

THE INFLUENCE OF CULTURE, ATTENTION, AND VISUAL FEEDBACK ON
PERCEPTUAL GROUPING

By

Tiffany A. Carther-Krone (Lazar)

A Thesis submitted to the Faculty of Graduate Studies at
The University of Manitoba
in partial fulfilment of the requirements of the degree of

DOCTOR OF PHILOSOPHY

Department of Psychology
University of Manitoba
Winnipeg, Manitoba, Canada

Copyright © 2021 by Tiffany A. Carther-Krone (Lazar)

Abstract

What factors influence how we perceive the world around us? This dissertation describes a series of experiments using traditional cognitive and psychophysical methodologies, functional magnetic resonance imaging (fMRI), and advanced visuomotor paradigms to explore the effects of culture, attention, and visual feedback on visual perception. In the first study, psychophysical methodologies were used to test the potential mechanism underlying differences in global processing by examining the relative contributions of the magnocellular and parvocellular pathways in mediating global and local visual processing in Asian and Caucasian groups. Participants completed the Navon hierarchical letters task under divided-attention conditions, indicating whether a target letter “H” was present in stimuli that were either unbiased, or biased to predominantly process low-spatial frequency information through the magnocellular or parvocellular pathways. Caucasians processed stimuli more globally than Asians when low-spatial frequency information was projected through the parvocellular pathway. Asians showed a global processing advantage when low-spatial frequency information was projected through the magnocellular pathway, and to a lesser extent to the parvocellular pathway. These findings suggest that the global processing bias found in each group depends on the pathway through which visual information was transmitted. In the second study, fMRI was used to examine perceptual grouping under inattention and divided-attention conditions. Results showed involvement of the right supramarginal gyrus in grouping specifically under conditions of inattention, suggesting that even during implicit grouping complex processing occurs. In the third study, early, middle and late visuomotor control were examined in the context of the Sander Parallelogram illusion to better understand how visual feedback impacts our perceptual system’s ability to group elements of our environment together. Consistent with the Two Visual Streams Hypothesis, results showed a more robust illusion effect for perceptual estimations compared to grasping a target. An illusion effect was also observed when participants were asked to grasp targets under both early and no vision conditions, supporting the notion that while the two streams are distinct, they also interact. Collectively, this work demonstrates that perception is shaped by many factors, and that those factors - in different amounts - can alter how we perceive the world around us.

Acknowledgments

There are many individuals I would like to thank who have guided, supported, and contributed to the completion of this dissertation. First and foremost, I would like to thank my supervisor, Dr. Jonathan Marotta, for his guidance, support and patience throughout the completion of this dissertation. Thank you for always being on my side, for pushing me out of my comfort zone, and for never being anything less than supportive as I figured out a work/family life balance over the past years. I would also like to thank my committee member, Dr. Jane Lawrence-Dewar, for all the time, expertise and support she has given me over the years. Thank you for hosting me during my visits to Thunder Bay to run the fMRI study, for the BrainVoyager tutorials and for all the coffee dates / mentoring sessions. I also want to thank my other committee members, Dr. Cheryl Glazebrook and Dr. Chase Figley, for all the time they graciously committed to committee meetings and reading over dissertations drafts. This dissertation wouldn't be what it is today without their meaningful and constructive feedback. Thank you to all the members of the *Perception and Action lab* that have come and gone over the years as I've worked my way through this academic journey, especially to Ryan Langridge, who graciously listened to me talk through one too many methodological conundrums and statistical analyses. My PhD journey also wouldn't have been the same without Alyse Sukovieff – it was truly an honour and pleasure getting to know you while we worked our way through graduate school together. And finally, to my family and friends outside my academic world – thank you for your never-ending support and encouragement over the years. Especially to my parents, mom and dad, you have always believed in me, listened to me, and supported me. And to my people — my husband, Chris, and our beautiful children, Olivia and Theo. Through it all you three have witnessed the highs and lows the most during this journey. There aren't enough words in the world to describe how much you mean to me, we really are “in it to win it”. Lastly, I wanted to acknowledge that this work was supported by a scholarship from the National Sciences and Engineering Research Council of Canada.

Dedication

This dissertation is dedicated to my parents, whom I am certain didn't imagine seeing me through three decades of school when they enrolled me in kindergarten at 5 years old. The amount of time they have spent helping me with homework, encouraging me, and funding my academic endeavors is unquestionably a testament to their unending love and support. Thank you, mom and dad, for making me into the person I am today. I love you.

Table of Contents

Abstract	ii
Acknowledgments.....	iii
Dedication	iv
List of Tables	viii
List of Figures.....	ix
Permission Statements	x
CHAPTER I: GENERAL INTRODUCTION	1
The Two Visual Streams Hypothesis.....	1
The Human Visual System	2
Evidence for the Two Visual Streams Hypothesis	4
Global/Local Processing	5
Perceptual Grouping	9
Neuroimaging Evidence.....	11
Perception and Action.....	12
Summary	16
References	17
CHAPTER II: PERCEPTION AND CULTURE	26
Method	29
Participants.....	29
General Procedure.....	30
Psychophysical Thresholds.....	30
Stimuli and Procedure.....	31
Results.....	33
Reaction Time Analysis	33
Accuracy Analysis	33
Adjusted Reaction Time Analysis using Inverse Efficiency Score (IES).....	35
Discussion	36
Conclusion	41
References.....	42
CHAPTER III: PERCEPTION AND ATTENTION.....	48
Method	50
Participants.....	50
Apparatus and Stimuli.....	51
Procedure	52

fMRI Image Acquisition	54
fMRI Data Preprocessing.....	54
Behavioral Data Analysis	55
GLM First-level Analysis	55
GLM Group Analysis	55
Results.....	56
Behavioral Results	56
Direct Query and Forced Choice Results.....	57
Correlation between Forced Choice Responses and Illusion Susceptibility.....	58
fMRI Results.....	59
Discussion	65
Perceptual Grouping and Attention	65
Grouped vs. Ungrouped Stimuli	66
Divided-Attention vs. Inattention Conditions.....	66
Brain Activity Related to the Interaction Between Grouping and Attention.....	68
Possible Limitations.....	68
Conclusion	70
References.....	71
CHAPTER IV: PERCEPTION AND VISUAL FEEDBACK	76
Method	80
Participants.....	80
Materials/Apparatus	80
Procedure	82
Data Analysis	86
Results.....	87
Grip Aperture Analysis	87
Time to Maximum Grip Aperture.....	90
Movement Time Analysis.....	90
Maximum Velocity and Wrist Deceleration Period.....	90
Discussion	91
Conclusion	96
References.....	97
CHAPTER V: GENERAL DISCUSSION	100
Limitations and Future Directions	100

Study 1: Perception and Culture	100
Study 2: Perception and Attention	102
Study 3: Comparison to Existing Models of Motor Control.....	102
Significance.....	105
Conclusion	106
References.....	108
APPENDIX 1: CONSENT FORM FOR STUDY 1.....	110
APPENDIX 2: CONSENT FORM FOR STUDY 2.....	112
APPENDIX 3: CONSENT FORM FOR STUDY 3.....	122

List of Tables

Table 3.1 Activation Regions for Grouping in Inattention and Divided-Attention Conditions ...	63
Table 4.1 Unadjusted Effects of the Illusion (in cm).....	88
Table 4.2 Paired Sample T-Tests on the Illusion Effects Across Visual Conditions (in cm).....	89

List of Figures

Figure 1.1 The Human Visual System.....	3
Figure 2.1 The Three Types of Stimuli Used to Bias Processing.....	32
Figure 2.2 Accuracy Results.....	34
Figure 2.3 Inverse Efficiency Score Results.....	36
Figure 3.1 Stimulus Backgrounds and Time Course of Trial Events.....	52
Figure 3.2 Behavioral Results of the Perceptual Grouping Task.....	58
Figure 3.3 Main Effects Analysis.....	60
Figure 3.4 Interaction and Simple Effects.....	62
Figure 3.5 Beta Values from Interaction.....	63
Figure 4.1 Sander Parallelogram Illusion.....	81
Figure 4.2 Experimental Set Up.....	82
Figure 4.3 Procedural Timing Used in the Experiment.....	85
Figure 4.4 Mean Peak Aperture.....	88
Figure 4.5 Overall Effect of Condition.....	91

Permission Statements

1. Carther-Krone, T.A. & Marotta, J.J. (*Submitted to Vision Research*). The influence of magnocellular and parvocellular visual information on global processing in Caucasian and Asian populations.
2. Carther-Krone, T.A., Lawrence-Dewar, J., Collegio, A.J., Nah, J.C., Shomstein, S, & Marotta, J.J. (2020). Neural correlates of perceptual grouping under conditions of inattention and divided-attention. *Perception*, 49(5), 495- 514.
3. Carther-Krone, T.A., Senanayake, S.S. & Marotta, J.J. (2020). The influence of the Sander Parallelogram Illusion and early, middle and late vision on goal-directed reaching and grasping. *Experimental Brain Research*, 238, 2993-3003.

