

BEHAVIOURAL AND NEUROIMAGING EVIDENCE OF SPEED-TUNED  
DIRECTIONAL ANISOTROPIES IN GLOBAL MOTION PERCEPTION

by

AMY ELIZABETH ZWICKER  
B.Sc.H., Acadia University, 2003

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF  
THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF ARTS

in

THE FACULTY OF GRADUATE STUDIES  
(Psychology)

THE UNIVERSITY OF BRITISH COLUMBIA

August 2005

© Amy Elizabeth Zwicker, 2005

## Abstract

Research has suggested that directional anisotropies, or asymmetries, exist for global motion perception, yet there are inconsistencies among these results. The purpose of this study was to examine directional anisotropies in motion perception, to determine what motion parameters affect anisotropies, and to investigate cortical activation that may contribute to anisotropies. In Experiment 1, coherence thresholds were obtained from 40 subjects for direction discrimination of moving random dot patterns. Lower thresholds were found for centripetal and horizontal motion relative to centrifugal and vertical, respectively, when the speed of motion was 8 deg/s. For motion that was 1 deg/s, lower thresholds were found for upward motion relative to downward. These anisotropies were retested in 4 subjects in Experiment 2 with a detection paradigm; the fast motion anisotropies were confirmed but the slow motion anisotropy was not. Six participants completed an fMRI experiment in which the BOLD response to slow and fast directions of motion was measured. V5/MT+ was functionally defined; within this ROI greater activity was found for fast vertical motion relative to horizontal and fast centripetal motion relative to centrifugal. There were no differences in cortical activity for directions of slow motion. Both the behavioural and fMRI studies suggest that there are global motion pathways tuned to different speeds of motion. Within these speed-tuned pathways, there is support for unique directional anisotropies in global motion processing.

## Table of Contents

Abstract	ii
Table of Contents	iii
List of Tables	v
List of Figures	vi
Acknowledgements	vii
Introduction	1
<i>Directional Anisotropies in Motion Processing</i>	1
<i>The Motion Pathway</i>	4
<i>The Middle Temporal Area (MT)</i>	4
<i>Direction Processing in MT: Single Cell Recording</i>	5
<i>Direction Processing in MT: Neuroimaging</i>	6
<i>Speed of Motion</i>	7
<i>The Current Study</i>	8
Experiment 1: Discrimination of Motion Direction	9
Methods	9
<i>Participants</i>	9
<i>Apparatus</i>	9
<i>Stimuli</i>	9
<i>Procedure</i>	11
Results	13
Experiment 2: Detection of Motion Direction	18
Method	18
<i>Participants</i>	18
<i>Apparatus</i>	18

	iv
<i>Stimuli</i>	18
<i>Procedure</i>	20
<i>Results</i>	20
Experiment 3: Cortical Activation for Motion Direction	23
<i>Methods</i>	23
<i>Participants</i>	23
<i>Data Acquisition</i>	23
<i>Stimuli and Experimental design</i>	24
<i>Data Analysis</i>	28
<i>Results</i>	29
<i>MT Localizer</i>	29
<i>Coherent Motion Analyses</i>	29
Discussion	33
<i>Speed of Motion</i>	34
<i>Direction of Motion</i>	35
<i>Speed and Direction of Motion</i>	37
<i>Neuroimaging Evidence of Speed- and Direction-Tuned Motion Responses</i>	40
<i>Conclusions</i>	43
References	44
Appendix A: Global Motion Stimuli	50
Appendix B: Mean Accuracy Scores for Responses Made during the fMRI Scans.	52
Appendix C: Single Subjects Brain Maps Obtained from MT Localizer	53
Appendix D: Group Brain Maps Obtained from MT Localizer	55
Appendix E: Group Brain Maps of Motion Responsive Areas	56

## List of Tables

Table 1: Functionally defined V5/MT+ clusters.

30

Table 2. ROI Analysis in V5/MT+.

32

## List of Figures

Figure 1. Mean coherence thresholds for horizontal and vertical motion at both slow and fast speeds.	14
Figure 2. Mean coherence thresholds illustrating the centripetal direction preference for fast motion.	16
Figure 3. Mean coherence thresholds for upward and downward slow motion.	17
Figure 4. Mean coherence thresholds for direction detection.	22
Figure 5. Coherent motion fMRI block design.	25
Figure 6: FMRI Global Motion Stimuli.	27
Figure 7. Bilateral V5/MT+ group ROI.	31

## Acknowledgements

I would like to thank my supervisor, Deborah Giaschi, for her guidance and supervision in all aspects of this study; Carmen Webber, Simon Au Young, Barry Chai, and Bruce Bjornson for their help with the fMRI portion of this study; Jane Wang for helping to run participants, and Craig Chapman for programming the stimuli.

## Introduction

The human visual system is adept at integrating many local motion features in order to extract a global motion percept (Watamaniuk, 1993). The overall direction of an array of moving dots, for example, is perceived by integrating the component directions of the individual dots. This is characteristic of the way in which a *global* percept arises from *local* features. Psychophysical data, summarized below, suggest that there are directional anisotropies (asymmetries) in global motion perception; however, consistent anisotropies have yet to emerge from this research. This study examines the effect of motion parameters, namely speed of motion, on the perception of motion direction and cortical activation in motion-sensitive cortical area V5/MT+.

V5/MT+, although it is just one of the motion-sensitive cortical areas, was deemed the most appropriate cortical region to begin to investigate the association between perceptual and cortical responses to direction and speed of motion. This is because the importance of V5/MT+ for motion processing has been clearly demarcated in single-cell recording, human and monkey lesion studies, and functional neuroimaging studies. There is a close homology between monkey MT and human V5/MT+ (Orban et al., 2003); because it is well established that such a homology exists, one is able to allow monkey single-cell recording and lesion studies to inform studies of cortical regions in humans. Other highly motion sensitive areas such as V3A do not share such a close homology between monkey and human (Orban et al., 2003; Tootell et al., 1997).

### *Directional Anisotropies in Motion Processing*

Psychophysical techniques have been used to show that directional anisotropies do exist in global motion perception. These asymmetries are not unique to global motion; asymmetrical motion perception has been noted for local motion and for visual

tracking of moving objects (namely, smooth pursuit eye movements). These findings have implications for processing throughout the visual pathway. Ohtani and Ejima (1997) found a preference for downward local motion in the lower visual field and concluded that it may be due to a discrepant number of local motion detectors in V1 and V3 tuned to downward versus upward motion. In the smooth pursuit literature, behavioural techniques have shown that the gain of horizontal pursuit is better than the gain of vertical pursuit (e.g. Rottach et al., 1996). Smooth pursuit eye movements, like global motion processing, depend on the medial temporal area (MT) and the middle superior temporal area (MST) (Newsome, 1987; Newsome, Wurtz, Dürsteler, & Mikami, 1985). Anisotropic pursuit of moving stimuli suggests that direction processing within MT and MST may be asymmetrical.

One trend that does seem to stand out in the motion literature is the difference between horizontal and vertical motion perception. Not only is horizontal pursuit of objects better than vertical pursuit, direction discrimination and detection of horizontal global motion have been found to occur at lower coherence thresholds than discrimination and detection of vertical global motion perception (Raymond, 1994). This suggests greater sensitivity to horizontal motion, when compared to vertical motion. Also, greater extrastriate cortical responses have been found using magnetoencephalography (MEG) for horizontal apparent motion as opposed to vertically moving bars (Naito, Kaneoke, Osaka, and Kakigi, 2000).

While horizontal motion is often compared to vertical motion, so too is centripetal (inward) motion compared to centrifugal (outward) motion. Across studies, centripetal and centrifugal motion have each been cited as the preferred direction of motion. Ball and Sekuler (1980) found faster reaction times (RTs) to centrifugal motion when compared to centripetal motion along the horizontal axis. The stimulus used in this

study consisted of 100%-coherent motion of dots. Using the same stimulus they were not able to differentiate between centripetal and centrifugal motion when the motion was presented along the vertical meridian. Dumoulin, Baker, and Hess (2001) have also found evidence of a centrifugal motion bias when using a second-order (contrast-defined) motion stimulus. When a first-order (luminance-defined) stimulus was used, no difference was found between centrifugal and centripetal motion perception. Thus evidence does exist for a centrifugal motion bias, when second-order or suprathreshold motion is tested.

There is, on the other hand, mounting evidence to suggest a centripetal preference in global motion processing. Edwards and Badcock (1993) found that participants were more sensitive to motion that moved centripetally towards a central point rather than centrifugally away from a central point. This was true when participants viewed central random dot kinematograms (RDKs); the centripetal bias decreased at eccentricities greater than 16 deg. Raymond (1994) also noted a centripetal preference in global motion perception. Where Edwards and Badcock noted a strong centripetal bias for foveal motion presentation, which decreased with peripheral presentation, Raymond instead found a centripetal bias for stimuli presented at 5 deg of eccentricity or greater, but not for foveally presented stimuli. This centripetal preference was evidenced by increased sensitivity to upward motion in the lower visual field, rightward motion in the left hemifield, and leftward motion in the right hemifield. Directional isotropy was found in the superior visual field. There is some evidence to support cortical motion processing that favours centripetal motion. Naito et al. (2000) found a greater MEG response in the extrastriate cortex for centripetally directed apparent motion in the superior visual field. In a previous study, they had shown that these responses correlated with perception of the motion (Kawakami, Kaneoke, &

Kikigi, 2000). That is, the neural response measured by MEG was correlated with the participants' subjective ratings of smoothness of the apparent motion stimuli. This fits with monkey studies that show a strong correlation between MT response properties and behavioural performance on direction discrimination tasks (e.g. Newsome, Britten, & Movshon, 1989). It is a reasonable step then, to predict that processing in the motion pathway may reflect behavioural patterns of direction perception.

### *The Motion Pathway*

Primate studies have delineated both subcortical and cortical components that contribute to motion processing. The subcortical magnocellular (M) visual pathway includes M cells in the retina and two magnocellular layers in the lateral geniculate nucleus (LGN), all of which have transient response properties and are subsequently well suited for motion processing (DeYoe & Van Essen, 1988). Subcortical motion signals project to the primary visual cortex (V1); cells in V1 as well as V2 and V3 respond preferentially to particular directions of motion (DeYoe & Van Essen, 1988; Fellerman & Van Essen, 1987). Because the receptive fields of these neurons are comparatively small, V1, V2, and V3 are often associated with the processing of local motion. Immediately anterior to V3 is a distinct cortical region, V3A (Tootell et al., 1997). V3A has larger receptive fields than earlier occipital regions and in humans (more so than monkeys), neurons in V3A are motion and direction selective (Tootell et al. 1997). These early cortical areas project to extrastriate cortical areas, MT and MST, which are accredited with processing global motion due to their larger receptive field sizes (Newsome & Paré, 1988).

### *The Middle Temporal Area (MT)*

Research conducted first with monkeys (e.g. Maunsell & Van Essen, 1983; Newsome & Paré, 1988) has mapped MT as a small region located in the lateral

posterior temporal lobe. Anterior to MT is area MST, the principle projection site of MT (Born & Tootell, 1992). Neuroimaging with humans later revealed that cortical area V5, found in the temporo-parietal-occipital junction, is the probable human homolog of monkey areas MT and MST (Zeki, Watson, Lueck, Friston, Kennard, & Frackowiak, 1991); this area is often referred to as V5/MT+ (or simply MT). The precise V5/MT+ stereotaxic location has been shown to vary in humans by as much as 2.7 mm but it shares a relationship with sulcal patterns within each brain (Watson et al., 1993). V5/MT+ is consistently located at the junction of the ascending limb of the inferior temporal sulcus and the lateral occipital sulcus (Dumoulin et al., 2000; Watson et al., 1993).

The importance of MT for motion processing has been evidenced in lesion studies; lesions to MT impair visual motion perception (e.g. Marcar, Zihl, & Cowey, 1997; Newsome & Paré, 1988). Unilateral MT lesions in both monkeys (Newsome & Paré, 1988) and humans (Plant, Laxer, Barbaro, Schiffman & Nakayama, 1993; Schenk & Zihl, 1997) have confirmed that motion processing in MT maps to the contralateral visual hemifield. In addition to lesion studies, the important role of MT in motion processing has also been demonstrated with functional neuroimaging (e.g. Rees, Friston, & Koch, 2000), single cell recording and psychophysical techniques (e.g. Britten, Shadlen, Newsome, & Movshon, 1992). Indeed, V5/MT+ is the most well-studied cortical motion area.

#### *Direction Processing in MT: Single Cell Recording*

After demonstrating the importance of MT in motion processing, researchers have begun to investigate the response of MT to different motion parameters such as speed and direction. Recording from single cells in monkey MT, it has been estimated

that 80% (Maunsell & Van Essen, 1983) to as many as 96% (DeAngelis & Uka, 2003) of MT cells are tuned to a particular direction of motion.

While it is clear that the majority of neurons in MT respond to a particular direction of motion, it is not clear if this area responds equally well to all directions of motion. There is some physiological evidence for a centrifugal bias; Albright (1989) found a greater distribution of macaque MT neurons tuned to centrifugal motion relative to centripetal motion, however, these neurons were limited to those responding to the peripheral visual field. DeAngelis and Uka (2003) on the other hand, recorded from 501 macaque MT cells and found that these cells were tuned to all directions of motion across a broad range of speeds. They found no evidence of a centrifugal preference in direction tuned neurons. All told, the physiological basis for direction anisotropies has been understudied.

#### *Direction Processing in MT: Neuroimaging*

Functional neuroimaging techniques, including positron emission tomography (PET), magnetoencephalography (MEG), and functional magnetic resonance imaging (fMRI), have allowed the study of motion processing in the human cortex. Neuroimaging studies of V5/MT+ have consistently confirmed that this region responds preferentially to motion moving in a coherent direction relative to random motion (e.g. Braddick et al., 2001; Nakamura et al., 2003). FMRI has also been used to study sub-regions within the V5/MT+ complex. Morrone and her colleagues (2000) have shown that this region can be parsed into a section that responds specifically to translational motion (upward and downward motion) and a section that responds specifically to optic flow (circular, radial and spiral) motion. The sub-region tuned to translational motion was found to be more dorsal and posterior to the region that responded instead to optic flow motion. These fine grained analyses of V5/MT+ are advancing knowledge of

direction processing in this region, yet possible preferences among translational directions (e.g. upward, downward, leftward or rightward motion) or among optic flow directions (e.g. expanding or contracting radial motion) have not been sufficiently addressed.

One study has pitted centripetal apparent motion against centrifugal and horizontal apparent motion against vertical. Naito et al. (2000) found stronger magnetic responses in the extrastriate cortex for centripetal motion in the superior visual field, and for horizontal motion relative to vertical motion. The origin of these responses was in the occipito-parietal-temporal region, but could not be specified further.

### *Speed of Motion*

Speed, like direction, is a defining parameter of motion. Also like direction, neurons in MT are tuned to speed of motion. Estimates of speed-tuned neurons suggest that virtually all of MT neurons are tuned to particular speeds. Recording from multi-unit and single-unit sites, Liu and Newsome (2003) found that 92.2% of MT neurons were speed-tuned (tuning range: approximately 2 octaves); DeAngelis and Uka (2003) recorded from single cells and estimated that 99% were tuned to speed.

Both physiological and fMRI studies have been used to determine if V5/MT+ activation varies as a function of speed. Recording from monkey MT neurons, optimal responses have been acquired for speeds between 4 and 16 deg/s (e.g. Cheng, Hasewage, Saleem & Tanaka, 1994; Rodman & Albright, 1987). An fMRI study revealed that speeds of 4 and 8 deg/s optimally activated human V5/MT+ neurons (Chawla et al., 1999). Speeds within this range may be processed distinctly from slower and faster speeds outside of this range. Edwards, Badcock, and Smith (1998) have found that global motion extraction may rely on at least two speed-tuned independent systems, one tuned to slower speeds and the other specializing in faster

speeds. They created global motion stimuli that contained both slow and fast moving dots ranging from speeds of 1.2 to 10.8 deg/s. They found that when the motion signal was carried by dots moving at the slow speed of 1.2 deg/s, noise dots that moved at a speed of 4.8 deg/s or greater had no effect on the extraction of the signal direction. From this they concluded that there is a global motion system sensitive only to a small range of slowly moving stimuli. They found a similar effect when the speed of signal motion was fast and the noise dots moved slowly. Slow moving noise dots presented less interference than faster moving noise dots. Again, they concluded that there must also be a global motion system that specializes in processing faster motion. Direction perception within these speed-tuned pathways has not been addressed.

