. S., & Timney, B. (2014). Effects of visual field size and speed on acceleration and deceleration perception [Abstract]. *Perception ECVF Abstract Supplement*, *43*, 41.
- Mueller, A. S., & Trick, L. M. (2012). Effect of vantage point on change detection in road traffic scenes [Abstract]. *Canadian Journal of Experimental Psychology*, *66*, 270.
- Mueller, A., & Trick, L. M. (2010). Detection of changes in driving environments: Effects of task relevance and size [Abstract]. *Canadian Journal of Experimental Psychology*, *64*, 307.