The above publications appear as Chapters 2, 3 and 4 in this dissertation. Copyright permissions have been obtained from all co-authors and the publishers, *American Psychological Association*, *Springer*, *SAGE Publications*, allows the right to include these publications in a thesis or dissertation without special permission. As primary author, I was responsible for the conception of the studies, literature searches, conducting the experiments and analyses, interpreting the findings and writing of the complete dissertation.

CHAPTER I: GENERAL INTRODUCTION

“The act of ‘seeing’ seems so effortless that it is difficult to appreciate the vastly sophisticated – and poorly understood – machinery that underlies the process” (Eagleman, 2001, p. 920). To complicate matters even more, what one person sees can be vastly different from what another person sees, even when the environment is the same. Visual perception, which is a process by which the brain is constantly organizing and interpreting incoming sensory information to represent and understand the environment, is fundamental to our ability to navigate and give meaning to visual information in our surrounding world. Without accurate perception, the world around us would appear as meaningless and fragmented. Yet, our perception of the world is influenced by many factors, such as our cultural identity, the way we orient our attention, and the amount of visual feedback available when viewing our environment. On the most simplistic level, the study of visual perception examines how the perceptual system receives and processes incoming information from the eyes. However, there are many stages to this system, and factors such as culture, attention and visual feedback all have the potential to influence how we interpret the world around us. To provide context for the series of experiments presented in this dissertation, this chapter first provides an overview of the visual system, followed by a summary of the concepts relevant to the research as a whole, and concludes with a brief introduction to the research undertaken in the present dissertation.

The Two Visual Streams Hypothesis

As humans, we experience only one unitary visual representation of the world that allows us to both perceive and interact with our surroundings. While it was originally assumed that vision was driven by a single visual stream, this notion began to evolve in the 1960’s when Schneider (1967) first proposed the existence of two visual streams: one for localization (superior colliculus) and one for identification (visual cortex). Following this, similar proposals for independent visual streams were put forth in monkeys and frogs (Trevarthen, 1968; Held, 1970; Ingle, 1973), eventually leading to a breakthrough by Ungerleider and Mishkin (1982) who demonstrated that while a distinction between localization and identification exists, it lies entirely within the cerebral cortex rather than between cortical and subcortical areas, as had been previously proposed. Their seminal lesion studies in monkeys led to the establishment of the dorsal and ventral streams as processing spatial (“where”) and visual (“what”) features, respectively. However, by the early 1990’s a competing theory of dual visual processing had

emerged, suggesting that perception vs. action (or “what vs. how”) better characterized the division of labor between the ventral and dorsal streams (Goodale & Milner, 1992). According to this account, the ventral stream mediates conscious visual judgments, allowing us to perceive the world around us and store it in our memories, while the dorsal stream operates in real time and mediates planning and executing visually guided actions (Goodale et al., 2004; Goodale & Milner, 2006).

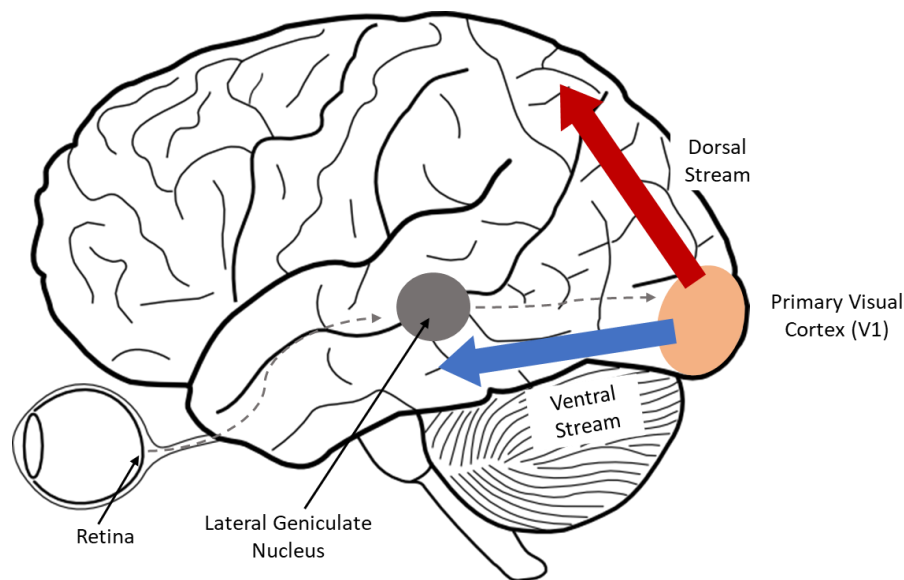
The Human Visual System

Despite how easily we are able to see and interact with our visual environment, the human visual system is complex. From the moment light falls on the retina, the process of sight begins. Specialized photoreceptor cells in the retina transform light into chemical energy, which is then propagated to the lateral geniculate nucleus (LGN), located within the thalamus (Figure 1.1). Connections from the LGN relay information from the retina to both primary and secondary visual areas via the geniculostriate pathway. The LGN is made up of 6 layers. The four dorsal layers of the LGN consist of parvo cells, which transmit information necessary for perception of color (Lee et al., 1988) and fine details to the primary visual cortex. Parvo cells have small cell bodies and show high spatial resolution, but low temporal resolution, resulting in good detection of fine details, but a slow and prolonged response (Tootell et al., 1988b; Merigan et al., 1991). The two ventral layers of the LGN consist of magno cells, and due to the high temporal resolution of these cells, transmit information necessary for the perception of form, movement, depth, and small differences in brightness very quickly to the primary visual cortex (Breitmeyer, 1975; Lupp et al., 1976). Unlike the parvo cells, magno cells have large cell bodies, are color-blind, and are not able to detect fine details, showing low spatial resolution, but high sensitivity to contrast (Derrington & Lennie, 1984; Tootell et al., 1988b). A third, less studied koniocellular channel is also found within the geniculostriate pathway, which is thought to provide a blue-yellow color opponency (Lee, 2004; Swanson & Cohen, 2003). From the LGN, all three of these layers propagate information to the primary visual cortex (area V1) and then to prestriate cortex (area V2). Together, areas V1 and V2 form the basis of color, form and motion perception before information is conveyed to higher brain regions (Shipp, 2006). After information passes through V2, the dissociation between dorsal and ventral streams begins, such that the dorsal stream receives mainly magnocellular inputs and the ventral stream receives mainly parvocellular inputs (Livingstone & Hubel, 1984). Within the dorsal stream, information

associated with interpreting motion, representing the location of objects, and allowing for control of movement is conveyed from area V2 to the posterior parietal lobe. Anatomically, the posterior parietal cortex is divided into the superior parietal lobe (SPL) and the inferior parietal lobe (IPL), which is separated by the intraparietal sulcus (IPS). Within the ventral stream, information associated with the recognition of color, form, texture and object recognition is conveyed from area V2 to the inferotemporal cortex (Grill-Spector, 2003).

Figure 1.1

The Human Visual System



Although both streams are considered to act nearly independently, their interaction has been shown to be important for allowing both streams to function properly. While properties such as texture, temperature and weight are not necessarily evident when looking at novel objects, they are extracted through interaction with the object, which in turn can influence kinematic responses such as movement time and grip force (Brenner & Smeets, 1996; Dubrowski & Carnahan, 2004; Gordon et al., 1991). This newly learned information obtained via the dorsal stream is stored in the ventral stream and can be accessed by the dorsal stream the next time a similar object is encountered. This ensures quick retrieval of kinematic parameters, which increases the overall efficiency of the visuomotor system (Gordon et al., 1993; Haffenden

& Goodale, 2000). This indicates that while the dorsal and ventral streams are driven by their own independent functions, they do not act in isolation.