### *The Current Study*

The purpose of the current study is two-fold. First, psychophysical experiments will be used to address the discrepancies noted in directional anisotropies. Secondly, speed of motion will be studied as a parameter that may affect direction perception. It is predicted that speed of motion will affect the ability to extract coherent motion signals, thus speed may be a parameter that has led to contradictory directional anisotropies. Based on previous research, it is expected that direction discrimination will be best for motion in the range of 4 to 8 deg/s; direction anisotropies will be examined at an optimal speed (8 deg/s) and at a slower speed (1 deg/s) using both a direction discrimination paradigm (Experiment 1) and a detection paradigm (Experiment 2). If it is the case that there are multiple speed-tuned global motion pathways (e.g. Edwards et al., 1998), it is possible that direction processing within speed-tuned pathways may differ. Translational motion will be used to test leftward, rightward, upward and downward motion perception. These directions will be tested in a full-field display and in hemifields. By testing these directions in hemifields, it will be possible to compare the

direction that is toward fixation (centripetal motion), and the opposite direction, which is away from fixation (centrifugal motion).

In a final experiment, a link will be drawn between psychophysical findings and underlying cortical activation. Motion perception is often ascribed to cortical area V5/MT+, given its important role in motion processing. Direction and speed processing will be examined with fMRI in the third experiment to determine if V5/MT+ activity varies as a function of motion direction and speed.

## **Experiment 1: Discrimination of Motion Direction**

### **Methods**

#### *Participants*

Forty university students (32 female), each with normal or corrected-to-normal vision, participated in this experiment. Participants had a mean age of 21.4 years (age range = 17-28 years) and they received course credit for their participation. This study was approved by the University of British Columbia's behavioural research ethics board.

#### *Apparatus*

Random-dot kinematograms (RDks), the experimental stimuli, were generated with custom Matlab code programmed on a Macintosh G4 computer. The stimuli were displayed on a 17" Apple Trinitron CRT with a pixel resolution of 1024 x 768 and frame rate of 75 Hz. Participants viewed the stimuli binocularly from a distance of 57 cm and responded by pressing designated buttons on a gamepad.

#### *Stimuli*

RDks subtending  $768 \text{ deg}^2$  served as our global motion stimuli (width: 32 deg, height: 24 deg). These stimuli included 768 white dots on a black background with a central green fixation cross (dot density:  $1.0 \text{ dot/deg}^2$ , dot diameter: 0.1 deg, dot

luminance:  $100 \text{ cd/m}^2$ ). Dots in these displays can be programmed to move coherently in one direction, or randomly in all directions. By varying the proportion of coherent "signal" dots relative to random "noise" dots, sensitivity to global motion is evidenced as the lowest coherence level necessary to accurately determine the direction of motion. For full-field conditions, the coherently moving dots (the motion signal) were selected from the entire display of 768 dots. In the hemifield conditions, the coherently moving dots were selected from just the 384 dots subtending one half of the display. The remaining 384 noise dots in the other half of the display were programmed to move in random directions.

The dots had a limited lifetime and were presented in eight successive frames for each trial (frame duration: 53.3 ms, trial duration: 426.4 ms). The limited lifetime dots were repositioned from frame to frame to create apparent motion; the speed of this motion was 1 deg/s in the slow speed condition and 8 deg/s for the fast speed condition. These different speeds were created by changing the displacement distance of the dots between frames. From frame to frame, "noise" dots were repositioned in random directions whereas "signal" dots were displaced in a designated direction. Whether a dot represented a signal or noise dot was determined randomly in each frame; the prior history of a dot did not affect its future designation as a signal or noise dot. The percentage of signal dots in a trial necessary for accurate direction discrimination was used to determine the minimum motion coherence threshold.

There were 10 experimental conditions derived from a combination of four motion directions (up, down, left, and right) and five visual field locations (full-field, bottom hemifield, top hemifield, left hemifield, and right hemifield). These 10 conditions are depicted in Appendix A. The four motion directions were paired such that both upward and downward motion trials were included in each of the five vertical motion

conditions. Both leftward and rightward motion trials were included in each of the five horizontal motion trials. The first experimental condition presented horizontal movement of dots in a full-field display. Signal dots moved either left or right in each trial; the direction of motion was chosen randomly on each trial. The second and third experimental conditions also presented horizontal movement of the signal dots, however, the signal dots were confined to the left half of the display for condition 2 and to the right half of the display for condition 3. In these conditions, incoherently moving noise dots were presented on the other half of the screen. Similarly, condition 4 presented horizontally moving signal dots in just the superior half of the display whereas condition 5 presented horizontal motion in the inferior half of the display, with randomly moving noise dots in the opposing halves.

Conditions 6 through 10 were identical to the first five conditions except the motion was vertical. Thus condition 6 was a full-field RDK with upward and downward movement of the signal dots. Condition 7 consisted of vertical movement of signal dots in the left-hemifield and in condition 8, the signal dots were confined to the right-hemifield. Condition 9 presented vertically moving signal dots in the superior portion of the screen and in condition 10, the vertically moving signal dots were displayed in the inferior portion of the screen. As with the horizontal conditions, the opposing side of the display in each of the hemifield conditions contained incoherently moving noise dots. These 10 experimental conditions were designed such that they could be run with a dot speed of 1 deg/s or 8 deg/s.

### *Procedure*

The experimental conditions each consisted of an adaptive staircase presentation of motion trials that began with 100% coherence and proceeded with a 2-down-1-up method until one of two criteria were met: either a) 20 reversals were

obtained, or b) a maximum of 80 trials was completed. A minimum of 50 trials was necessary in each experimental condition. The coherence level decreased first in 20% increments. After the third reversal, the step size was halved at each reversal. The staircase was programmed such that the coherence could not decrease below 1%. Participants controlled the rate of trial presentation using a single button press on a game pad to initiate each trial and responded by pressing one of two designated buttons on the game pad to indicate their choice of leftward or rightward motion in the horizontal conditions, or, upward or downward motion in the vertical conditions.

The experiment was conducted in a dimly lit room and participants viewed the stimulus binocularly. Participants were instructed to fixate on the central green cross throughout each condition, and their task was to discriminate the global direction of the moving dots. Prior to completion of the experimental conditions, each participant completed three practice staircases. The practice staircases were identical to the experimental stimuli except that they contained only 20 trials. The three conditions chosen for the practice staircases were: 1) a full-field vertical motion condition, 2) a left hemifield horizontal condition, and 3) a top hemifield vertical condition. All participants confirmed at this point that they had received enough practice. Participants then completed the 10 experimental conditions, the order of which was counterbalanced with a Latin square. Twenty of the participants completed the conditions with the slow speed of motion whereas the other 20 participants completed the conditions with the faster speed of motion.

Because a 2-AFC paradigm was adopted, participants could respond correctly 50% of the time through chance alone. The data were fit with a Weibull function and the point of inflection (maximum slope) was used as the threshold level (Strasburger, 2001). The point of inflection for a Weibull function with two response choices

represents 82% accuracy. Three coherence thresholds were determined for each condition, for each participant. These thresholds were for: 1) all trials in the condition, 2) trials for one motion direction, and 3) trials for the other motion direction. This resulted in horizontal, leftward, and rightward thresholds for the horizontal conditions, and vertical, upward and downward thresholds for the vertical conditions.

There were two main analyses performed on the data. The first examined the difference between horizontal and vertical motion, and the second contrasted centripetal motion with centrifugal motion; these motion patterns were studied at both the slow and faster speed. In order to deal with a few aberrant coherence thresholds, outliers that were beyond a z-score of 2.0 were removed from the data and replaced with the mean coherence value for the particular condition. This resulted in the removal of 7 of 640 scores (or 1.1%).

## Results

Fast horizontal and vertical thresholds were tested in the full field and it was found that horizontal motion thresholds ( $M = 8.3\%$ ,  $SE = 0.7\%$ ) were significantly lower than vertical motion thresholds ( $M = 10.6\%$ ,  $SE = 1.0\%$ ),  $F(1,19) = 7.41$ ,  $p < .05$ . However, horizontal motion thresholds did not differ from vertical thresholds when the speed of motion was slow. These means are shown in Figure 1.

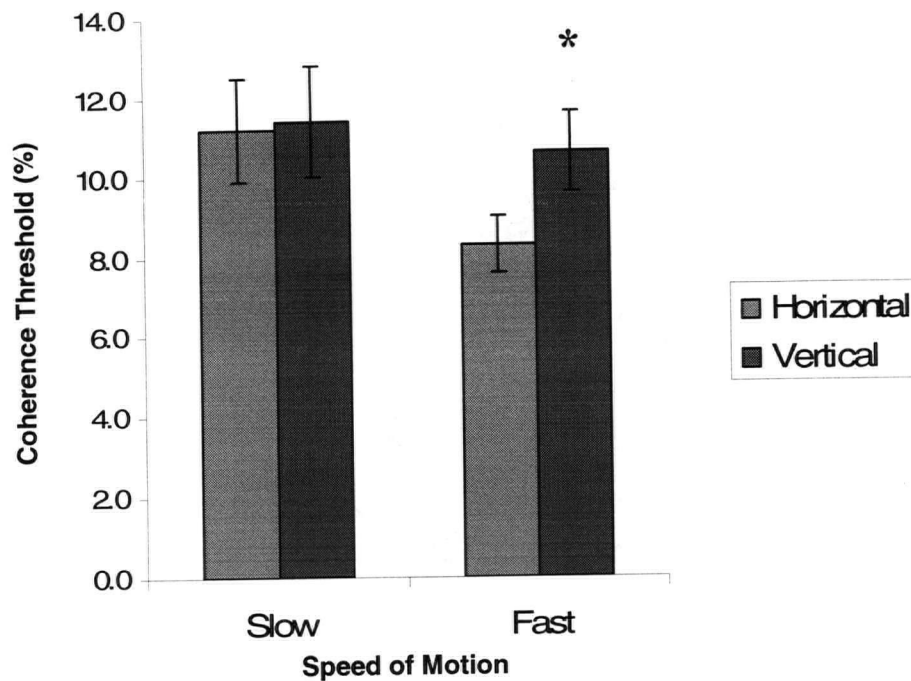


Figure 1. Mean coherence thresholds for horizontal and vertical motion at both slow and fast speeds. The error bars represent standard error of the mean and the asterisk (\*) represents a significant comparison;  $p < .05$ .

A second analysis tested for a centripetal motion preference; this would be evidenced by an interaction between direction of motion and location. Specifically, we expected to find that the leftward motion threshold would be lower in the right hemifield while the rightward motion threshold would be lower in the left hemifield. Similarly, in the top hemifield, the downward motion threshold would be lower whereas in the bottom hemifield, the upward motion threshold would be lower. While the interaction between direction of motion and location was highly significant,  $F(9, 342) = 4.90$ ,  $p < .001$ , so too was the interaction between direction, location, and speed of motion,  $F(9, 342) = 2.63$ ,  $p < .01$ . Accordingly, the significant 3-way interaction was probed with two, 2-way

analyses comparing direction of motion and location at the slow speed, and at the faster speed.

The interaction between direction of motion and location was highly significant at the fast speed,  $F(9, 171) = 4.75$ ,  $p < .001$ . Upon finding a significant main effect of direction of motion in each of the four hemifields, the two directions corresponding to centripetal and centrifugal for each particular hemifield were tested with a pairwise comparison (using the Bonferroni adjustment for multiple comparisons). In the left hemifield, the rightward motion threshold ( $M = 7.4\%$ ,  $SE = 0.9\%$ ) was significantly lower than the leftward motion threshold ( $M = 13.0\%$ ,  $SE = 1.3\%$ ;  $p < .001$ ) whereas the leftward motion threshold ( $M = 8.3\%$ ,  $SE = 1.3\%$ ) was significantly lower than the rightward threshold ( $M = 12.9\%$ ,  $SE = 1.3\%$ ;  $p < .05$ ) when tested in the right hemifield. The downward motion threshold in the top hemifield ( $M = 7.3\%$ ,  $SE = 1.0\%$ ) was significantly lower than the upward motion threshold ( $M = 11.5\%$ ,  $SE = 1.1\%$ ;  $p < .01$ ). The centripetal preference noted in these three hemifields did not reach significance when tested in the bottom hemifield ( $p = .12$ ). However, the centripetal direction appeared to be favoured, such that the upward motion threshold ( $M = 9.3\%$ ,  $SE = 1.4\%$ ) was lower than the downward motion threshold ( $M = 15.0\%$ ,  $SE = 2.2\%$ ). Refer to Figure 2.

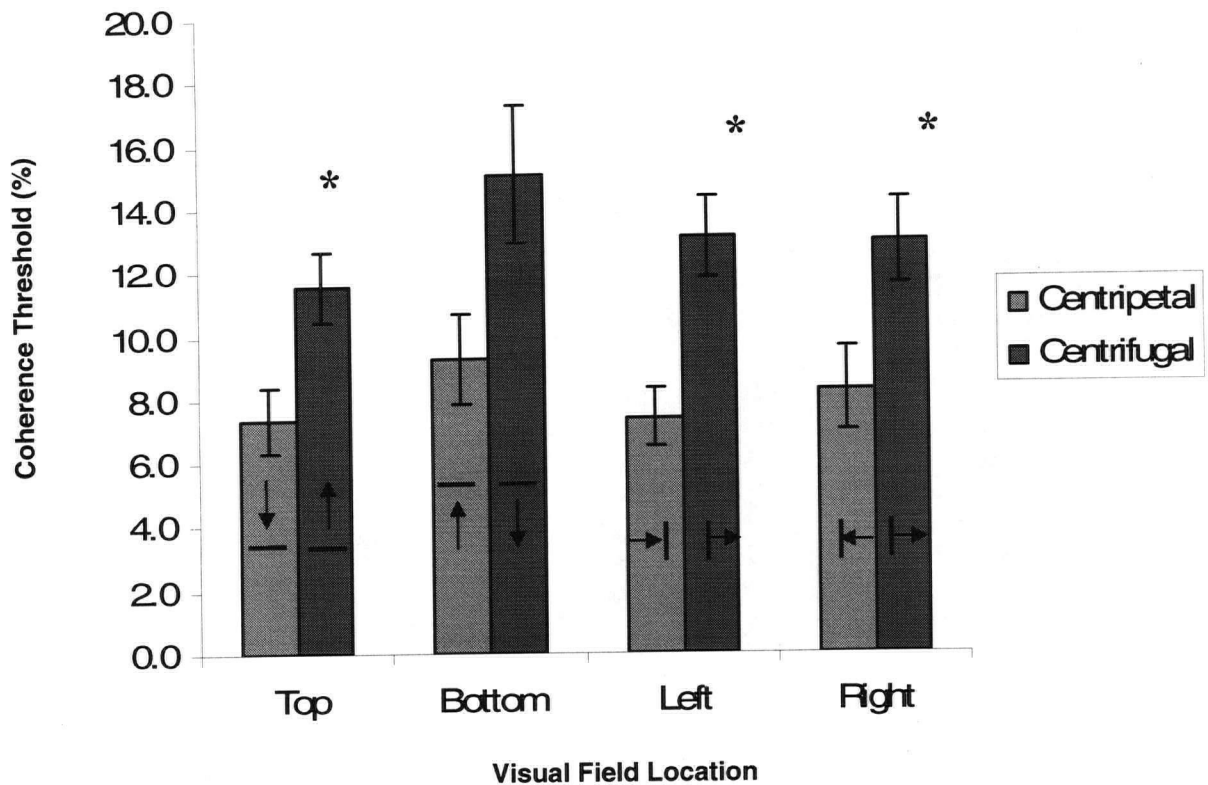


Figure 2. Mean coherence thresholds illustrating the centripetal direction preference for fast motion. The error bars represent standard error of the mean and asterisks (\*) represent significant comparisons;  $p < .05$ . Arrows represent motion direction toward, or away from, the meridian.