Evidence for the Two Visual Streams Hypothesis

Evidence for the dissociation between action and perception most notably comes from Patient D.F., who acquired profound visual form agnosia following bilateral ventral stream damage caused by carbon monoxide poisoning. What was most striking about Patient D.F. was that while she showed impairments on ventral stream tasks, such as using hand movements to form either the shape or orientation of an object, she performed as well as controls on dorsal stream tasks, such as reaching and orienting her wrist in a 'posting' task (Goodale et al., 1991). Similarly, even though she was not able to report the width of a rectangular block, she could still modify her grip size to the width of the block so that she could pick it up without any issue. Basically, her perceptual deficits were linked to damage to her ventral stream while her spared visuomotor skills were attributed to her dorsal stream (Goodale et al., 1991; Goodale et al., 1994; James et al., 2003; Milner et al., 1991).

Consistent with this dissociation was a complementary finding in patients who acquired optic ataxia following bilateral dorsal stream damage. These patients showed difficulties making spatially accurate reaches and were unable to rotate their wrist or pre-configure their hand posture when reaching out to grasp objects of different orientation or size (Jeannerod, 1986a; Jakobson et al., 1991; Jeannerod et al., 1994). However, they could still report where targets were located relative to themselves and what they looked like. In other words, patients with optic ataxia showed impairments in action but intact perceptual abilities. This double dissociation between patient D.F. and those with optic ataxia has been the most influential evidence for the Two Visual Streams Hypothesis since its inception.

The ability for Patient D.F. to accurately perform actions despite an impaired awareness of the object suggests that visual awareness of the physical properties of a target object does not limit the ability to effectively interact with the object. This has been most notably demonstrated in individuals with action-blindsight, a deficit arising from lesions to area V1. When these individuals were shown visual stimuli within their impaired hemifield, even though they were unable to consciously perceive the stimuli, they were still able to demonstrate visually guided pointing and tracking within their scotoma (Perenin & Jeannerod, 1975; Weiskrantz et al., 1974). This suggests that these patients are not completely insensitive to visual input and that visual

information can be received by the dorsal stream via other intact subcortical visual structures. However, since the ventral stream depends primarily on V1 for visual input, visual perception cannot occur when V1 is damaged.

The notion that action can occur without awareness has also been examined in neurotypical participants by inducing action-blindsight using transcranial magnetic stimulation (TMS), a noninvasive method for altering brain excitability (Ro, 2008). By applying TMS to area V1, input to the dorsal stream was restricted to those from outside V1, and participants became “unaware” of the presented stimuli. However, even when participants were unaware of the stimuli, their reaching actions were no different than what was observed for conscious vision, suggesting that the primary visual cortex is not completely necessary for visually guided actions and that a functionally intact extrageniculate projection to the dorsal pathway bypasses V1 and inputs into the dorsal stream. This residual visuomotor ability has been attributed to the superior colliculus, a midbrain structure involved in controlling saccadic eye movements (Perry & Cowey, 1984). This structure sends projections from the retina via the optic chiasm to dorsal stream areas via the pulvinar nucleus of the thalamus. This is further supported by research in which no physical manipulations of the brain have occurred, showing that in the absence of conscious visual awareness, automatic and online limb adjustments arising from a change in target location can still occur (Bridgeman et al., 1979; Goodale et al., 1986), and that appropriate size scaling of reach trajectories is independent of conscious visual awareness of the size of the target (Binsted et al., 2007; Heath et al., 2008). These studies show that visuomotor processes are retained in the midst of a clinical or experimental disruption to early visual processing areas (i.e., area V1) because extrageniculate projections to the dorsal stream can proxy for V1 inputs.

Global/Local Processing

Within the ventral visual pathway, perception of our visual environment relies on our ability to group local elements in our environment together to create coherent representations of the world. This is driven by a set of principles put forth by Gestalt psychologists describing that the way we group elements together relies on constructs such as proximity or similarity (Wertheimer, 1923). For example, reading requires grouping letters by proximity into words on a page, while a plate flanked by a fork and knife can be grouped together into a dining set. While individuals are able to quickly and efficiently group individual features of a scene together to form a whole, a phenomenon known as the ‘global precedence effect’ (Fabre-Thorpe et al.,

2001; Torralba et al., 2006; Navon, 1977), the extent to which a bias is shown towards global percepts is not equally evident between individuals, can be influenced by individual characteristics and can change over time.

For example, older individuals (Lux et al., 2008) and musicians (Stoesz et al., 2007) have been shown to prefer local compared to global processing. Lux et al. (2008) examined older and younger participants in a directed attention task in which participants were instructed to detect a target letter that occurred at a prespecified local or global level. Findings showed that individuals in the young group had faster reaction times to global targets while older subjects showed faster reaction times to local targets. In a follow up divided-attention task where participants were instructed to detect a target at either the global or local level, individuals in the young group were slightly quicker to detect the global targets while individuals in the older group were slightly quicker to detect the local targets. Stoesz et al. (2007) compared global/local processing between musicians and nonmusicians, showing that musicians outperformed nonmusicians on the Group Embedded Figures Test and on the Block Design test, both of which involve manipulating smaller features of an overall design to complete the given task.

Research involving sex-dependent processing styles have also demonstrated differences in global/local processing, showing stronger global processing in men and stronger local processing in women (Roalf et al., 2006; Razumnikova & Vol'f, 2011; Pletzer et al., 2014). Even more interestingly, whether or not one shows a global processing bias can be influenced by a person's mood (Gasper & Clore, 2002; Fredrickson & Branigan, 2005). For example, when participants were asked to write about a happy and positive life event, they were more likely to match the figures in the Kimchi-Palmer task, which involves making similarity judgments between two comparison figures (one globally-biased, the other locally-biased) to a target figure, based on their global features (rather than local features) than participants who wrote about a sad and negative life event (Gasper & Clore, 2002). Fredrickson and Branigan (2005) also showed that compared to participants in a neutral mood state, participants in a positive mood were more likely to match figures based on their global configurations, while participants in a negative mood were more likely to match figures based on local elements. Individuals induced into a state of negative affect have been found to show a local compared to global processing bias (Gasper & Clore, 2002), while individuals induced into a state of positive affect have been found

to show a preference for global processing (Fredrickson & Branigan, 2005). As such, global processing is not absolute and appears to be influenced by individual characteristics.

Cross-cultural research comparing Western Caucasian populations (i.e., Canadians, Americans, British and Australians) and East Asian populations (i.e., Chinese and Japanese) has shown that East Asians have a tendency to process objects and scenes more globally than Western Caucasians (Chua, Boland, & Nisbett, 2005; Masuda & Nisbett, 2001; 2006; Nisbett & Masuda, 2003; Nisbett & Miyamoto, 2005). For example, Kitayama, Duffy, Kawamura, and Larsen (2003) presented Western Caucasians and East Asians a vertical line within a square frame and asked them to report the length of the line (the framed-line task). Results showed that East Asians were better than Western Caucasians at the relative task, which required global selective attention (i.e., reporting the relative length by referencing the surrounding frame), while Western Caucasians were better than East Asians at the absolute task, which required local selective attention (i.e., reporting the absolute length without referencing the surrounding frame). Based on the notion that Western Caucasians perform better on tasks emphasizing independent (absolute) dimensions while East Asians perform better on tasks emphasizing interdependent (relative) dimensions, Hedden et al. (2008) administered an fMRI study in which participants made either absolute judgments (ignoring visual context) or relative judgments (considering visual context) during a simple visuospatial task. While results showed no culture effects on behavioral performance, fMRI results showed that achieving the equivalent levels of behavioral performance required more sustained attentional effort for the absolute task in East Asians and for the relative task in Western Caucasians.