An interaction was also found between motion direction and visual field location when the speed of motion was slow,  $F(4.84, 92.04) = 2.74$ ,  $p < .05$ . However, this interaction did not favour centripetal directions of motion. Using the Bonferroni adjustment for multiple comparisons it was found that upward motion thresholds were significantly lower than downward thresholds in each of the four hemifields (see Figure 3). Upward motion thresholds were found to be significantly lower than leftward and rightward thresholds when tested in the bottom hemifield, however, not in the other

hemifields. Leftward and rightward motion did not differ significantly from one another in any of the four hemifields. Given that visual field location did not play a critical role in the slow motion coherence thresholds, a simpler analysis comparing all four motion directions was conducted for the full-field condition. A main effect of motion direction was found in the full-field,  $F(3, 57) = 3.795$ ,  $p < .02$ . Using the Bonferonni correction for multiple comparisons again it was found that upward motion thresholds ( $M = 6.35\%$ ,  $SE = 1.2\%$ ) were significantly lower than downward thresholds ( $M = 13.4\%$ ,  $SE = 1.8\%$ ,  $p < .02$ ). There were no other significant contrasts between motion directions in the full-field condition.

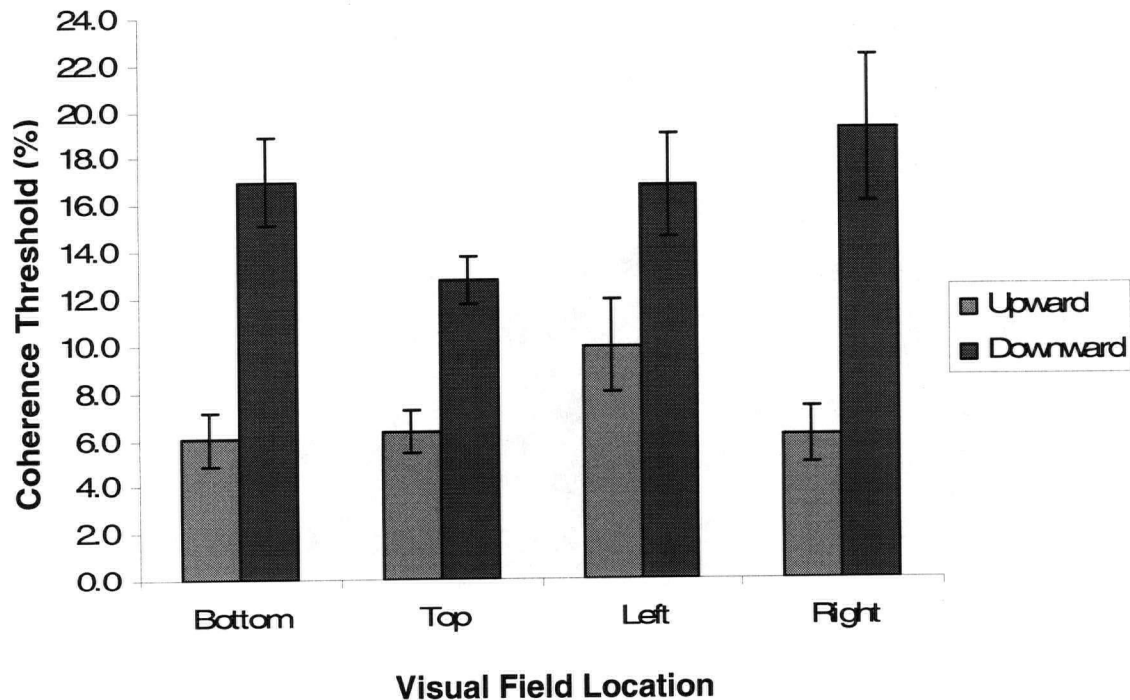


Figure 3. Mean coherence thresholds for upward and downward slow motion. Error bars represent standard error of the mean; all four contrasts are significant ( $p < 0.05$ ).

Experiment 1 showed that thresholds were lower when motion was horizontal relative to vertical and centripetal relative to centrifugal when the speed of motion was fast. Lower thresholds were also observed for upward motion relative to downward when the speed of motion was slow. While the discrimination method used in this first experiment is suitable for measuring horizontal and vertical thresholds (thresholds for which both trial directions within a condition contribute), thresholds obtained for individual trial directions are vulnerable to any response bias that participants may have. For that reason, centripetal and centrifugal fast motion and upward and downward slow motion were retested with a detection experiment.

## **Experiment 2: Detection of Motion Direction**

### **Method**

#### *Participants*

Four participants completed Experiment 2. All four participants were female and were obtained from the sample included in Experiment 1. The participants all had normal or corrected-to-normal vision, and had a mean age of 24.5 years (age range = 21-28 years).

#### *Apparatus*

See experiment 1.

#### *Stimuli*

RDKs identical to those in Experiment 1 (refer to Appendix A) were used as the stimuli for Experiment 2. However, each trial now included two successive intervals as opposed to one. On each trial, one of the two intervals was randomly assigned to present coherent motion while the other interval contained randomly moving dots. As in

Experiment 1, the dots had a limited lifetime and were presented in eight successive frames for each interval (frame duration: 53.3 ms, interval duration: 426.4 ms). The two intervals were separated by an interstimulus interval of 213.2 ms thus the total trial length was 1066 ms. The percentage of signal dots necessary for accurate detection of the coherent motion interval was the minimum motion coherence threshold measured in this experiment.

There were 10 experimental conditions designed to further test the findings of Experiment 1. The first two conditions presented slow (1 deg/s) signal motion in a full-field display. Condition 1 contained trials of slow upward motion in the coherent interval, and randomly directed motion in the incoherent interval. The second condition presented trials with slow downward motion in the coherent interval. The last eight conditions tested the centripetal and centrifugal motion direction in each of the four hemifields. The coherent interval in these trials presented signal motion in one hemifield and random motion in the opposite hemifield (as in Experiment 1). The incoherent interval contained random motion. Conditions 3, 4, 5, and 6 tested centripetal motion by presenting leftward motion in the right hemifield, rightward motion in the left hemifield, upward motion in the bottom hemifield, and downward motion in the top hemifield, respectively. The final four conditions presented the centrifugal direction for each of the four hemifields (condition 7: leftward motion in the left hemifield, condition 8: rightward motion in the right hemifield, condition 9: upward motion in the top hemifield, and condition 10: downward motion in the bottom hemifield). The eight hemifield conditions contained fast motion (8deg/s). These coherent intervals were identical to the global motion stimuli used in Experiment 1 except that each condition now included trials of only one motion direction as opposed to the paired motion directions included in Experiment 1 conditions.

### *Procedure*

The experiment was conducted in a dimly lit room and participants viewed the stimulus binocularly. Participants were instructed to fixate on the central green cross throughout each condition, and their task was to determine which of the two intervals contained coherent motion. All participants completed two practice sessions. Participants then completed the 10 experimental conditions, the order of which was counterbalanced.

Each of the 10 experimental conditions was completed in the same manner. The coherence level in the coherent intervals was initially 100% and was adjusted throughout the condition according to a 2-down-1-up method. The condition ended when one of two criteria were met: either a) 20 reversals were obtained, or b) 50 trials were completed. Participants controlled the rate of trial presentation using a single button press on a game pad to initiate each trial and responded by pressing one of two designated buttons on the game pad to indicate whether the first or second interval contained coherent motion. Because a 2-AFC paradigm was adopted, participants could respond correctly 50% of the time through chance alone. Coherence thresholds were determined by fitting a Weibull function to the data as in Experiment 1. Because only one motion direction was tested in each condition, only one coherence threshold was obtained for each condition. Two analyses were completed, the first to test upward and downward direction detection, and the second to test centripetal and centrifugal direction detection.

### *Results*

It was found in Experiment 1 that upward motion thresholds were lower than downward motion thresholds when the speed of motion was slow; this finding was not

replicated using a detection paradigm. Upward motion was detected at the average threshold of 14.0% ( $SE = 2.5\%$ ) coherence whereas downward motion was detected at the average threshold of 12.4% ( $SE = 1.0\%$ ) coherence,  $t(3) = -0.677$ ,  $p > .50$ .

Planned comparisons were used to compare centripetal and centrifugal coherence thresholds obtained in this detection experiment. In accordance with the results of Experiment 1, centripetal motion thresholds were found to be lower than centrifugal thresholds when the speed of motion was fast. The threshold for leftward motion in the right hemifield ( $M = 10.8\%$ ,  $SE = 0.6\%$ ) was significantly lower than the rightward coherence threshold ( $M = 15.9\%$ ,  $SE = 1.3\%$ ;  $t(3) = 3.621$ ,  $p < .05$ ) whereas the rightward motion threshold ( $M = 8.6\%$ ,  $SE = 3.1\%$ ) was significantly lower than the leftward threshold ( $M = 12.2\%$ ,  $SE = 3.2\%$ ) when tested in the left hemifield,  $t(3) = 6.462$ ,  $p < .01$ . The threshold for upward motion ( $M = 6.7\%$ ,  $SE = 1.6\%$ ) in the bottom hemifield was significantly lower than the threshold for downward motion ( $M = 12.1\%$ ,  $SE = 1.7\%$ ;  $t(3) = 2.912$ ,  $p < .05$ ). While the threshold for downward motion ( $M = 9.0\%$ ,  $SE = 1.8\%$ ) was lower than the upward motion threshold ( $M = 14.3\%$ ,  $SE = 1.2\%$ ) in the top hemifield, this comparison did not reach the traditional significance level,  $t(3) = 2.317$ ,  $p < .10$ . These means are depicted in Figure 4.

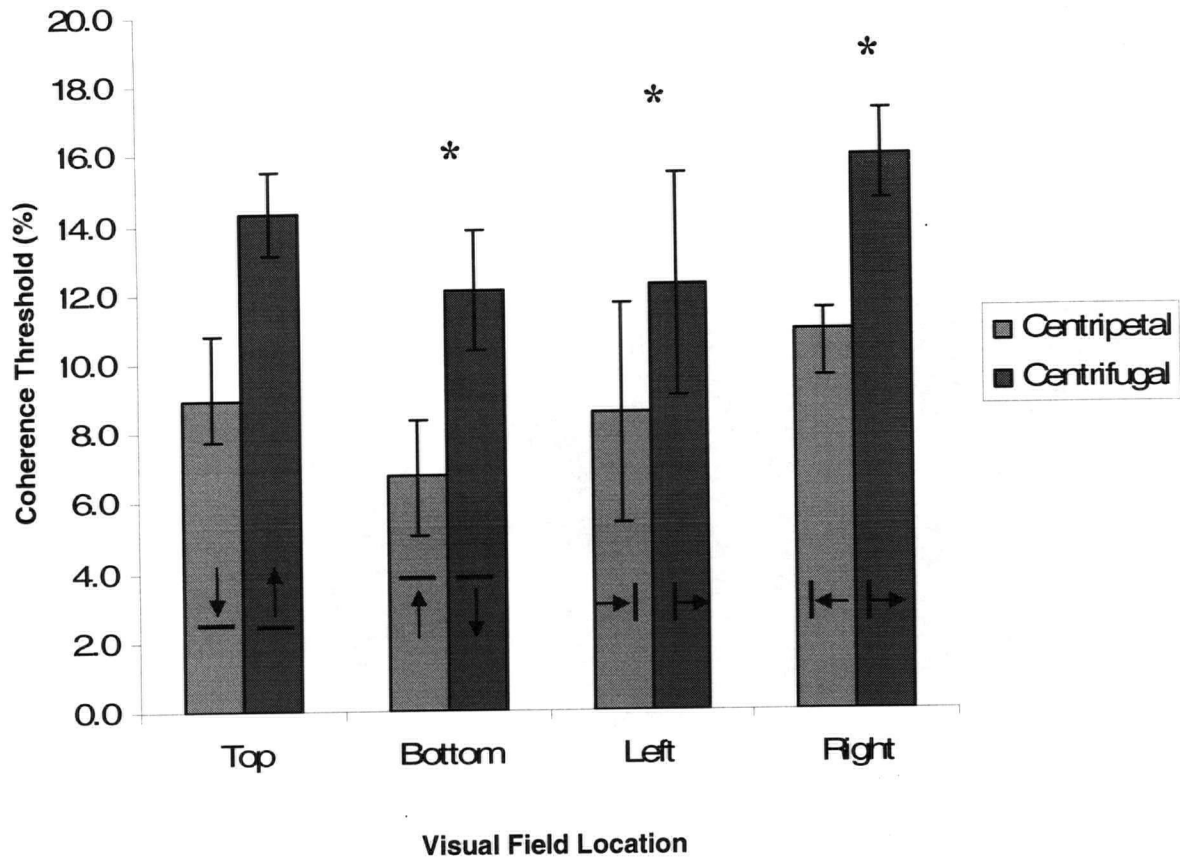


Figure 4. Mean coherence thresholds for fast motion detection; the error bars represent standard error of the mean and asterisks (\*) represent significant comparisons;  $p < .05$ . Motion direction is depicted by arrows pointing inward toward the meridian or outward away from the meridian.

To summarize the perceptual anisotropies found in this study, both Experiments 1 and 2 showed greater sensitivity for centripetal motion relative to centrifugal motion when the speed of motion was fast. Fast motion also led to increased sensitivity for horizontal motion relative to vertical. Directional anisotropies were not consistently observed for slow motion. Although, slow upward motion resulted in lower coherence thresholds in Experiment 1, Experiment 2 showed that participants did not in fact detect upward motion better than downward. It was concluded that in Experiment 1 lower

threshold were found for upward motion because the discrimination paradigm used in that study was vulnerable to response bias. Accordingly, horizontal, vertical, centripetal and centrifugal motion directions were chosen to investigate the cortical basis for direction anisotropies. In the following experiment, fMRI was used to study the BOLD (blood oxygenation level-dependent) response to these directions of motion at fast and slow speeds of motion.

### **Experiment 3: Cortical Activation for Motion Direction**

#### **Methods**

##### *Participants*

Seven participants completed this experiment for course credit; however, the data from one participant was excluded due to imaging artifacts. The six remaining participants (4 female) had a mean age of 21.3 years, all were right handed, and all had normal or corrected-to-normal vision.

##### *Data Acquisition*

Each participant completed a scanning session that lasted approximately one hour. During this session, echo-planar imaging (EPI) was used to collect images during nine T2\*-weighted functional scans (TE = 30 ms, TR = 2000 ms). The field of view (FOV) was 240 mm; 3 mm isotropic voxels were acquired using an 80 x 80 mm matrix. The images were reconstructed with a 128 x 128 mm matrix which resulted in an effective voxel size of 1.88 x 1.88 x 3 mm. Volumes were collected in 36 interleaved axial slices (slice thickness: 3 mm, inter-slice gap: 1 mm). At the end of the scanning session a high-resolution anatomic brain image was collected. Transverse slices were acquired with a T1-weighted scan that was 6 minutes and 34 seconds in duration (FOV: 256 mm, matrix: 256 x 256, voxel size: 1 x 1 x 1 mm).

### *Stimuli and Experimental design*

*Coherent Motion Stimuli.* RDKs similar to those used in Experiments 1 and 2 were viewed by participants while lying in a Philips Gyroscan Intera 3 Tesla MRI scanner with a phased array head coil (SENSE). The stimuli were back projected with an LCD projector (resolution: 800 x 600; refresh rate: 75 Hz) onto a screen that was 53 cm behind the participant's head and viewed through a mirror that was 15 cm from the participant's eyes. The stimuli were composed of white dots (dot diameter: 0.1 deg, dot density: 0.5 dot/deg<sup>2</sup>) on a black background and contained a central white fixation cross (stimulus width: 25.2 deg; height: 19.4 deg).

Eight coherent motion conditions were created by crossing four motion directions (horizontal, vertical, centripetal, and centrifugal) with two dot speeds (slow: 1 deg/s; fast: 8 deg/s). All eight conditions were based on the same block design and were 288 s in duration (see Figure 5). Each condition was composed of four cycles; the cycles included three blocks of moving dots (motion blocks) presented in alternation with three blocks of stationary dots (control blocks). The motion blocks were 14 s in duration and contained 14 trials of moving dots whereas the control blocks were 10 s in duration and contained 10 trials in which an arrowhead alternated position on the central fixation cross. Each trial was composed of a 600 ms moving dot/arrow presentation followed by a 400 ms inter-trial response phase. The three motion blocks in each cycle differed only in that the first presented motion at 85% coherence, the second contained motion at a 25% coherence level, and the third contained randomly directed motion (0%

coherence).

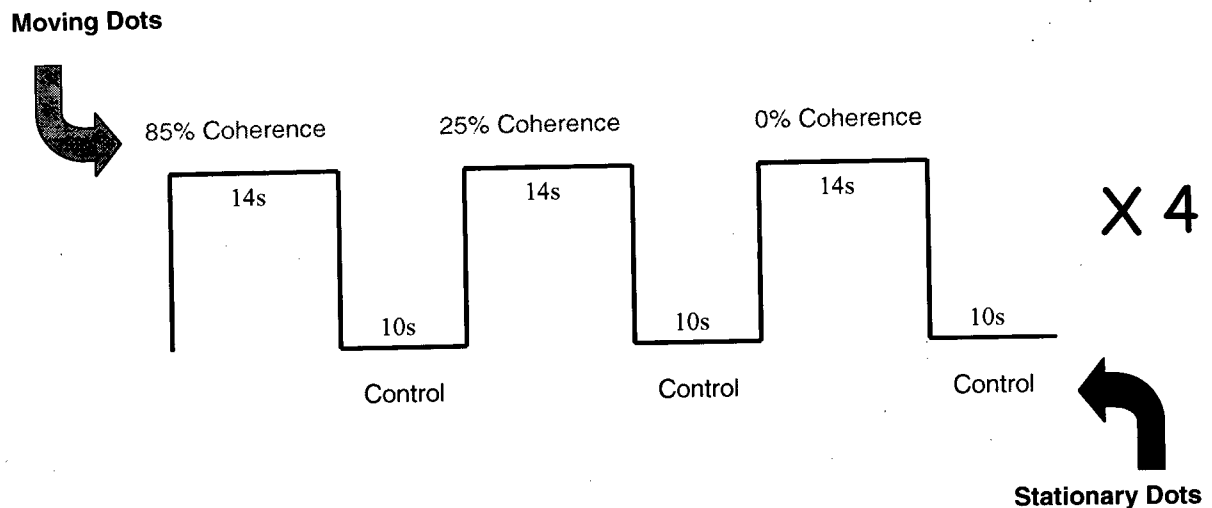


Figure 5. Coherent motion block design. The diagram depicts one of four cycles in each functional run.

Each trial in the motion and control blocks randomly presented one of two directions of motion. For the slow horizontal and fast horizontal conditions, motion and arrow direction was randomly chosen to be left or right on each trial. Similarly, the slow vertical and fast vertical conditions contained upward and downward trials. The horizontal and vertical motion stimuli were much like the horizontal and vertical full-field stimuli used in Experiment 1. Trials in the centripetal motion conditions presented dots that moved from the left and right sides inward toward the center, or from the top and bottom, inward toward the center. The control blocks in the centripetal conditions contained double arrowheads pointed either inward along the horizontal plane or inward along the vertical plane. Motion trials in the centrifugal condition randomly alternated between trials of dots that moved from the center outward toward the left and right, and

trials in which the dots moved outward toward the top and bottom. The centrifugal control blocks presented double arrowheads pointing outward along the horizontal meridian or outward along the vertical meridian (See Figure 6). Participants had the task on all trials of pressing one of two buttons to indicate the direction of motion/arrows. Accuracy of behavioural responses was recorded and is presented in Appendix B.

*MT Localizer.* The MT localizer condition contained grey dots on a black background and was also constructed with a block design. There were two blocks, each 14 s in duration, in each cycle. The motion blocks contained dots that alternated 8 times between radial inward and outward motion, changing direction every 1.75 s. During the control blocks, the dots were stationary. The MT localizer had six cycles and was 168 s in duration. Participants viewed this task passively.

Participants practiced each of the coherent motion tasks prior to entering the scanner. In the scanner, all participants viewed the MT localizer first. Half of the participants then completed the four slow coherent motion tasks (slow horizontal, slow vertical, slow centripetal and slow centrifugal) followed by the four fast coherent motion tasks (fast horizontal, fast vertical, fast centripetal and fast centrifugal). The remaining participants completed the four fast conditions followed by the four slow conditions.

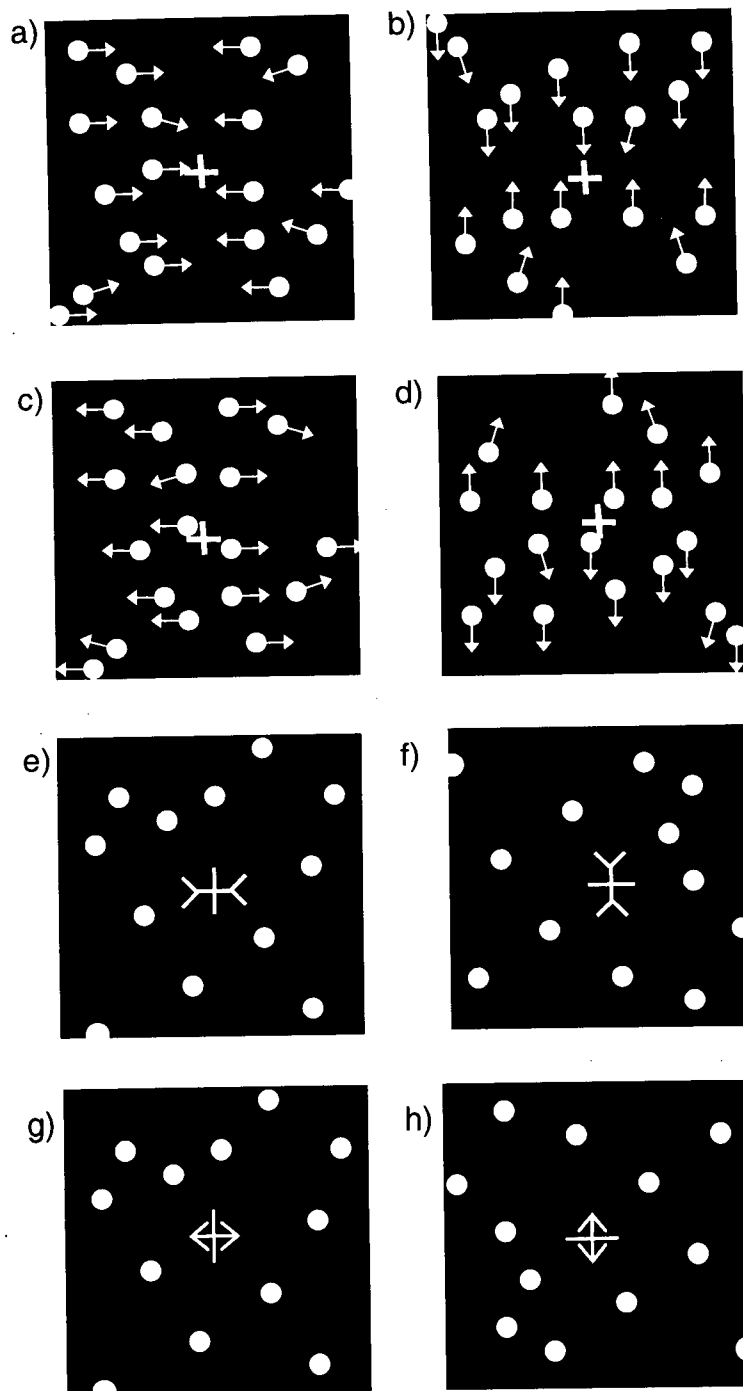


Figure 6: fMRI Global Motion Stimuli. Centripetal motion trials are shown in a) and b); centrifugal motion trials are shown in c) and d). The arrow discrimination task used in the control blocks is shown in e) and f) for the centripetal conditions, and in g) and h) for the centrifugal conditions.

## *Data Analysis*

Data preprocessing and statistical analysis were conducted with Brain Voyager QX (Brain Innovation B.V.). Prior to analysis, inter-slice time differences were removed from the data with a slice time correction. Temporal high pass filtering was used to remove low frequency trends from the data (e.g. physiological and scanner noise). All volumes were aligned to the first volume of each run to correct for motion. The functional volumes were co-registered with the anatomic image, and the data were normalized to stereotaxic space (Talairach & Tournoux, 1988).

The general linear model was used to model the data. Two fixed effects models were constructed with subject-specific predictors and confounds (the mean signal level of each condition, for each participant). The first model was designed to analyze data collected during the MT localizer scan. This model included subject-specific “motion” predictors, “stationary” predictors, and confounds for all six subjects. Including subject-specific predictors in the model allows contrasts to be tested in both single subject and group analyses. Accordingly, this model was used to functionally locate MT in the group and in single subjects. A boxcar function, convolved with a hemodynamic response function, was used to model the motion and stationary conditions, and maps of the  $t$  statistic were created, correcting for multiple comparisons.

Images collected during all eight coherent motion scans were analyzed with a model that contained subject-specific predictors for each motion direction, speed, coherence level, and baseline condition, as well as confounds. Contrasts were again modeled with a boxcar function, convolved with a hemodynamic response function. A series of contrasts were first tested in a group analysis of the whole brain. A correction for multiple comparisons was used in this analysis. A series of contrasts was then tested in a group analysis in the functionally defined MT region of interest (ROI). Due to

the limited number of comparisons in a ROI analysis,  $t$  scores were deemed significant at  $p < .05$ , uncorrected. The ROI analysis was replicated in single subjects.

## Results

### *MT Localizer*

Table 1 includes the coordinates and statistics for probable V5/MT+. Voxels in this region were identified by contrasting radial motion with stationary dots. There was a robust signal in V5/MT+ in the group analysis and in 4 of the 6 participants (see brain pictures in Appendix C and D). The locations of V5/MT+ in the individual subject analyses were in agreement with the region defined in the group analysis, thus the group map was used to define an MT ROI for further ROI analyses.

The ROI analyses tool in Brainvoyager QX uses a region-growing method to define ROI's. A voxel within the active V5/MT+ region was selected; the tool spreads this selection to include suprathreshold neighboring voxels, stopping when the boundaries of the functional cluster have been reached. A left and right group MT ROI was defined in this manner (see figure 7).

### *Coherent Motion Analyses*

A series of contrasts between motion directions and speeds were first computed in a whole-brain group analysis, corrected for multiple comparisons. This whole brain analysis lacked sufficient power to produce significant results for any of these subtle contrasts. Using the defined V5/MT+ region, direction and speed contrasts were then computed in a more powerful ROI analysis.

Table 1

Functionally defined V5/MT+ clusters.

<i>Cortical Region</i>	<i>Coordinates</i>			<i>Number of Voxels</i>	<i>t- score</i>	<i>p-value</i>
	<i>x</i>	<i>y</i>	<i>z</i>			
<i>Group</i>						
L V5/MT+	-45	-66	0	888	6.978	0.00000004
R V5/MT+	40	-60	0	527	5.776	0.00000012
<i>Subject 1</i>						
L V5/MT+	-47	-66	-1	660	6.565	0.00000004
R V5/MT+	46	-64	-1	556	6.368	0.00000006
<i>Subject 4</i>						
L V5/MT+	-39	-64	-8	290	5.497	0.00000020
R V5/MT+	47	-63	-12	100	5.375	0.00000024
<i>Subject 5</i>						
L V5/MT+	-44	-67	-1	149	5.495	0.00000019
R V5/MT+	44	-68	3	247	5.819	0.00000009
<i>Subject 6</i>						
L V5/MT+	-49	-66	-1	515	6.569966	0.00000003
R V5/MT+	48	-65	-2	336	6.502024	0.00000005

Note. Coordinates are given in stereotaxic space (Talairach & Tournoux, 1988) for the most active voxel in the cluster, the *t*-statistic is the average for the cluster, as is the *p*-value. For subjects 3 and 4, there was little activation during the MT localizer task; V5/MT+ could not be defined in these subjects.

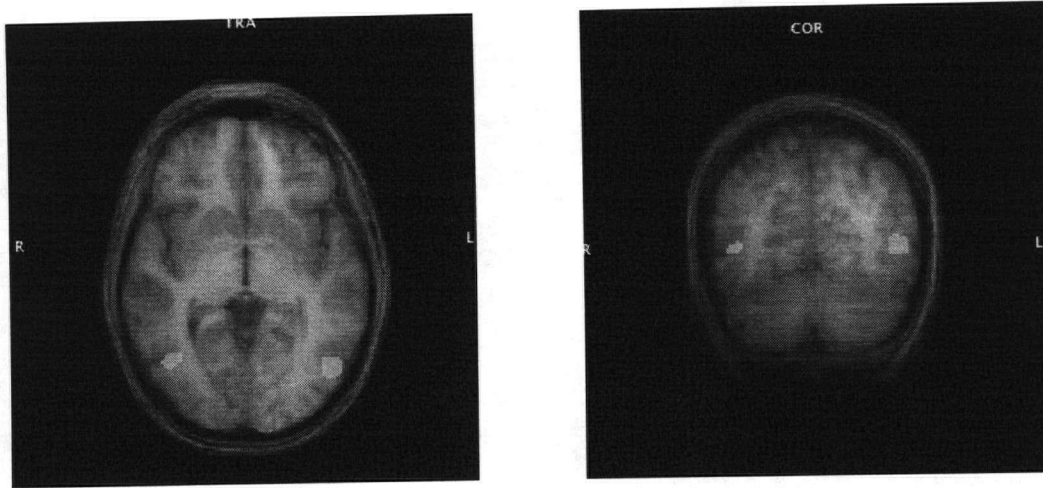


Figure 7. The shaded area represents the bilateral V5/MT+ group ROI. The region was defined from a map of the  $t$  statistic and is superimposed on the average anatomic from all 6 participants. Left: axial slice, Right: coronal slice.

The bilateral V5/MT+ ROI included 1455 voxels. The direction, speed, and coherence contrasts computed in this region are summarized in Table 2. Within this ROI it was found that greater cortical activity ensued from fast motion, regardless of the coherence level of the motion (contrasts 1-3). When coherence level was tested directly, it was found that V5/MT+ responded more to 25% coherent and 0% (incoherent) motion, than to 85% coherent motion (contrast 4-5). V5/MT+ activity did not differ when the motion coherence was 0% or 25% (contrast 6). The cortical response in V5/MT+ was then compared when the stimulus motion was horizontal and vertical. Greater cortical activity was found for vertical motion, but only when the speed of motion was fast. Horizontal and vertical motion did not differentially activate the ROI when the speed of motion was slow (contrasts 7-10). Similarly, centripetal and centrifugal motion differentially activated the ROI when the speed of motion was fast, but not slow. Fast centripetal motion resulted in stronger V5/MT+ activation than did fast centrifugal motion (contrast 11-14).

Table 2.

ROI Analysis in V5/MT+.