In another study, McKone et al. (2010) used Navon letters (e.g., large E made up of small Vs) to directly quantify the global/local attention bias between Western Caucasians and East Asians. Relative to Western Caucasians, East Asians showed a strong global advantage, identifying target letters faster when they appeared at the global level. These findings also extended to the second generation (Asian-Australians), although it was weakened when compared to recent immigrants. These findings suggest that East Asians show more effective global-selective attention compared to Western Caucasians. Following this framework, Lao, Vizioli and Caldara (2013) examined the underlying neural mechanisms and the temporal dynamics of this processing difference by recording the electrophysiological signals of Western Caucasian and East Asian individuals while they actively matched geometric Navon shapes

(circle, cross, diamond, square, triangle). Participants judged whether a target and an adapter Navon figure were identical, global congruent, local congruent, or different. They focused their analysis on the P1 component, which is a positive deflection peaking about 100 ms after stimulus onset on the occipital scalp surface and is larger for attended compared to unattended information. Results indicated that East Asians showed a greater sensitivity to global congruency relative to Western Caucasians, as indexed by an early P1 component.

Studies involving eye movements have suggested that this difference in perception may be driven by culture-specific tuning towards visual spatial frequency information (Miellet et al., 2013). Research involving face recognition has shown that Western Caucasians preferentially process high spatial frequency information from foveal vision and are more biased to local processing in hierarchical stimuli, while East Asians preferentially process contextual information by relying on extra-foveal vision during face recognition, favoring globally-based holistic stimulus processing (Miellet et al., 2013). East Asians have also been shown to rely on extra-foveal vision more than Western Caucasians when detecting low-level visual stimuli (Boduroglu, Shah, & Nisbett, 2009) and for change detection of complex real-world stimuli (Masuda & Nisbett, 2001). Using a visual change detection paradigm, Bodouroglu et al. (2009) demonstrated that East Asians were better than Western Caucasians at detecting color changes when a layout of a set of colored blocks was expanded to cover a wider region. East Asians were also found to be slower at detecting changes in the center of a screen, supporting the notion that East Asians rely more heavily on extra-foveal vision than Western Caucasians. Masuda and Nisbett (2001) showed that after viewing an underwater scene of fish and other objects, Western Caucasians tended to remember the more salient fish on the foreground, while Japanese also recalled items in the background, suggesting that Western Caucasians tend to pay more attention to focal information, while East Asians pay more attention to contextual information. While these studies support the notion that East Asians allocate their attention more broadly than Western Caucasians, it should also be acknowledged that some studies have failed to replicate these differences. For example, Caparos et al. (2012) found that Japanese college students from Kyoto University were as globally oriented as British college students from Goldsmiths University of London. In another study, Zhou et al. (2008) failed to replicate Kitayama et al.'s (2003) findings that Western Caucasians more accurately estimated absolute than relative length in the framed-line task. Similarly, in examining eye movements, some studies have not found

the same evidence that East Asians integrate objects with backgrounds while Western Caucasians focus more on focal objects (Evans et al., 2009; Rayner et al., 2007; Mielle et al., 2010). As such, the extent to which attention influences cultural perception across Western and Eastern cultures remains to be clarified. Based on previous research showing that culture-specific tuning towards visual spatial frequency information can influence perception, chapter 2 will explore the notion that differences in global processing between Caucasians and Asians are driven by differences in the means by which low spatial frequency information is projected through the visual system.

Perceptual Grouping

One of the most striking ideas to arise from the Two Visual Streams Hypothesis is the notion that what we consciously see is not necessarily what controls our visually guided actions. While our interaction with the world is usually based on voluntary movements, it seems logical that these movements would be governed by what we consciously perceive. However, studies involving visual illusions have demonstrated that this is not always the case. This was first put forth by Aglioti et al. (1995), who used the Ebbinghaus illusion, a size-contrast illusion in which two target circles of equal size are surrounded by a circular array of either smaller or larger circles presented side by side, to show that grip aperture scaling was refractory to the illusion. The relative size of the two target circles was varied so that on some trials they appeared perceptually different but were equivalent in size, while on other trials they were physically different but appeared perceptually equivalent. Perceptual judgments were found to be affected by the illusion, but grip aperture scaling was largely determined by the true size of the target circle and not its illusory size. As a result, on trials where participants judged two circles of different size to be the same, they nevertheless used a wider grip aperture to retrieve the larger circle. Interestingly, while our visuomotor system appears in many cases to be immune to visual illusions, our perceptual system appears susceptible even in situations where we are not able to indicate that we saw the illusion.

While our attentional system facilitates our ability to perceive the world, it is limited in that we are not able to report on everything we see. However, even input we cannot report on can influence how we perceive our visual environment. Classical theories of visual perception suggest that Gestalt grouping is a fast and efficient process occurring automatically, without attention or effort (Julesz, 1981; Marr, 1982; Neisser, 1967, Treisman, 1982). However,

opposing accounts argue that little, if any, perceptual organization can occur without attention (Ben-Av et al., 1992).

Ben-Av et al. (1992) used a dual-task experiment to show that participants were not able to explicitly report perceptual groups while attention was simultaneously engaged in a demanding task not involving the groups. The effects obtained under a divided-attention condition where perceptual grouping was a secondary task was compared with those obtained when it was the primary task. Results showed that grouped patterns were harder to identify in the divided-attention condition, suggesting that more attentional resources were required compared to the full-attention (primary) task. Since participants were not able to explicitly report the perceptual groups under divided-attention conditions, it was thought that grouping could also not occur preattentively. Mack et al. (1992) developed an “inattention paradigm” to test whether perceptual grouping would occur not only in the absence of attention to certain elements, but also when there was not even an intention to perceive the elements. Their findings were that participants were unable to report anything about how the elements in the background were grouped when surprise questions were given at the end of the experiment asking participants if they noticed a pattern, and to indicate or guess at which pattern they may have seen when given a choice. Since the task required focused attention, Mack et al. (1992) argued that if preattentive grouping had occurred, then participants should have been able to accurately answer the surprise questions. They also concluded that grouping could not have occurred preattentively and that perceptual organization required attention.

However, Moore and Egeth (1997) argued that an inability to explicitly report grouping when attention is engaged in a simultaneously demanding task does not necessarily mean that perceptual grouping in itself requires attention. They suggested that it was possible that grouping did occur in Mack et al.’s (1992) study, but the location of the grouped elements might not have been encoded since remembering was not explicitly demanded. Using an implicit measure to examine perceptual grouping under preattentive conditions, participants were asked to judge the length of line segments presented along with background elements that were entirely task-irrelevant. The background elements were arranged so that, if perceptually grouped, they could induce either the Ponzo illusion, a classic depth illusion in which two converging oblique lines form a depth cue that modulates the perceived length of two horizontal lines superimposed on the converging lines, or the Müller-Lyer illusion, a visual illusion in which the length of two

identical lines appears to be different depending on the orientation of the wings attached to their ends (inward vs. outward). Their results showed that participants were not aware of the background illusions but consistently judged their responses in accordance with an illusion-based response, suggesting that perceptual grouping can occur without attention. Russell and Driver (2005) extended these results using their own measure of inattentive visual grouping by means of a change-detection task. They found that when task-irrelevant background elements were grouped by colour similarity into columns, rows, or pseudorandomly, the background grouping influenced the accuracy of change judgments for the change detection task, even though background grouping or its change usually could not be explicitly reported when questions were asked after the task was completed. These results further confirm that perceptual grouping can occur even when the individual is unaware of the background stimuli.

Neuroimaging Evidence

Although behavioral studies have provided ground-breaking insights into how attention influenced perceptual grouping, brain imaging studies using functional magnetic resonance imaging (fMRI), a non-invasive method used to examine brain activity, has furthered our knowledge exponentially regarding the functional architecture of visual processing in the brain. Brain imaging studies exploring the role of attention in perceptual grouping have shown that damage to posterior parietal cortex (PPC), a brain region involved in attentional control, disrupts grouping (Zaretskaya, Anstis, & Bartels, 2013). Other processes involving grouping, such as global pattern coding, also seem to depend on intact attentional brain regions, such as the intraparietal cortex, suggesting that attention related brain regions are important in modulating grouping in regions such as the lateral occipital cortex (LOC), which are typically thought to respond to perceptual groups (Lestou, Lam, Humphreys, Kourtzi, & Humphreys, 2014). However, these studies all involve the recruitment of attentional processes, and as a result, previous findings showing that the inferior intraparietal sulcus is a brain region common to perceptual grouping in general may actually be specific to perceptual grouping when attentional processes are involved. Thus, brain studies involving preattentive perceptual grouping are important for determining which brain regions overlap, and which brain regions are responsible for perceptual grouping specifically.

Although little is known about the brain regions activated by preattentive perceptual grouping alone, research comparing perceptually grouped to ungrouped stimuli under full

attention conditions has shown that brain regions common to all forms of perceptual grouping are areas V1 and V2 (Ross, Grossberg & Mingolla, 2000). Other areas that have been shown to be involved in perceptual grouping are the inferior parietal cortex, middle temporal gyrus and prefrontal cortex (Seymour, Karnath & Himmelbach, 2008). Further research by Xu and Chun (2007) comparing grouped stimuli to ungrouped stimuli also found that the inferior intraparietal sulcus represents perceptually grouped items even when grouping is task-irrelevant. However, it is unclear whether the same regions would be activated when attention is implicitly directed towards the grouped stimuli, further emphasizing the importance of conducting research that directly compares brain regions activated under inattention conditions to those of attentional conditions. Chapter 3 will examine this notion more closely, focusing on what can be gleaned from the similarities and differences found in the brain during a perceptual grouping task performed under inattention and divided-attention conditions.

Perception and Action

Vision is one of the most robust sensory inputs used for the control of goal directed actions (Woodworth, 1899). Although the ventral stream is primarily responsible for the perception of visual scenes and the dorsal stream involves perception for action, there is still much to be learned about how the way we perceptually organize our world influences how we interact with it. Studies using visual illusions have shown that while the perceptual stream is affected by visual illusions, the action stream succumbs less to illusions as demonstrated by grasping tasks in which maximum grip aperture (maximum distance between the thumb and index finger) is not influenced by the illusion (Aglioti et al., 1995; Gentilucci, Chieffi, Daprati, Saetti, & Toni, 1996; Haffenden & Goodale, 1998). Aglioti et al. (1995) showed that the Ebbinghaus illusion, an illusion of object size, did not deceive the hand when participants were asked to reach out and pick up objects that were perceived to be larger or smaller than their actual size. Similar results were found by Gentilucci et al. (1996), who used the Müller-Lyer illusion to study how different amounts of visual feedback affects visuomotor control. It was found that pointing movements performed in the context of the illusion under conditions of full vision, non-visual feedback, and in two no-vision conditions where visual memory was required in no delay (0 second) and 5 second delay conditions resulted in a gradual increase of illusion susceptibility from no-vision to full-vision conditions, suggesting that the perceptual stream and action stream may interact, and that the strength of this interaction depends on how much visual

feedback the participant is allowed to use. Haffenden and Goodale (1998) also used the Ebbinghaus illusion to study the effects of the illusion on perception and action. However, unlike Aglioti et al. (1995), no visual feedback from the hand or target was available after initial viewing. Consistent with Aglioti et al. (1995), they found that perceptual judgments were biased in the direction of the illusion, but grip aperture scaling was largely determined by the physical size of the target, further confirming the notion that grip aperture is determined by the true size of an object even when perception of object size is distorted by a visual illusion. Together these studies support the Two Visual Streams Hypothesis, demonstrating that perceptual judgements are affected by the visual context associated with the illusory configurations, while goal-directed action movements tend to be immune to these perceptual biases. This notion that the ventral stream is affected by illusory visual context while the dorsal stream remains immune is thought to rely on the way each of the streams code visual-spatial information. Specifically, the ventral stream is involved with the allocentric coding of space, incorporating visual information about the target's relationship to its surroundings, while the dorsal stream is involved with the egocentric coding of space, relying on a body-based frame of reference (Haffenden and Goodale 1998).

However, other studies have shown that actions are not immune to illusory context. When vision is only available before movement onset, the outcome reflects the perceptual bias of the illusion, showing shorter aiming movements in pointing studies (Elliott and Lee 1995) and smaller peak grip apertures in reaching and grasping studies (Bruno and Franz 2009; Franz, Hesse, and Kollath 2009; Haffenden and Goodale 1998) when dealing with perceptually smaller targets compared to perceptually larger targets. These differences in illusory susceptibility suggest that movement planning, which occurs before the movement is initiated, is controlled by a different process than the online control that occurs once the movement is initiated. Glover and Dixon's (2001, 2002) Planning-Control Model (PCM) posits that movement preparation processes occurring during the planning phase of a movement incorporates allocentric information and results in illusion susceptibility, while online control processes occurring during the movement itself depends on egocentric visual information resulting in decreased susceptibility to visual illusions. Although this model helps to address some of the discrepancies involving illusion susceptibility in the literature, it does not explain why other studies have found that illusory information available during movement planning and execution have additive

effects on final movement bias (see Franz, Gegenfurtner, Bühlhoff, and Fahle 2000; Glazebrook et al. 2005; Handlovsky, Hansen, Lee, and Elliott 2004; Mendoza, Elliott, Meegan, Lyons, and Welsh 2006). These studies demonstrate that while online control processes may be less influenced by the visual context in which a target is presented, they are not completely immune to allocentric visual information. This suggests that perhaps there is more than one process involved in online visual control.

Recent studies have expanded on the notion that there is a dichotomous set of visual coding processes, proposing that there are multiple processes involved in visual online control. More specifically, Elliott et al. (2010) proposed that there are two processes involved in visual online regulation: a process early in the movement concerned with comparisons between actual and expected consequences, and another later on in the movement involved in providing information about the relative positions of the limb and target. This former part of the movement is related to impulse regulation, which involves monitoring the expected and actual limb positions in the initial parts of the movement trajectory, while the latter part of the movement relates to limb-target regulation such that the position of the limb is compared to the position of the target in order to facilitate trajectory amendments. However, this research relies on visual feedback for the duration of the movement and does not explain how visual online control changes based on reduced visual feedback.

Kennedy, Bhattacharjee, Hansen, Reid and Tremblay (2015) examined the point at which online vision during the reach has the most influence on endpoint consistency when participants were asked to make rapid reaches to a target. Results showed that endpoint consistency was comparable to that of full-vision trials when vision was provided during early and middle points along the reach. The late window was not found to be useful to implement online trajectory amendments and did not differ significantly from no vision conditions. This suggests that early visuomotor control contributes the most to modulations in endpoint precision and online correction measures. However, the manipulation of vision in this study was determined based on limb velocity criteria, resulting in early, middle and late time windows of different duration. As such, the outcomes within each condition may have been influenced by the amount of vision rather than when vision was provided. Nonetheless, this research shows that the availability of visual feedback during different points along the reach time course can influence the end goal, highlighting the important influence that visual feedback can have on goal-directed movements.

One caveat to consider when using visual illusions to examine the influence of perception on action is the effect that attention towards non-target stimuli has on goal-directed actions. Action-centered theories and models of attention suggest that attentional distribution is influenced by a to-be-performed action, and the capture of attention by a stimulus automatically activates an action plan designed to interact with that stimulus. In the seminal paper on action-centered attention by Tipper et al. (1992), participants were instructed to complete aiming movements from a home position to one of nine buttons arranged in a 3 x 3 grid. Underneath each potential target location was a red and yellow light-emitting diode (LED), which indicated to the participant which button was the to-be-responded-to target button and the to-be-ignored distractor button, respectively. Participants were instructed to aim to and touch the target location and ignore the yellow distractor LED. From this, two key patterns of distractor interference emerged. First, when participants reached to targets in the middle row, distractors appearing in the row nearest to the starting position of the hand caused more interference than distractors farther from the starting position of the hand (the proximity-to-hand effect). Second, when participants reached to targets in the middle column, distractors on the same side of space as the reaching arm caused more interference than distractors on the opposite side of space (the ipsilateral effect). This suggests that both target and distractor capture attention and simultaneously activate responses to interact with each button. This parallel processing suggests that distractors activate a competing motor response alongside the target-directed response. This finding is supported by other previous research demonstrating that both temporal (Meegan & Tipper, 1998) and kinematic (Welsh, Elliott & Weeks, 1999; Welsh & Elliott, 2004, 2005) characteristics of goal-directed actions are affected by the presence of distracting stimuli. In the context of the visual illusion research, these findings emphasize the importance of considering the influence that attention directed at nontarget stimuli (i.e., the perceptually grouped components of the illusion) has on the processing of the target, particularly when visual stimuli is placed in the space between the hand starting position and the target.