<b>Contrast</b>	<b>t-score</b>	<b>p-value</b>
1. Slow Motion vs. Fast Motion (Combined across coherence level)	-6.02	< 0.0001
2. Slow Motion vs. Fast Motion (85% Coherence)	-5.24	< 0.0001
3. Slow Motion vs. Fast Motion (25% Coherence)	-6.02	< 0.0001
4. 85% Coherent Motion vs. 25% Coherent Motion	-2.41	< 0.0200
5. 85% Coherent Motion vs. 0% Coherent Motion	-2.22	< 0.0300
6. 25% Coherent Motion vs. 0% Coherent Motion	0.19	ns
7. Fast Horizontal vs. Fast Vertical (85% Coherence)	-6.13	< 0.0001
8. Slow Horizontal vs. Slow Vertical (85% Coherence)	0.39	ns
9. Fast Horizontal vs. Fast Vertical (25% Coherence)	-6.75	< 0.0001
10. Slow Horizontal vs. Slow Vertical (25% Coherence)	0.87	ns
11. Fast Centripetal vs. Fast Centrifugal (85% Coherence)	3.74	<0.0002
12. Slow Centripetal vs. Slow Centrifugal (85% Coherence)	1.43	ns
13. Fast Centripetal vs. Fast Centrifugal (25% Coherence)	4.87	< 0.0001
14. Slow Centripetal vs. Slow Centrifugal (25% Coherence)	1.41	ns

Note. Contrasts were computed in bilateral V5/MT+ across all subjects. *p*-values are uncorrected.

## Discussion

The psychophysical results obtained in this study suggest that there are directional anisotropies in global motion processing. The fMRI data reveal that greater V5/MT+ activation exists for many of the directions for which perceptual sensitivity was heightened. Importantly, both the psychophysical and fMRI data show that speed of motion is a determining factor in global motion direction anisotropies. While directional anisotropies were found only for fast motion, and not slow, V5/MT+ activation was also increased for fast motion relative to slow. Previous research has suggested that there may be independent speed-tuned global motion pathways (Edwards et al., 1998); the current study supports speed-tuned global motion processing and has identified speed-tuned directional anisotropies.

Research of global motion processing has revealed conflicting directional anisotropies. For example, some studies contrasting centripetal and centrifugal motion have found that sensitivity is greater for centripetal motion (e.g. Edwards & Badcock, 1993; Raymond, 1994) while other studies have concluded that sensitivity is greater for centrifugal motion (e.g. Ball & Sekuler, 1980; Dumoulin et al. 2001). It is difficult to reconcile many of the directional anisotropies in the literature. It was the goal of this study not only to replicate directional anisotropies, but to determine factors that may lead to the noted variance. Speed of motion was identified as one such factor. It is difficult to conclude if speed led to the discrepancies in past research. In those studies that observed heightened centrifugal motion perception, speed was either not specified (Dumoulin et al., 2001) or changed throughout the stimulus presentation from stationary to 5.3 deg/s (Ball & Sekuler, 1980). Raymond (1994) found increased sensitivity for centripetal motion using a stimulus speed of 5 deg/s and as did Edwards & Badcock

(1993) whose stimuli were stationary at fixation and increased in speed to 6 deg/s in the periphery. None of these studies explored speed as a motion parameter.

### *Speed of Motion*

In keeping with single cell recording (Cheng et al., 1994; Rodman et al., 1987) and fMRI studies (Chawla et al., 1999), I found that V5/MT+ activation was significantly stronger for fast motion (8 deg/s) relative to slow (1 deg/s). The psychophysical data in this study did not reveal a significant difference between slow and fast motion perception (collapsed across directions), but there was a trend for greater fast motion sensitivity.

Given that single cell response properties in monkey MT parallel perceptual responses in motion discrimination tasks (Newsome et al., 1989), one would expect that the increased response in V5/MT+ for faster motion found in our study and previously (Chawla et al., 1999), would be matched by the psychophysical data. That is, one would expect greater sensitivity (lower thresholds) for faster motion as opposed to slow. It may be that this contrast lacked sufficient power in Experiment 1 given that this was the one motion variable tested between-subjects, as opposed to within-subjects. A more sensitive test in which both slow and fast motion were tested within subjects may show that sensitivity for these two speeds does in fact differ.

As noted in the study by Chawla et al. (1999) the V5/MT+ response to speed depicts an inverted "U"-shaped function. The current study replicates half of this function in that an optimal V5/MT+ speed (8 deg/s) was compared only to a slower speed (1 deg/s). By comparing an 8 deg/s motion with a faster speed of motion in behavioural and imaging studies, there is room to further test if patterns of cortical responses to speed should lead to reliable differences in perceptual responses to optimal and sub-optimal motion speeds. While a close link has been posed between

single cell responses and perceptual responses in monkeys (e.g. Newsome et al., 1989), direct tests of a similar link in humans are increasingly feasible with neuroimaging techniques.

### *Direction of Motion*

The directional anisotropies found in this study for faster speed confirm patterns reported previously; namely that centripetal directions of motion are perceived more accurately than centrifugal directions of motion (Edwards & Badcock, 1993; Raymond, 1994). Similarly, it was found that horizontal motion was perceived more accurately than vertical motion (Raymond, 1994). There is little evidence to refute a horizontal motion bias; however, the centripetal motion bias found in this study is challenged by the centrifugal bias noted by Ball and Sekuler (1980) and Dumoulin et al. (2001).

The current study differs from the studies by Ball and Sekuler (1980) and Dumoulin et al. (2001); these differences may account for the discrepancies in the results. First, this study tested the sensitivity to motion direction by obtaining minimum coherence threshold scores. Edwards and Badcock (1993) and Raymond (1994) also found centripetal motion biases when studying motion sensitivity at threshold levels. The stimulus used by Ball and Sekuler contained dots moving in 100% coherence. It is unclear whether direction perception should be identical for threshold and suprathreshold stimuli. It is possible that the cortical mechanisms involved in discrimination of 100% coherent motion may differ from motion discrimination at a lesser coherence level. At 100% coherence, one need not integrate motion signals across the visual field; any individual dot provides an accurate motion signal. As such, stimuli with lower coherence may depend more heavily on global mechanisms. The centripetal bias found in this study and previously (Edwards & Badcock, 1993; Raymond, 1994) may reflect anisotropic processing in *global* motion cortical regions

such as V5/MT+ and V3A. The centrifugal bias found by Ball & Sekuler (1980) may better inform us of anisotropic processing of *local* motion in earlier occipital regions such as V1, V2, and V3.

It was for this reason that the coherence levels of the fMRI stimuli used in this study were chosen to be 85% and 25%. Both of these levels require global integration to accurately discriminate the motion, yet 85% is well above expected thresholds, and 25% is very near expected thresholds. (Note that the accuracy data in Appendix B shows that accuracy for the 25% coherence conditions is near 82%, which is the appropriate threshold level obtained from a Weibull function based on a two-choice response task.) Thus these two levels were designed to be suprathreshold and threshold stimulus levels. The cortical response to coherence levels was compared in V5/MT+ and greater activation was found for 25% coherent motion relative to 85% coherent motion. This study was not designed to map the V5/MT+ response to motion coherence level, but this contrast does indicate a greater cortical response for stimuli near perceptual threshold.

It is not surprising that the centrifugal bias found by Dumoulin and his colleagues (2001) was not replicated in this study. Our stimulus was defined by luminance contours (a first-order motion stimulus) whereas their study used a second-order (contrast-defined) motion stimulus. Differences in directional anisotropies could arise from differences in the way first- and second-order motion is processed. Many motion studies have focused solely upon luminance-based motion stimuli (Culham, He, Dukelow, & Verstraten, 2001); further research must be done to determine if directional anisotropies for first- and second-order stimuli are comparable.

### *Speed and Direction of Motion*

The directional anisotropies just described apply only to the faster stimulus speed in our study. When the speed of motion was slow, no reliable direction anisotropies were uncovered. It should be noted that the first psychophysical experiment resulted in significantly lower thresholds for upward motion relative to downward. That experiment used a discrimination task in which upward and downward motion were paired within a condition. Because participants had to decide on each trial which of the two directions were present if participants displayed any response bias for one of the two directions, their accuracy would be artificially increased for that direction, and decreased for the paired direction. It was suspected that response bias could have led to the difference between upward and downward slow motion perception. Accordingly, a detection experiment was designed to remove any possibility of response bias from this comparison. Upward motion was tested separately from downward motion using a 2-interval task. An interval with some proportion of coherent motion (either upward or downward motion) was paired with an incoherent motion interval. Because participants no longer were to discriminate between the two directions, there could be no bias for one direction or the other. It was found in this experiment that upward and downward motion thresholds did not differ from one another. It seems that the difference found in the first experiment was not one of perceptual sensitivity to the two directions, but instead a bias in response patterns. The same lengths were taken to further test increased centripetal motion sensitivity found in the first experiment. Increased sensitivity for centripetal motion relative to centrifugal motion was, however, replicated in Experiment 2 when tested with a detection paradigm.

The differences between directional anisotropies in slow and fast global motion processing have interesting implications. Using similar speeds to those in our study, Edwards et al. (1998) found that global motion extraction may rely on at least two independent systems, one tuned to slower speeds (below 4.8 deg/s) and the other specializing in faster speeds between (4.8 and 10.2 deg/s). The speed-tuned global motion mechanisms suggested by Edwards and his colleagues are strengthened by our findings. Our slow speed of 1 deg/s and fast speed of 8 deg/s fall within the slow and fast speed-tuned global motion systems they proposed. While they were able to identify the existence of these two global motion mechanisms, the current study has shown different properties of these speed-tuned global motion mechanisms. We were able to demonstrate unique patterns of direction discrimination for faster global motion, relative to slow motion, and provide support for these speed-tuned directional anisotropies in cortical processing.

Further studies should investigate speeds faster than those used in this study and in the study by Edwards and his colleagues. Chawla et al. (1999) found that V5/MT+ responded best to speeds between 4 and 8 deg/s; the BOLD response in this region decreased for speeds slower *and* faster than this range. It may be that the isotropic pattern of direction perception found for the slow speed in our study would be replicated for speeds that are both slower and faster than optimal speeds of 4-8 deg/s. Directional anisotropies were observed in our study only for the optimal speed of 8 deg/s; anisotropies were not found for slower motion and perhaps would not be found for motion exceeding 8 deg/s. In keeping with the speed-tuned pathways identified by Edwards and his colleagues, this would suggest that there are more than 2 speed-tuned pathways. These speed-tuned pathways would delineate motion processing of optimal

speeds (approximately 4-8 deg/s) and speeds that are not optimal (speeds that are slower *and* faster than 4-8 deg/s).

Alternatively, testing motion directions at speeds faster than those used in our study could instead show that directional anisotropies persist at speeds greater than 8 deg/s. If that were the case, the isotropic direction processing at slow speeds and anisotropic direction processing at fast speeds may be better attributed to a model that includes just two motion processing pathways.

Others have suggested the presence of fast and slow motion pathways as well. Gegenfurtner and Hawken (1996) proposed a fast motion channel that is sensitive to luminance contrasts and a slow motion channel that specializes in colour processing. Such fast and slow motion pathways may correspond to the M pathway and parvocellular (P) pathway, respectively (Gegenfurtner & Hawken, 1996). These pathways remain segregated from the retina to cortex as they pass through their respective parvocellular and magnocellular layers of the LGN, and they consequently have distinct functional properties. Cells in the P pathway are almost exclusively colour-opponent whereas those in the M pathway are much more sensitive to black and white as opposed to colour (Shapley, 1995). However, both the M and P pathways are capable of processing most types of visual information. To illustrate this, Merigan, Byrne, and Maunsell (1991) have shown that motion direction and speed can both be discriminated based entirely on input from the P pathway following M pathway lesions. Despite this evidence that the P pathway is capable of motion processing, Merigan and his colleagues concluded that the M pathway probably conveys the large majority of motion information in the absence of M pathway lesions, especially for faster speeds of motion. Single cell recording from MT has also shown that the P pathway makes weak,

but definite contributions to MT (Maunsell, Nealey, & DePriest, 1990) which indicates that the P pathway is capable of conveying motion information.

It was not the purpose of this study to investigate the subcortical visual pathways, yet, the account of motion processing in the M and P pathway coincides with the neuroimaging data collected in this study. If the P pathway is involved in slow motion processing and the M pathway, in fast motion processing, one would expect less V5/MT+ activation in response to slow motion since P pathway contributions to V5/MT+ are weaker than those of the M pathway (Maunsell et al., 1990). In keeping with this hypothesis, greater V5/MT+ activation was found for faster motion than for slow. Whether this finding is best attributed to the speed-tuning of the cells within V5/MT+, or to the motion input from the P and M pathways deserves further attention.

#### *Neuroimaging Evidence of Speed- and Direction-Tuned Motion Responses*

Much of the focus in this study has been to determine if cortical activation in V5/MT+ paralleled behavioural evidence of speed-tuned directional anisotropies. The activity in this region provides a strong building block from which to understand these anisotropies. In accordance with the psychophysical findings, slow motion did not result in differential activation of V5/MT+ for horizontal motion, when compared to vertical, or centripetal motion, relative to centrifugal. Yet these same direction contrasts did result in significant activation differences when the speed of motion was fast. Activation in V5/MT+ was significantly greater for centripetal motion, relative to centrifugal; this mirrors the heightened psychophysical sensitivity for centripetal motion. Surprisingly though, it was not horizontal motion, the direction to which participants also showed greater perceptual sensitivity, that led to greater V5/MT+ activity. It was instead vertical motion that produced a greater BOLD response in the V5/MT+ ROI.

This puzzling finding could reflect the inclusive nature of the ROI in this study. It is often the case that neuroimaging studies do not distinguish MT from MST; this is a difficult task given their neighboring location and similar functions. Yet it is possible. Morrone and her colleagues (2000) distinguished between MT and MST based on the response of these areas to motion direction. They compared upward and downward coherent motion to incoherent motion as well as radial motion to incoherent motion; the use of a motion baseline was intended to isolate the response to motion *direction* and not simply the response to motion. They found that MT responded more strongly to translational directions whereas MST responded better to radial directions of motion. The MT localizer used in our study was composed of radial motion, however, the radial motion was instead contrasted with stationary dots. Radial motion is ideal for activating the MT complex. Contrasting motion with stationary dots elicits a response from motion sensitive cortical regions; radial motion was used specifically because it includes all directions of motion thereby eliciting a strong response from V5/MT+ neurons regardless of their directional tuning. This stimulus is commonly used to localize the MT complex (e.g. Huk, Dougherty, & Heeger, 2002; Tootell & Taylor, 1995; Watson et al., 1993; Zeki et al., 1991), despite its inability to distinguish MT from MST. Given the findings of Morrone and her colleagues, a more sensitive test for cortical responses to translational motion may be achieved by isolating MT from MST. Naito et al. (2000) did find a larger MEG response in the extrastriate cortex for horizontal motion as opposed to vertical motion; responses were also greater for centripetal motion when compared to centrifugal motion. Because MEG has poor spatial resolution, the study by Naito et al. could not specify the exact extrastriate cortical regions from which their MEG responses were obtained but suggests that horizontal and vertical motion should

be studied further to determine the cortical basis for increased perceptual sensitivity to horizontal motion.

With exception to the discrepancy between fast horizontal/vertical perceptual sensitivity and V5/MT+ activation, patterns of directional anisotropies in motion perception were easily reconciled with the BOLD responses observed in V5/MT+. It is likely that the increased BOLD response for centripetal directions and fast speeds of motion reflects an increase in the number of neurons that respond to these parameters, or an increase in the magnitude of the response in these neurons. Clearly V5/MT+ is an important cortical region for global motion processing. That is not to say that it is the only important cortical region that may further our understanding of directional anisotropies. Included in Appendix E are brain maps obtained from contrasting many of the motion conditions with the baseline (stationary dot) condition. V5/MT+ activation is robust in these maps, but so too is V1 and V3A activation. V1 has been studied extensively with single cell recording, and direction and speed selectivity have been noted (DeYoe & Van Essen, 1988). The V1 activation observed in response to the motion stimuli in this study likely ensues from the local motion signals within the stimulus.