The aim of Chapter 4 is to examine how goal-directed movements are influenced by the availability of visual feedback. While previous studies have focused on the early and late portions of the movement trajectory (Elliott et al. 2010; Grierson and Elliott 2009; Roberts et al. 2013) as well as limb velocity to designate time course windows (Kennedy et al. 2015), this study isolates early, middle and late portions of the movement trajectory using predefined time

windows based on each participant's own natural movements to gain a better understanding of how goal-directed movements are influenced by visual feedback.

Summary

Taken together, it is clear that the functional architecture underlying the human visual system is complex, relying on many different cortical and subcortical brain regions acting both together and in isolation. While information arriving at the early visual cortex is already subserved by two pathways, the magnocellular and parvocellular pathways, the Two Visual Streams Hypothesis further divides the visual system into two streams: vision for perception (ventral stream) and vision for action (dorsal stream) (Goodale & Milner, 2006). Although much research has focused on the differences and similarities between the two visual streams, establishing where they go and how they work, there is still much to be discovered about how the visual system is affected by other influential factors in our day-to-day lives, such as culture, attention, and visual feedback. The purpose of the series of experiments that follows is to use functional magnetic resonance imaging (fMRI), advanced visuomotor paradigms and traditional cognitive and psychophysical methodologies to explore how our perception of the world is influenced by our cultural identity (Chapter 2), the way we orient our attention (Chapter 3) and the amount of visual feedback available when viewing our environment (Chapter 4). In a broader sense, these studies seek to explain why one person can see a visual scene differently from what another person sees even when the environment is the same.

References

- Aglioti, S., DeSouza, J.F.X., & Goodale, M.A. (1995). Size-contrast illusions deceive the eye but not the hand. *Current Biology*, *5*, 679-685.
- Ben-Av, M.B., Sagi, D., & Braun, J. (1992). Visual attention and perceptual grouping. *Perception and Psychophysics*, *52*, 277-294.
- Binsted, G., Brownell, K., Vorontsova, Z, Heath, M., & Saucier, D. (2007). Visuomotor system uses target features unavailable to conscious awareness. *PNAS*, *104*(31), 12669-12672.
- Boduroglu, A., Shah, P., & Nisbett, R.E. (2009). Cultural differences in allocation of attention in visual information processing. *Journal of Cross-Cultural Psychology*, *40*(3), 349–360. doi: 10.1177/0022022108331005
- Breitmeyer, B.G. (1975). Simple reaction time as a measure of the temporal response properties of transient and sustained channels. *Vision Research*, *15*, 1411-1412.
- Brenner, E. & Smeets, J.B.J. (1996). Size illusion influences how we lift but not how we grasp an object. *Experimental Brain Research*, *111*, 473-476.
- Bridgeman, B., Lewis, S., Heit, G., & Nagle, M. (1979). Relation between cognitive and motor-oriented systems of visual position perception. *Journal of Experimental Psychology: Human Perception and Performance*, *5*, 692-700.
- Bruno, N., & Franz, V.H. (2009). When is grasping affected by the Müller-Lyer illusion?: A quantitative review. *Neuropsychologia*, *47*(6):1421-1433. doi:10.1016/j.neuropsychologia.2008.10.031
- Caparos, S., Ahmed, L., Bremner, A.J., de Fockert, J.W., Linnell, K.J., & Davidoff, J. (2012). Exposure to an urban environment alters the local bias of a remote culture. *Cognition*, *122*(1), 80-85. doi: 10.1016/j.cognition.2011.08.013
- Chua, H.F., Boland, J.E., & Nisbett, R.E. (2005). Cultural variation in eye movements during scene perception. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 12629-12633. doi: 10.1073/pnas.0506162102
- Derrington, A.M. & Lennie, P. (1984). Spatial and temporal contrast sensitivities of neurons in lateral geniculate nucleus of macaque. *Journal of Physiology*, *357*, 219-240.
- Dubrowski, A., & Carnahan, H. (2004). Grip force when grasping moving cylinders. *International journal of industrial ergonomics*, *34*(2), 69-76.

- Eagleman, D.M. (2001). Visual illusions and neurobiology. *Nature Reviews Neuroscience*, 2, 920-926.
- Elliott, D., & Lee, T.D. (1995). The role of target information on manual-aiming bias. *Psychological Research*, 58, 2-9. doi:10.1007/BF00447084
- Elliott, D., Hansen, S., Grierson, L.E., Lyons, J., Bennett, S.J., & Hayes, S.J. (2010). Goal-directed aiming: Two components but multiple processes. *Psychological Bulletin*, 136(6), 1023-1044. doi:10.1037//0033-2909.127.3.342
- Evans, K., Rotello, C.M., Li, X., & Rayner, K. (2009). Scene perception and memory revealed by eye movements and receiver-operating characteristic analyses: Does a cultural difference truly exist? *The Quarterly Journal of Experimental Psychology*, 62, 276-285. doi: 10.1080/17470210802373720
- Fabre-Thorpe, M., Delorme, A., Marlot, C., & Thorpe, S. (2001). A limit to the speed of processing in ultra-rapid visual categorization of novel natural scenes. *Journal of Cognitive Neuroscience*, 13(2), 1-10. doi: 10.1162/089892901564234
- Franz, V.H., Gegenfurtner, K.R., Bühlhoff, H.H., & Fahle, M. (2000). Grasping visual illusions: No evidence for a dissociation between perception and action. *Psychological Science*, 11(1), 20-25. doi:10.1111/1467-9280.00209
- Franz, V.H., Hesse, C., & Kollath, S. (2009). Visual illusions, delayed grasping, and memory: No shift from dorsal to ventral control. *Neuropsychologia*, 47(6), 1518-1531. doi:10.1016/j.neuropsychologia.2008.08.029
- Fredrickson, B.L., & Branigan, C. (2005). Positive emotions broaden the scope of attention and thought-action repertoires. *Cognition & Emotion*, 19(3), 313-332.
- Gaspar, K., & Clore, G. L. (2002). Attending to the big picture: Mood and global versus local processing of visual information. *Psychological Science*, 13(1), 34-40.
- Gentilucci, M., Chieffi, S., Deprati, E., Saetti, M. C., & Toni, I. (1996). Visual illusion and action. *Neuropsychologica*, 34, 369-376.
- Glazebrook, C.M., Dhillon, V.P., Keetch, K.M., Lyons, J., Amazeen, E., Weeks, D.J., & Elliott, D. (2005). Perception-action and the Müller-Lyer illusion: Amplitude or endpoint bias? *Experimental Brain Research*, 160(1), 71-78. doi:10.1007/s00221-004-1986-y

- Glover, S.R., & Dixon, P. (2001). Dynamic illusion effects in a reaching task: evidence for separate visual representations in the planning and control of reaching. *Journal of Experimental Psychology: Human Perception and Performance*, *27*(3), 560-572. doi:10.1037/0096-1523.27.3.560
- Glover, S.R., & Dixon, P. (2002). Dynamic effects of the Ebbinghaus illusion in grasping: Support for a planning/control model of action. *Perception & Psychophysics*, *64*(2), 266-278. doi:10.3758/BF03195791
- Goodale, M.A., Milner, A.D., Jakobson, L.S., & Carey, D.P. (1991). A neurological dissociation between perceiving objects and grasping them. *Nature*, *349*, 154-156.
- Goodale, M.A., Jakobson, L.S., & Keillor, J.M. (1994). Differences in the visual control of pantomimed and natural grasping movements. *Neuropsychologia*, *32*, 1159-1178. doi: 10.1016/0028-3932(94)90100-7
- Goodale, M.A. & Milner, A.D. (1992). Separate visual pathways for perception and action. *Trends in Neuroscience*, *15*, 20-25.
- Goodale, M.A. & Milner, A.D. (2006). One brain – two visual systems. *The Psychologist*, *19*(11), 660-663.
- Goodale, M.A., Westwood, D.A., & Milner, A.D. (2004). Two distinct modes of controls for object-directed action. *Progress in Brain Research*, *144*, 131-144.
- Goodale, M.A., Pelisson, D., & Prablanc, C. (1986). Large adjustments in visually guided reaching do not depend on vision of the hand or perception of target displacement. *Nature*, *320*, 748-750.
- Gordon, A.M., Forssberg, H., Johansson, R.S., & Westling, G. (1991). The integration of haptically acquired size information in the programming of precision grip. *Experimental Brain Research*, *83*(3), 483-488.
- Gordon, A.M., Westling, G., Cole, K.J., & Johansson, R.S. (1993). Memory representations underlying motor commands used during manipulation of common and novel objects. *Journal of neurophysiology*, *69*(6), 1789-1796.
- Grill-Spector, K. (2003). The neural basis of object perception. *Current opinion in neurobiology*, *13*(2), 159-166.
- Haffenden, A.M. & Goodale, M.A. (1998). The effect of pictorial illusion on prehension and perception. *Journal of Cognitive Neuroscience*, *10*, 122-136.

- Haffenden, A.M., & Goodale, M.A. (2000). The effect of learned perceptual associations on visuomotor programming varies with kinematic demands. *Journal of Cognitive Neuroscience*, *12*(6), 950-964.
- Handlovsky, I., Hansen, S., Lee, T.D., & Elliott, D. (2004). The Ebbinghaus illusion affects on-line movement control. *Neuroscience Letters*, *366*(3), 308-311.
doi:10.1016/j.neulet.2004.05.056
- Heath, M., Neely, K.A., Yakimishyn, J., & Binsted, G. (2008). Visuomotor memory is independent of conscious awareness of target features. *Experimental Brain Research*, *188*(4), 517-527.
- Hedden, T., Ketay, S., Aron, A., Markus, H.R. & Gabrieli, J.D.E. (2008). Cultural influences on neural substrates of attentional control. *Psychological Science*, *19*, 12-17. doi: 10.1111/j.1467-9280.2008.02038.x
- Held, R. (1970). Two modes of processing spatially distributed visual information. In F.O. Schmitt (Ed.) *The Neurosciences Second Study Program* (pp. 317–324). Cambridge, MA: MIT Press.
- Ingle, D.J. (1973). Evolutionary perspectives on the function of the optic tectum. *Brain, Behavior and Evolution*, *8*, 211–237.
- Jakobson, L.S., Archibald, Y.M., Carey, D.P., & Goodale, M. A. (1991). A kinematic analysis of reaching and grasping movements in a patient recovering from optic ataxia. *Neuropsychologia*, *29*, 803–809. doi: 10.1016/0028-3932(91)90073-H
- James, T.W., Culham, J., Humphrey, G.K., Milner, A.D. & Goodale, M.A. (2003). Ventral occipital lesions impair object recognition but not object-directed grasping: A fMRI study. *Brain*, *126*, 2463–2475.
- Jeannerod, M. (1986a). The formation of finger grip during prehension. A cortically mediated visuomotor pattern. *Behavioral Brain Research*, *19*, 99–116. doi: 10.1016/0166-4328(86)90008-2
- Jeannerod, M., Decety, J., & Michel, F. (1994). Impairment of grasping movements following a bilateral posterior parietal lesion. *Neuropsychologia*, *32*, 369–380. doi: 10.1016/0028-3932(94)90084-1
- Julesz, B. (1981). Textons, the elements of texture-perception, and their interactions. *Nature*, *290*(5802), 91-97.

- Kennedy, A., Bhattacharjee, A., Hansen, S., Reid, C., & Tremblay, L. (2015). Online vision as a function of real-time limb velocity: another case for optimal windows. *Journal of motor behavior*, *47*(6), 465-475. doi:10.1080/00222895.2015.1012579
- Kitayama, S., Duffy, S., Kawamura, T., & Larsen, J.T. (2003). Perceiving an object and its context in different cultures: A cultural look at new look. *Psychological Science*, *14*, 201-206. doi: 10.1111/1467-9280.02432
- Lao, J., Vizioli, L., & Caldara, R. (2013). Culture modulates the temporal dynamics of global/local processing. *Culture and Brain*, *1*(2-4), 158-174. doi: 10.1007/s40167-013-0012-2
- Lee, B.B. (2004). Paths to color in the retina. *Clinical & Experimental Optometry*, *87*, 239-248.
- Lee, B., Martin, P., & Valberg, A. (1988). The physiological basis of heterochromatic flicker photometry demonstrated in the ganglion cells of the macaque retina. *Journal of Physiology*, *404*, 323-347.
- Lestou, V., Lam, J.M.L., Humphreys, K., Kourtzi, Z., & Humphreys, G.W. (2014). A dorsal visual route necessary for global form perception: Evidence from neuropsychological fMRI. *Journal of Cognitive Neuroscience*, *26*(3), 621-634.
- Livingstone, M.S. & Hubel, D.H. (1984). Anatomy and physiology of a color system in the primate visual cortex. *Journal of Neuroscience*, *4*, 309-356.
- Lupp, U., Hauske, G., & Wolf, W. (1976). Perceptual latencies to sinusoidal gratings. *Vision Research*, *16*, 969-972.
- Lux, S., Marshall, J.C., Thimm, M., & Fink, G.R. (2008). Differential processing of hierarchical visual stimuli in young and older healthy adults: Implications for pathology. *Cortex*, *44*(1), 21-28.
- Mack, A., Tang, B., Tuma R., & Kahn, S. (1992). Perceptual grouping and attention. *Cognitive Psychology*, *24*, 475-501.
- Marr, D. (1982). *Vision: A computational investigation into the human representation and processing of visual information*. San Francisco: WH Freeman.
- Masuda, T., & Nisbett, R.E. (2001). Attending holistically versus analytically: Comparing the context sensitivity of Japanese and Americans. *Journal of Personality and Social Psychology*, *81*, 922-934. doi: 10.1037//0022-3514.81.5.922

- Masuda, T., & Nisbett, R.E. (2006). Culture and change blindness. *Cognitive Science*, 30, 381-399. doi: 10.1207/s15516709cog0000_63
- McKone, E., Davies, A.A., Fernando, D., Aalders, R., Leung, H., Wickramariyaratne, T., & Platow, M.J. (2010). Asia has the global advantage: Race and visual attention. *Vision Research*, 50, 1540-1549. doi:10.1016/j.visres.2010.05.010
- Meegan, D.V., & Tipper, S.P. (1998). Reaching into cluttered visual environments: Spatial and temporal influences of distracting objects. *Quarterly Journal of Experimental Psychology-Section A-Human Experimental Psychology*, 51(2), 225-250.
- Mendoza, J.E., Elliott, D., Meegan, D.V., Lyons, J.L., & Welsh, T.N. (2006). The effect of the Müller-Lyer illusion on the planning and control of manual aiming movements. *Journal of Experimental Psychology: Human Perception and Performance*, 32(2), 413-422. doi:10.1037/0096-1523.32.2.413
- Merigan, W.H., Katz, L.M., & Maunsell, J.H. (1991). The effects of parvocellular lateral geniculate lesions on the acuity and contrast sensitivity of macaque monkeys. *Journal of Neuroscience*, 11, 994-1001.
- Miellet, S., Vizioli, L., He, L., Zhou, X., & Caldara, R. (2013). Mapping face recognition information use across cultures. *Frontiers in psychology*, 4(34), 1-12. doi: 10.3389/fpsyg.2013.00034
- Miellet, S., Zhou, X., He, L., Rodger, H., & Caldara, R. (2010). Investigating cultural diversity for extrafoveal information use in visual scenes. *Journal of Vision*, 10(6), 21. doi: 10.1167/10.6.21
- Milner, A.D., Perrett, D.I., Johnston, R.S., Benson, P.J., Jordan, T.R., Heeley, D.W., ... & Davidson, D.L.W. (1991). Perception and action in 'visual form agnosia'. *Brain*, 114(1), 405-428.
- Milner, A.D., Dijkerman, H.C., Pisella, L., McIntosh, R.D., Tilikete, C., Vighetto, A., & Rosetti, Y. (2001). Grasping the past: Delay can improve visuomotor performance. *Current Biology*, 11, 1896-1901. doi:10.1016/s0960-9822(01)00591-7
- Moore, C.M. & Egeth, H. (1997). Perception without attention: Evidence of grouping under conditions of inattention. *Journal of Experimental Psychology: Human Perception and Performance*, 23(2), 339-352.