The other prominent motion region that emerged from motion-vs-baseline contrasts corresponds to probable V3A. Neurons in V3A are direction and speed selective; similar to V5/MT+, V3A responds best to fast speeds ranging from 4 to 16 deg/s (Chawla et al., 1999). While both of these areas likely play an important role in processing direction and speed of motion, it was not possible to study the BOLD response in these regions for the contrasts of interest to this study. Because contrasts of one motion direction with another direction, or one speed with another speed of motion are such subtle comparisons, the BOLD response did not differ in these regions,

or elsewhere in the brain, when whole-brain analyses were conducted. It was the increased power of a ROI analysis that allowed differences in the BOLD response to manifest in V5/MT+ for these subtle comparisons. Similar ROI analyses can certainly be used to study V1 and V3A responses with appropriate localization of these areas. It is the case that both V1 and V3A are occipital regions that can be retinotopically mapped (Tootell & Taylor, 1995; Tootell et al., 1997). Retinotopic mapping would allow the delineation of these regions for ROI analyses much like an MT localizer stimulus was used in this study to delineate V5/MT+ for ROI analyses.

### *Conclusions*

In sum, distinct psychophysical and neuroimaging responses for motion direction were observed in this study for fast motion, relative to slower motion. This suggests that there are at least two speed-tuned global motion mechanisms which each have unique directional anisotropies. A neural basis for much of these motion responses has been implicated in V5/MT+. Further investigations should address other cortical regions such as V1 and V3A to demarcate their role in directional anisotropies, and the dependency of these anisotropies on speed. These are cortical regions, in addition to V5/MT+, that may contribute to the behavioural findings revealed in this study.

## References

- Albright, T.D. (1989). Centrifugal bias in the middle temporal visual area (MT) of the macaque. *Visual Neuroscience*, 2, 177-188.
- Ball, K. & Sekuler, R. (1980). Human vision favors centrifugal motion. *Perception*, 9, 317-325.
- Barton, J.J.S., Sharpe, J.A., & Raymond, J.E. (1995). Retinotopic and directional defects in motion discrimination in humans with cerebral lesions. *Annals of Neurology*, 37, 665-675.
- Born, R.T. & Tootell, R.B.H. (1992). Segregation of global and local motion processing in primate middle temporal visual area. *Nature*, 357, 497-499.
- Braddick, O. J., O'Brien, J. M. D., Wattam-Bell, J., Atkinson, J., Hartley, T., & Turner, R. (2001). Brain areas sensitive to coherent visual motion. *Perception*, 30, 61-72.
- Britten, K.H., Shadlen, M.N., Newsome, W.T., & Movshon, J.A. (1992). The analysis of visual motion: A comparison of neuronal and psychophysical performance. *The Journal of Neuroscience*, 12, 4745-4765.
- Chawla, D., Buechel, C., Edwards, R., Howseman, A., Josephs, O., Ashburner, J., and Friston, K. J. (1999). Speed-dependent responses in V5: A replication study. *NeuroImage*, 9, 508-515.
- Cheng, K., Hasegawa, T., Saleem, K., & Tanaka, K. (1994). Comparison of neuronal selectivity for stimulus speed, length, and contrast in prestriate visual cortical areas V4 and MT of the macaque monkey. *Journal of Neurophysiology*, 71, 2269-2280.
- Culham, J., He, S., Dukelow, S., & Verstraten, F.A.J. (2001). Visual motion and the human brain: What has neuroimaging told us? *Acta Psychologica*, 107, 69-94.

- DeAngelis, G.C. & Uka, T. (2003). Coding of horizontal disparity and velocity by MT neurons in the alert macaque. *The Journal of Neurophysiology*, 89, 1094-1111.
- DeYoe, E.A. & Van Essen, D.C. (1988). Concurrent processing streams in monkey visual cortex. *Trends in Neurosciences*, 11, 219-226.
- Dumoulin, S. O., Bittar, R. G., Kabani, N. J., Baker, C. L., Le Goualher, G., Pike, G. B., and Evans, A. C. (2000). A new anatomical landmark for reliable identification of human area V5/MT: A quantitative analysis of sulcal patterning. *Cerebral Cortex*, 10, 454-463.
- Dumoulin, S. O., Baker, C. L., and Hess, R. F. (2001). Centrifugal bias for second-order but not first-order motion. *Journal of the Optical Society of America*, 18, 2179-2189.
- Edwards, M. & Badcock, D.R. (1993). Asymmetries in the sensitivity to motion in depth: A centripetal bias. *Perception*, 22, 1013-1023.
- Edwards, M., Badcock, D.R., & Smith, A.T. (1998). Independent speed-tuned global motion systems. *Vision Research*, 38, 1573-1580.
- Fellerman, D.J., & Van Essen, D.C. (1987). Receptive field properties of neurons in area V3 of macaque monkey extrastriate cortex. *The Journal of Neuroscience*, 4, 889-920.
- Gegenfurtner, K.R. & Hawken, M.J. (1996). Interaction of motion and colour in the visual pathways. *Trends in Neurosciences*, 19, 394-401.
- Huk, A.C., Dougherty, R.F., & Heeger, D.J. (2002). Retinotopy and functional subdivision of human areas MT and MST. *The Journal of Neuroscience*, 22, 7195-7205.

- Kawakami, O., Kaneoke, Y., & Kakigi, R. (2000). Perception of apparent motion is related to the neural activity in the human extrastriate cortex measured by magnetoencephalography. *Neuroscience Letters*, 285, 135-138.
- Liu, J. & Newsome, W. T. (2003). Functional organization of speed tuned neurons in visual area MT. *Journal of Neurophysiology*, 89, 246-256.
- Marcas, V.L., Zihl, J., & Cowey, A. (1997). Comparing the visual deficits of a motion blind patient with the visual deficits of monkeys with area MT removed. *Neuropsychologia*, 35, 1459-1465.
- Maunsell, J.H.R., Nealey, T.A., & DePriest, D.D. (1990). Magnocellular and parvocellular contributions to responses in the middle temporal visual area (MT) of the macaque monkey. *The Journal of Neuroscience*, 10, 3323-3334.
- Maunsell, J.H.R., & Van Essen, D.C. (1983). Functional properties of neurons in the middle temporal visual area (MT) of the macaque monkey: I. Selectivity for stimulus direction, speed and orientation. *The Journal of Neurophysiology*, 49, 1127- 1147.
- Merigan, W.H., Byrne, C.E., & Maunsell, J.H.R. (1991). Does primate motion perception depend on the magnocellular pathway? *The Journal of Neuroscience*, 11, 3422-3429.
- Morrone, M.C., Tosetti, M., Montanaro, D., Fiorentini, A., Cioni, G., and Burr, D.C. (2000). A cortical area that responds specifically to optic flow, revealed by fMRI. *Nature Neuroscience*, 3, 1322-1328.
- Naito, T., Kaneoke, Y., Osaka, N., & Kakigi, R. (2000). Asymmetry of the human visual field in magnetic response to apparent motion. *Brain Research*, 865, 221-226.
- Nakamura, H., Kashii, S., Nagamine, T., Matsui, Y., Hashimoto, T., Honda, Y., & Shibasaki, H. Human V5 demonstrated by magnetoencephalography using

random dot kinematograms of different coherence levels. *Neuroscience Research*, 46, 423-433.

Newsome, W.T. (1987). Visual cortical mechanisms for the control of smooth pursuit eye movements. *Archives of Neurology*, 44, 1210.

Newsome, W.T., Britten, K.H., & Movshon, J.A. (1989). Neuronal correlates of a perceptual decision. *Nature*, 341, 52-54.

Newsome, W.T. & Paré, E.B. (1988). A selective impairment of motion perception following lesions of the middle temporal visual area (MT). *The Journal of Neuroscience*, 8, 2201-2211.

Newsome, W.T., Wurtz, R.H., Dürsteler, M.R., & Mikami, A. (1985). Deficits in visual motion processing following ibotenic acid lesions of the middle temporal visual area of the macaque monkey. *The Journal of Neuroscience*, 5, 825-840.

Ohtani, Y. & Ejima, Y. (1997). Anisotropy for direction discrimination in a two-frame apparent motion display. *Vision Research*, 37, 765-767.

Orban, G.A., Fize, D., Peuskens, H., Denys, K., Nelissen, K., Sunaert, S., Todd, J., & Vanduffel, W. (2003). Similarities and differences in motion processing between the human and macaque brain: Evidence from fMRI. *Neuropsychologia*, 41, 1757-1768.

Plant, G.T., Laxer, K.D., Barbaro, N.M., Schiffman, J.S., & Nakayama, K. (1993). Impaired visual motion perception in the contralateral hemifield following unilateral posterior cerebral lesions in humans. *Brain*, 116, 1303-1335.

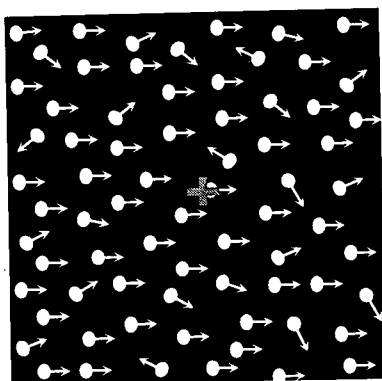
Raymond, J.E. (1994). Directional anisotropy of motion sensitivity across the visual field. *Vision Research*, 34, 1029-1037.

- Rees, G., Friston, K., & Koch, C. (2000). A direct quantitative relationship between the functional properties of human and macaque V5. *Nature Neuroscience*, 3, 716-723.
- Rodman, H.R & Albright, T.D. (1987). Coding of visual stimulus velocity in area MT of the macaque. *Vision Research*, 27, 2035-2048.
- Rottach, K.G., Zivotofsky, A.Z., Das, V.E., Averbuch-Heller, L., Discenna, A.O., Poonyathalang, A., & Leigh, R.J. (1996). Comparison of horizontal, vertical and diagonal smooth pursuit eye movements in normal human subjects. *Vision Research*, 36, 2189-2195.
- Schenk, T. & Zihl, J. (1997). Visual motion perception after brain damage: I. Deficits in global motion perception. *Neuropsychologia*, 35, 1289-1297.
- Shapley, R. (1995). Parallel neural pathways and visual function. In M. S. Gazzaniga (Ed.), *The Cognitive Neurosciences* (pp. 315-324). Cambridge, MT: The MIT press.
- Strasburger, H. (2001). Converting between measures of slope of the psychometric function. *Perception & Psychophysics*, 63, 1348-1355.
- Talairach, J. & Tournoux, P. (1988). *Coplanar Stereotaxic Atlas of the Human Brain*. Thieme, New York.
- Tootell, R.B. & Taylor, J.B. (1995). Anatomical evidence for MT and additional cortical visual areas in humans. *Cerebral Cortex*, 1, 39-55.
- Tootell, R. B., Mendola, J. D., Hadjikhani, N. K., Ledden, P. J., Liu, A. K., Reppas, J. B., Sereno, M. I., & Dale, A. M. (1997). Functional analysis of V3A and related areas in human visual cortex. *The Journal of Neuroscience*, 17, 7060-7078.
- Watamaniuk, S.N.J. (1993). Ideal observer for discrimination of the global direction of dynamic random-dot stimuli. *Journal of the Optical Society of America*, 10, 16-28.

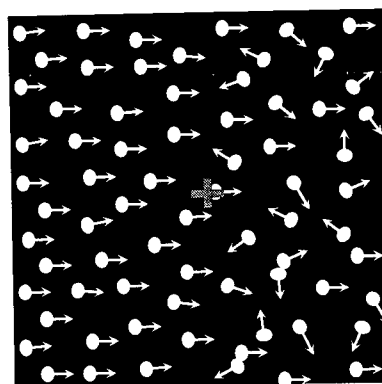
- Watson, J. D., Myers, R., Frackowiak, R. S., Hajnal, J. V., Woods, R. P., Mazziotta, J. C., Shipp, S., and Zeki, S. (1993). Area V5 of the human brain: Evidence from a combined study using positron emission tomography and magnetic resonance imaging. *Cerebral Cortex*, 3, 79-94.
- Zeki, S., Watson, J. D., Lueck, C., Friston, K. J., Kennard, C., & Frackowiak, R. S. J. (1991). A direct demonstration of functional specialization in the human visual cortex. *Journal of Neuroscience*, 11, 641-649.

## Appendix A: Global Motion Stimuli

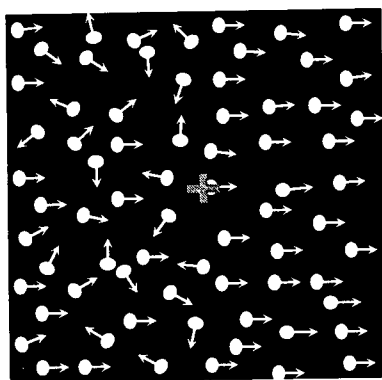
1)



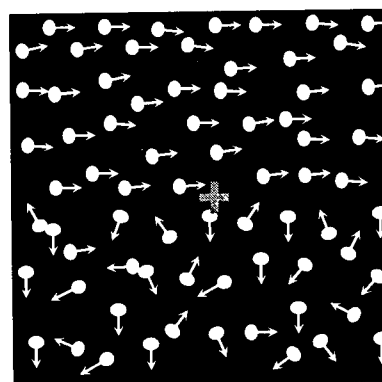
2)



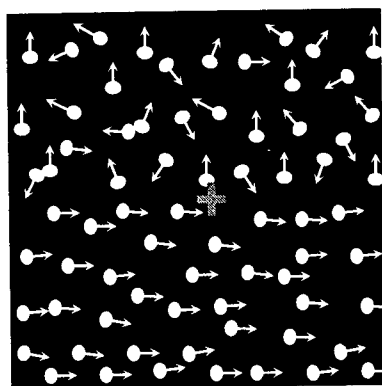
3)



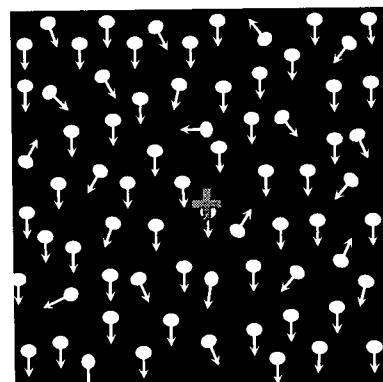
4)



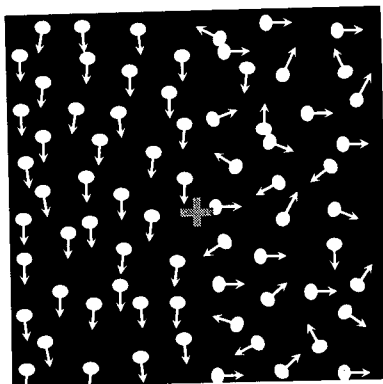
5)



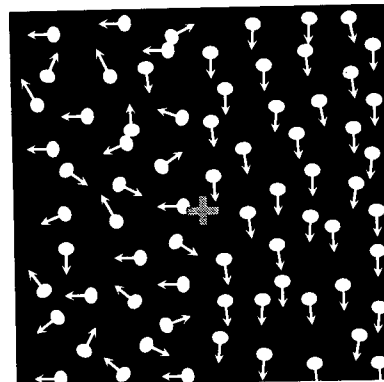
6)



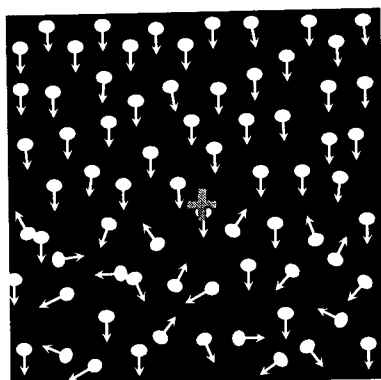
7)



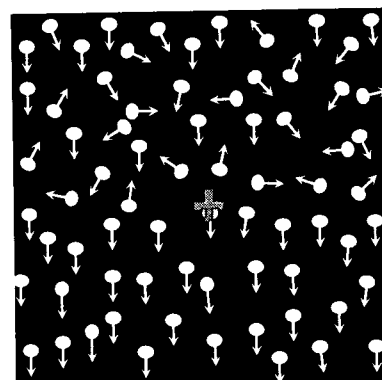
8)



9)



10)



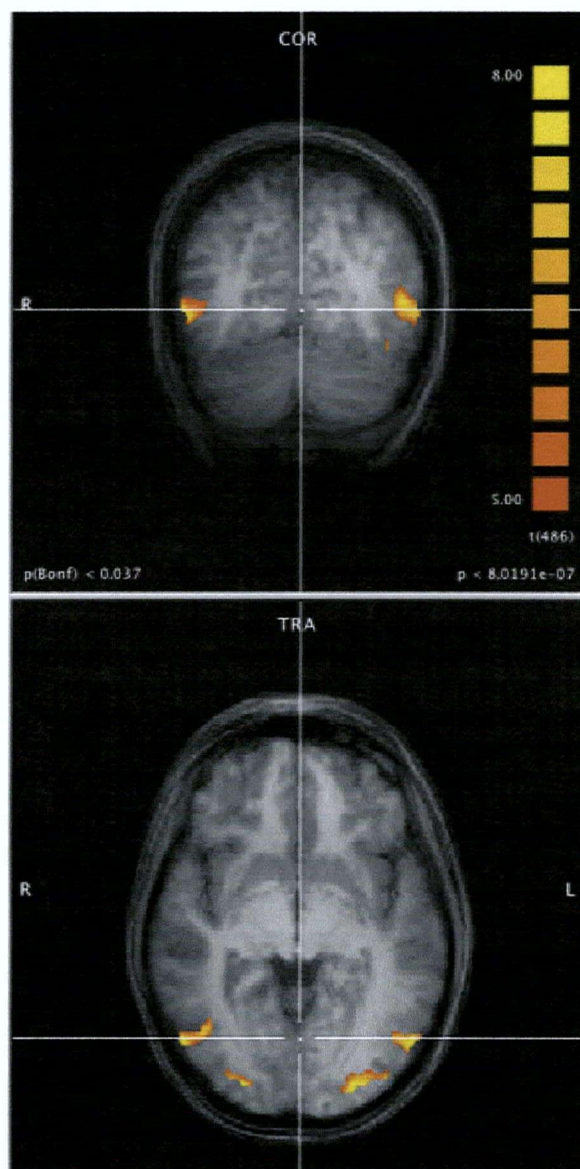
Note. The diagram depicts the 10 conditions of the Experiment 1 RDK stimuli. 1) Full-field Horizontal, 2) Left-hemifield Horizontal, 3) Right-hemifield Horizontal, 4) Top-hemifield Horizontal, 5) Bottom-hemifield Horizontal, 6) Full-field Vertical, 7) Left-hemifield Vertical, 8) Right-hemifield Vertical, 9) Top-hemifield Vertical, 10) Bottom-hemifield Vertical. Rightward motion trials are shown for conditions 1-5; these horizontal conditions also contained leftward motion trials. Downward motion trials are shown in conditions 6-10; these vertical conditions also included upward motion trials.

Appendix B: Mean Accuracy Scores for Responses Made during the fMRI Scans.

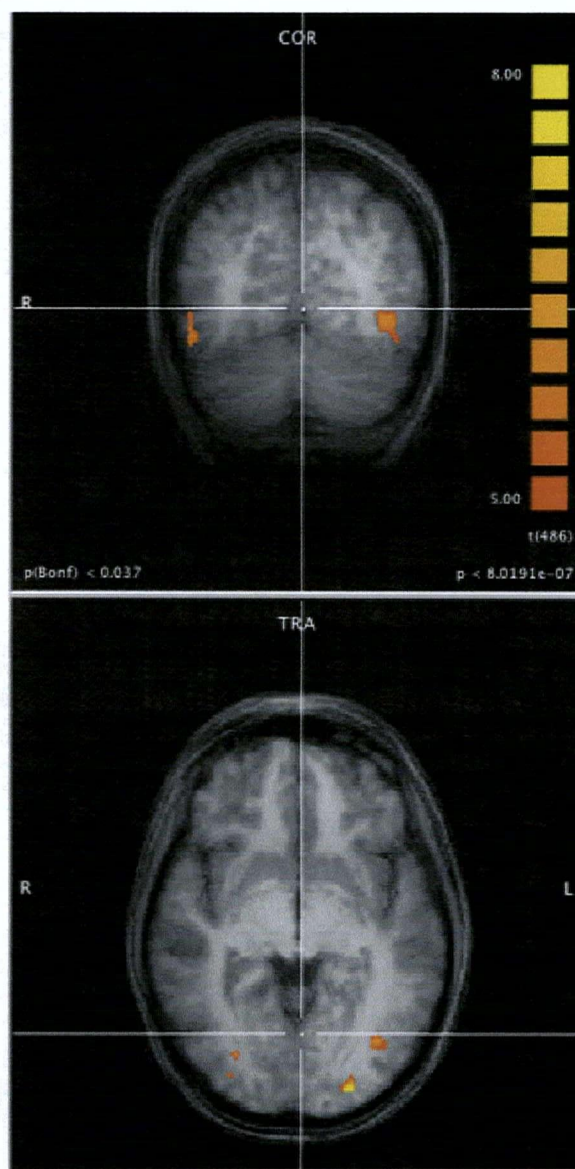
<i>Stimulus Condition</i>	<i>Mean Accuracy (%)</i>
Slow Horizontal	
85% Coherence	89.9
25% Coherence	78.0
Control	93.1
Slow Vertical	
85% Coherence	92.9
25% Coherence	82.4
Control	91.1
Slow Centripetal	
85% Coherence	86.3
25% Coherence	79.2
Control	84.4
Slow Centrifugal	
85% Coherence	83.6
25% Coherence	73.5
Control	77.6
Fast Horizontal	
85% Coherence	94.3
25% Coherence	81.0
Control	91.8
Fast Vertical	
85% Coherence	91.4
25% Coherence	86.0
Control	89.0
Fast Centripetal	
85% Coherence	88.1
25% Coherence	82.7
Control	88.6
Fast Centrifugal	
85% Coherence	90.8
25% Coherence	83.0
Control	81.0

Note. The behavioural task was to discriminate motion direction.

## Appendix C: Single Subject Brain Maps Obtained from MT Localizer



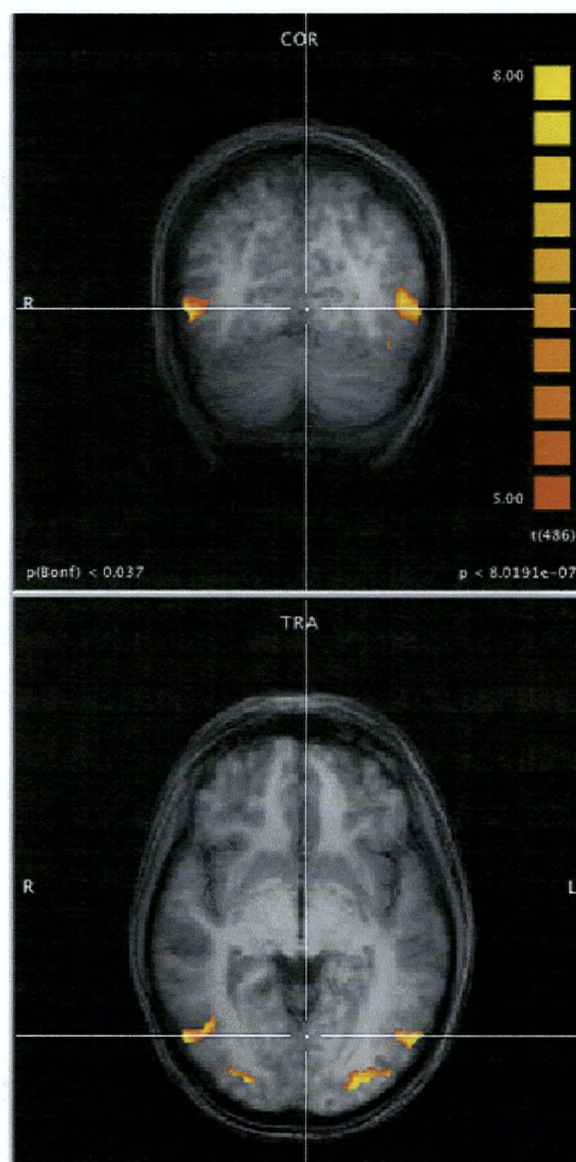
Subject 1 V5/MT+



Subject 4 V5/MT+

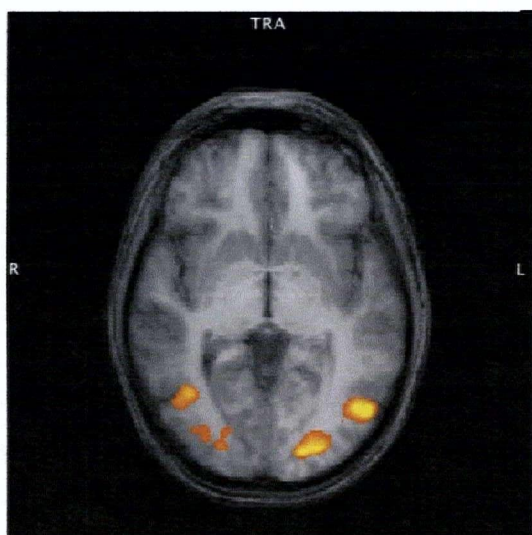


Subject 5 V5/MT+

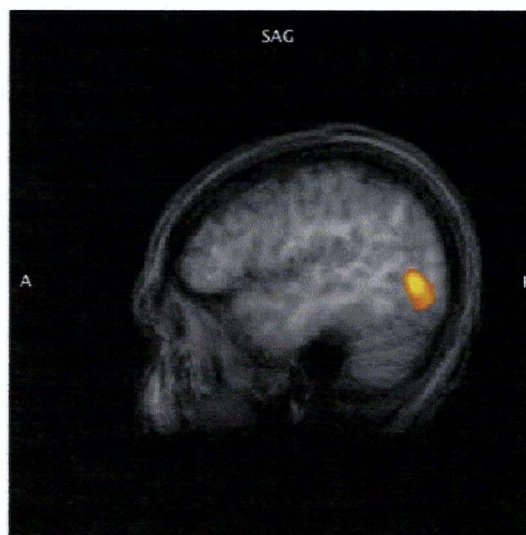


Subject 6 V5/MT+

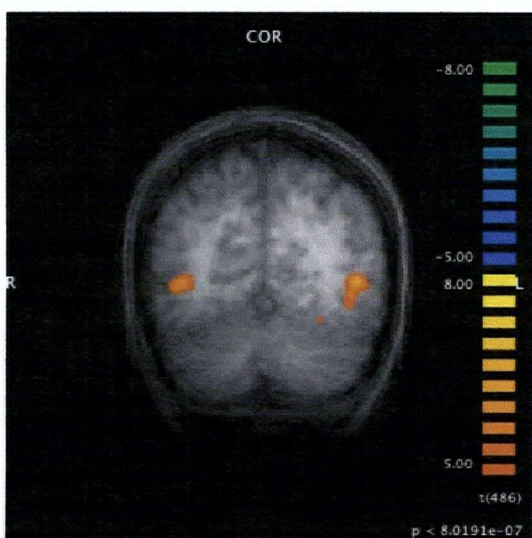
## Appendix D: Group Brain Maps Obtained from MT Localizer



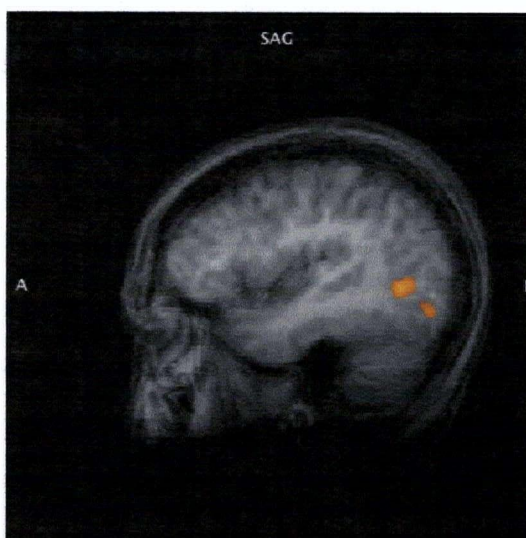
Group Axial V5/MT+



Group Left Sagittal V5/MT+



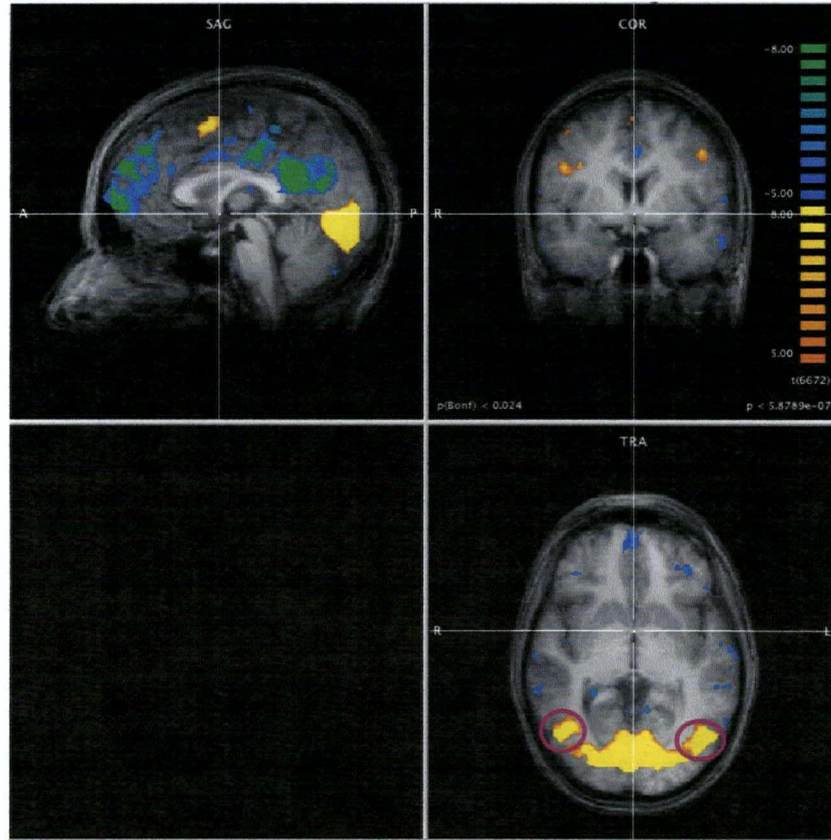
Group Coronal V5/MT+



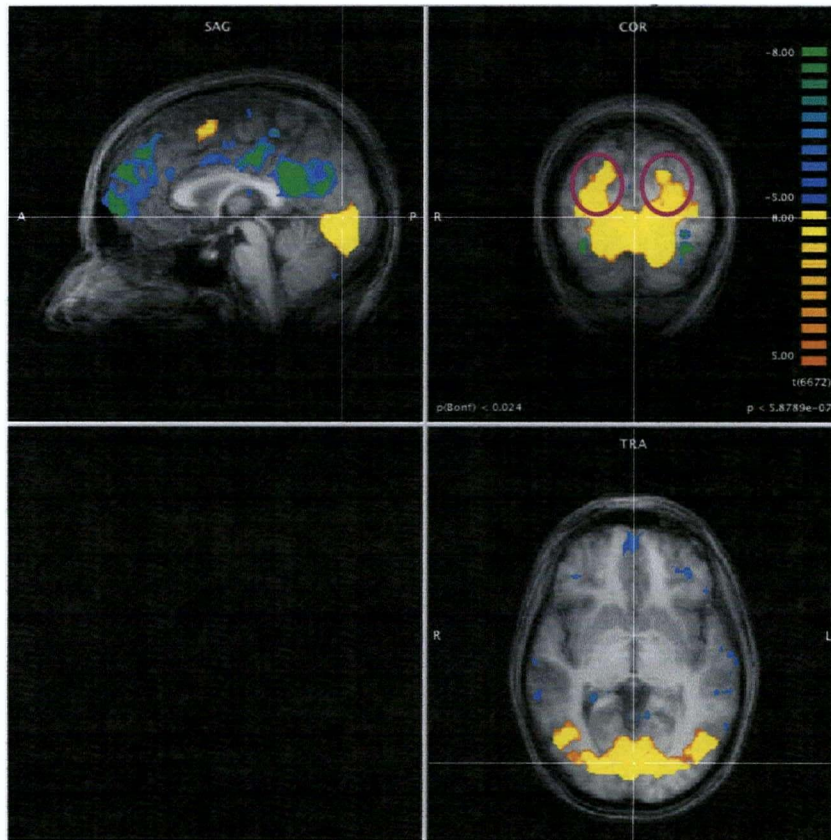
Group Right Sagittal V5/MT+

Appendix E: Group Brain Maps of Motion Responsive Areas

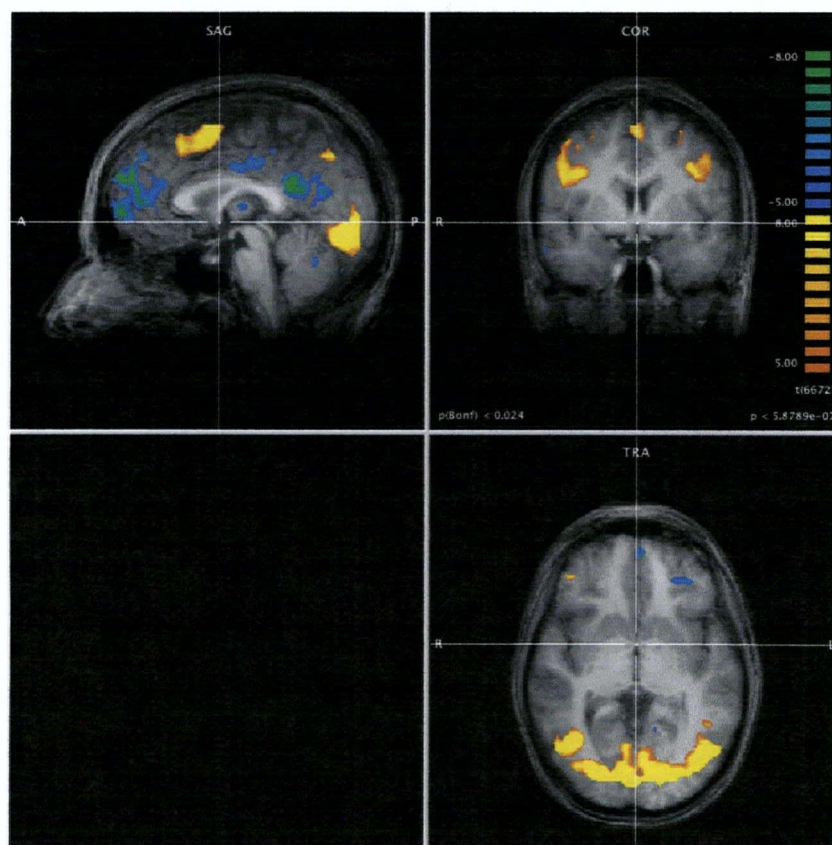
a)



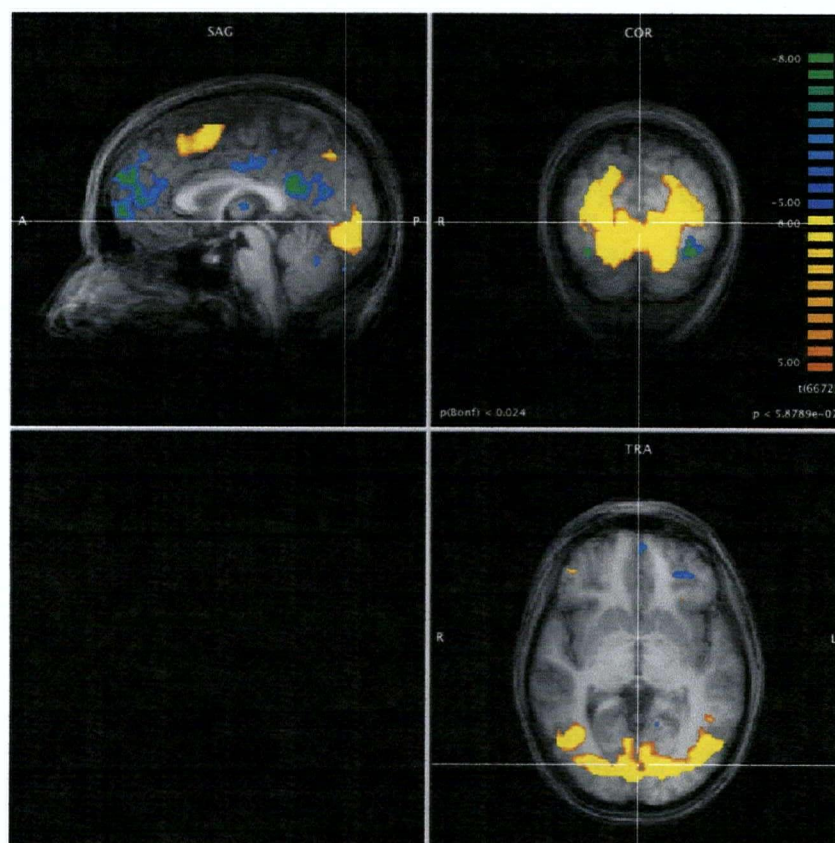
b)



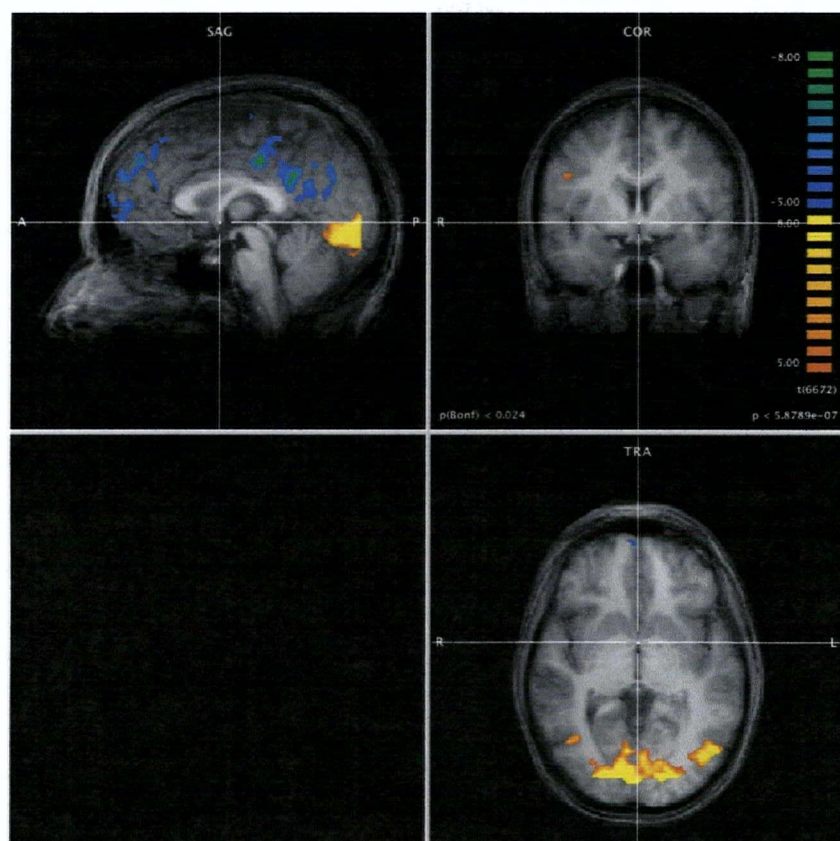
c)



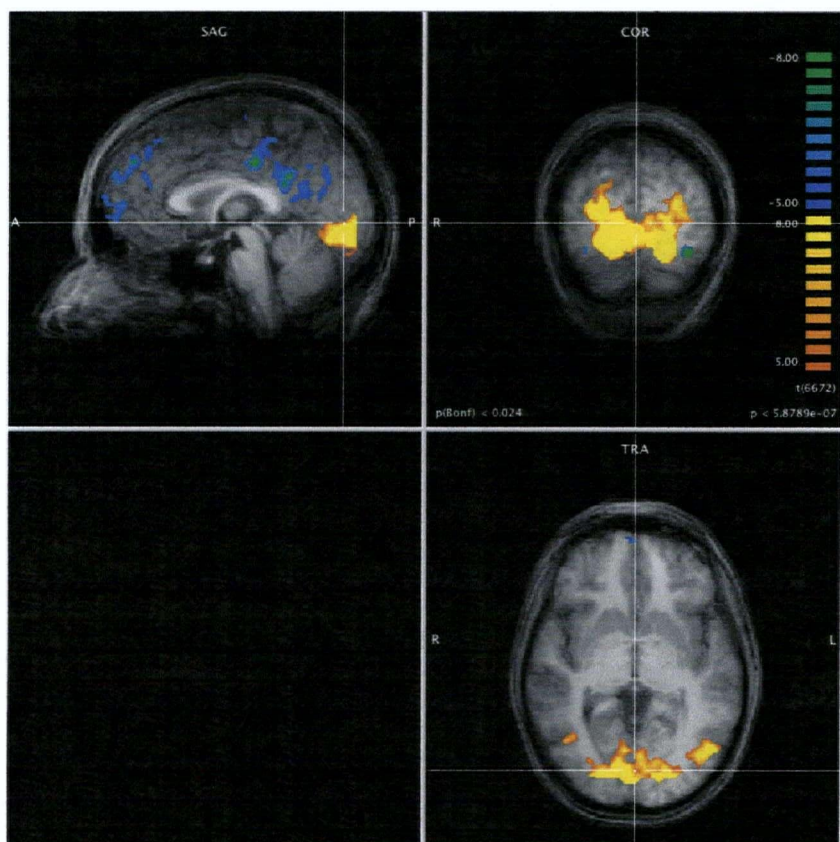
d)



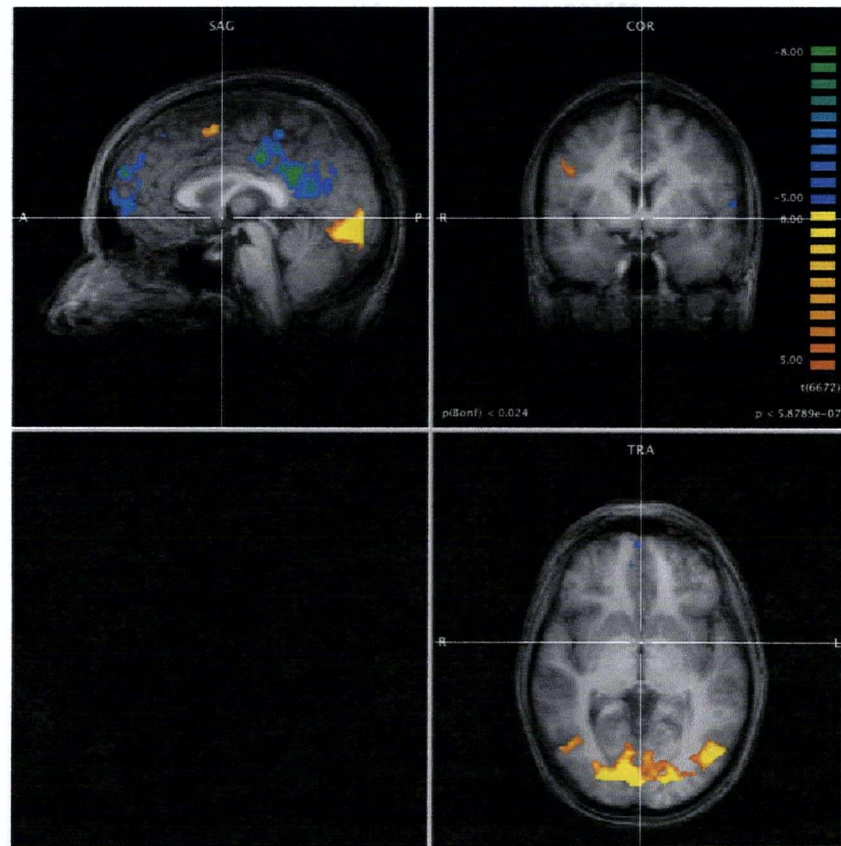
e)



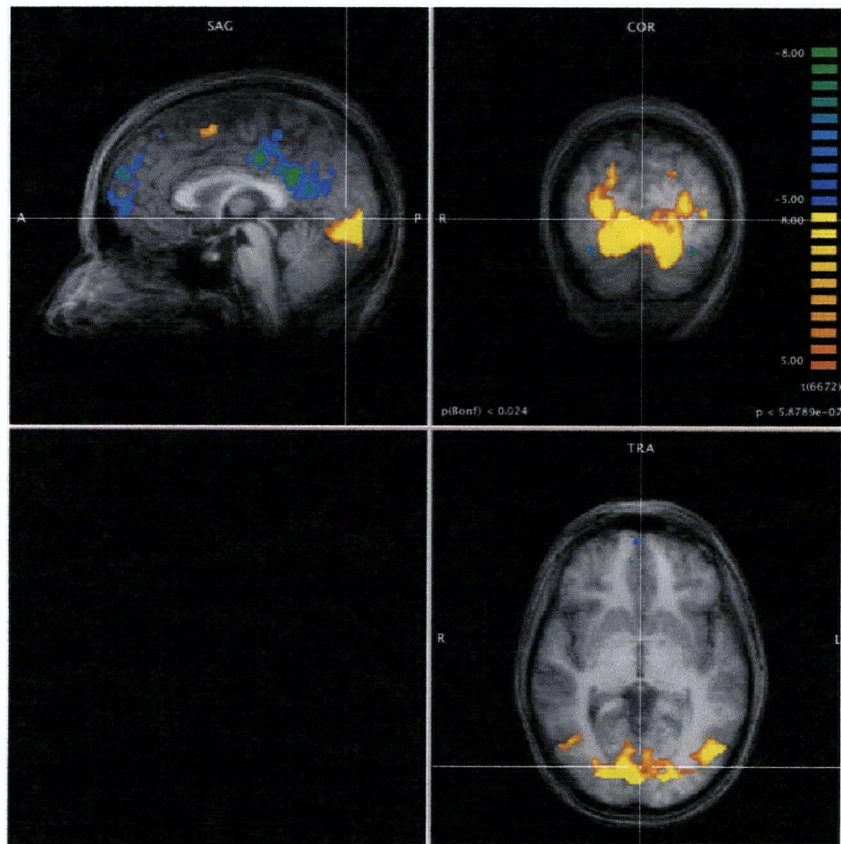
f)



g)



h)



Note. Orange-yellow on the colour scale indicates positive activation for each of the "motion vs. baseline" contrasts and blue-green indicates negative activation. Thus orange-yellow identifies cortical regions more active to the motion tasks, and blue-green identifies cortical regions more active during the baseline task. These contrasts were thresholded at  $p < .025$ , corrected.

- a) Fast motion vs. Baseline (Crosshair located at 0, 0, 0 Talairach coordinates).  
Left and Right V5/MT+ are circled in the axial view.
- b) Fast motion vs. Baseline (Crosshair located at 0, 77, 0 Talairach coordinates).  
Probable left and right V3A are circled in the coronal view. V1 is inferior to these regions.
- c) Slow motion vs. Baseline (Crosshair located at 0, 0, 0 Talairach coordinates)
- d) Slow motion vs. Baseline (Crosshair located at 0, 77, 0 Talairach coordinates)
- e) Fast Horizontal motion vs. Baseline (Crosshair located at 0, 0, 0 Talairach coordinates)
- f) Fast Horizontal motion vs. Baseline (Crosshair located at 0, 77, 0 Talairach coordinates)
- g) Fast Centripetal motion vs. Baseline (Crosshair located at 0, 0, 0 Talairach coordinates)
- h) Fast Centripetal motion vs. Baseline (Crosshair located at 0, 77, 0 Talairach coordinates)