- Navon, D. (1977). Forest before trees: The precedence of global features in visual perception. *Cognitive Psychology*, *9*, 353-383. doi: 10.1016/0010-0285(77)90012-3
- Neisser, U. (1967). *Cognitive psychology*. New York: Appleton-Century-Crofts.
- Nisbett, R.E., & Masuda, T. (2003). Culture and point of view. *Proceedings of the National Academy of Sciences*, *100*(19), 11163–11170. doi: 10.1073/pnas.1934527100
- Nisbett, R.E., & Miyamoto, Y. (2005). The influence of culture: Holistic versus analytic perception. *Trends in Cognitive Sciences*, *9*(10), 467–473. doi: 10.1016/j.tics.2005.08.004
- Perenin, M.T. & Jeannerod, M. (1975). Residual vision in cortically blind hemiphields. *Neuropsychologia*, *13*(1), 1-7.
- Perry, V.H. & Cowey, A. (1984). Retinal ganglion cells that project to the superior colliculus and pretectum in the macaque monkey. *Neuroscience*, *12*, 1125-1137.
- Pletzer, B., Petasis, O., & Cahill, L. (2014). Switching between forest and trees: Opposite relationship of progesterone and testosterone to global–local processing. *Hormones and behavior*, *66*(2), 257-266.
- Rayner, K., Li, X., Williams, C.C., Cave, K.R., & Well, A.D. (2007). Eye movements during information processing tasks: Individual differences and cultural effects. *Vision Research*, *47*, 2714-2726. doi: 10.1016/j.visres.2007.05.007
- Razumnikova, O.M., & Volf, N.V. (2011). Information processing specialization during interference between global and local aspects of visual hierarchical stimuli in men and women. *Human Physiology*, *37*(2), 137-142.
- Ro, T. (2008). Unconscious vision in action. *Neuropsychologia*, *46*(1), 379-383.
- Roalf, D., Lowery, N., & Turetsky, B.I. (2006). Behavioral and physiological findings of gender differences in global-local visual processing. *Brain and cognition*, *60*(1), 32-42.
- Ross, W.D., Grossberg, S., & Mingolla, E. (2000). Visual cortical mechanisms of perceptual grouping: Interacting layers, networks, columns, and maps. *Neural Networks*, *13*(6), 571-588.
- Russell, C. & Driver, J. (2005). New indirect measures of “inattentive” visual grouping in a change-detection task. *Perception and Psychophysics*, *67*(4), 606-623.
- Schneider, G.E. (1967). Contrasting visuomotor functions of tectum and cortex in the golden hamster. *Psychologische Forschung*, *31*, 52–62.

- Seymour, K., Karnath, H.O., & Himmelbach, M. (2008). Perceptual grouping in the human brain: Common processing of different cues. *Neuroreport*, *19*(18), 1769-1772.
- Shipp, S.D. (2006). Parallel visual pathways. *Advances in Clinical Neuroscience and Rehabilitation*, *6*, 21-23.
- Stoesz, B.M., Jakobson, L.S., Kilgour, A.R., & Lewycky, S.T. (2007). Local processing advantage in musicians: Evidence from disembedding and constructional tasks. *Music Perception*, *25*(2), 153-165.
- Swanson, W.H., & Cohen, J.M. (2003). Color Vision. *Ophthalmology Clinics of North America*, *16*, 179-203.
- Tipper, S.P., Lortie, C., & Baylis, G.C. (1992). Selective reaching: Evidence for action-centered attention. *Journal of Experimental Psychology: Human Perception and Performance*, *18*(4), 891-905. doi:org/10.1037/0096-1523.18.4.891
- Tootell, R.B., Silverman, M.S., Hamilton, S.L., Switkes, E., & De Valois, R.L. (1988b). Functional anatomy of macaque striate cortex: V. Spatial frequency. *Journal of Neuroscience*, *8*, 1610-1624.
- Torralba, A., Aude, O., Castelhana, M.S., & Henderson, J.M. (2006). Contextual guidance of eye movements and attention in real-world scenes: The role of global features in object search. *Psychological Review*, *113*(4), 766-786.
- Treisman, A. (1982). Perceptual grouping and attention in visual search for features and for objects. *Journal of Experimental Psychology: Human Perception & Performance*, *8*, 194-214.
- Trevarthen, C.B. (1968). Two mechanisms of vision in primates. *Psychologische Forschung*, *31*, 299-337.
- Ungerleider, L.G. & Mishkin, M. (1982). Two cortical visual systems. In *Analysis of visual behaviour*, (ed. D. J. Ingle, M. A. Goodale, and R. J. W. Mansfield), p.549-586. MIT Press, Cambridge, MA.
- Weiskrantz, L., Warrington, E.K., Sanders, M.D., & Marshall, J. (1974). Visual capacity in the hemianopic field following a restricted occipital ablation. *Brain*, *97*(1), 709-728.
- Welsh, T.N., Elliott, D., & Weeks, D.J. (1999). Hand deviations toward distractors Evidence for response competition. *Experimental Brain Research*, *127*(2), 207-212.

- Welsh, T.N., & Elliott, D. (2004). Movement trajectories in the presence of a distracting stimulus: Evidence for a response activation model of selective reaching. *The Quarterly Journal of Experimental Psychology Section A*, 57(6), 1031-1057.
- Welsh, T.N., & Elliott, D. (2005). The effects of response priming on the planning and execution of goal-directed movements in the presence of a distracting stimulus. *Acta Psychologica*, 119(2), 123-142.
- Wertheimer, M. (1923). Untersuchungen zur Lehre von der Gestalt II. *Psychologische Forschung*, 4, 301-350.
- Woodworth, R.S. (1899). Accuracy of voluntary movement. *The Psychological Review: Monograph Supplements*, 3(3), 1-114. doi:10.1037/h0092992
- Xu, Y. & Chun, M.M. (2007). Visual grouping in human parietal cortex. *PNAS*, 104(47), 18766-18771.
- Zaretskaya, N., Anstis, S., & Bartels, A. (2013). Parietal cortex mediates conscious perception of illusory Gestalt. *Journal of Neuroscience*, 33(2), 523-531. doi: 10.1523/JNEUROSCI.2905-12.2013
- Zhou, J., Gotch, C., Zhou, Y., & Liu, Z. (2008). Perceiving an object in its context – Is the context cultural or perceptual? *Journal of Vision*, 8, 1-5. doi: 10.1167/8.12.2

CHAPTER II: PERCEPTION AND CULTURE

Study 1: The Influence of Magnocellular and Parvocellular Visual Information on Global Processing in Caucasian and Asian Populations

Every day the human visual system is bombarded by vast amounts of visual information. Typically developing individuals are able to quickly and efficiently group individual features of a scene together to form a global whole, a phenomenon known as the ‘global precedence effect’ (Fabre-Thorpe et al., 2001; Torralba et al., 2006; Navon, 1977). However, recent research has shown that the relative preference for global versus local distribution of attention may differ based on culture.

Comparisons between Western Caucasian populations (i.e., Canadians, Americans, British and Australians) and East Asian populations (i.e., Chinese and Japanese) show that East Asians process objects and scenes more globally than Western Caucasians (Chua, Boland, & Nisbett, 2005; Masuda & Nisbett, 2001; 2006; Nisbett & Masuda, 2003; although see Caparos et al., 2012; Zhou et al., 2008; Evans et al., 2009; Rayner et al., 2007; Mielliet et al., 2010). For example, when individuals are asked to make absolute judgments (requiring local processing) and relative judgments (requiring global processing), East Asians perform better than Western Caucasians at the relative task while Western Caucasians perform better than East Asians at the absolute task (Kitayama et al., 2003). Similarly, an fMRI study showed that achieving equivalent levels of behavioral performance required more sustained attentional effort for the absolute task in East Asians and for the relative task in Western Caucasians (Hedden et al., 2008). When the global processing bias is directly compared between Western Caucasians and East Asians, a global advantage is found in East Asians relative to Western Caucasians, extending through to a second generation of Asian-Australians (McKone et al., 2010). An electrophysiological study examining the neural mechanisms and the temporal dynamics related to a global processing bias has shown a greater sensitivity to global congruency in East Asians relative to Western Caucasians, as indexed by an early P1 component (Lao et al., 2013).

Studies involving eye movements have suggested that perceptual differences may be driven by culture-specific tuning towards visual spatial frequency information (Mielliet et al., 2013). Face recognition studies show that Western Caucasians preferentially process high spatial frequency information from foveal vision and are more biased to local processing in hierarchical stimuli, while East Asians preferentially process contextual information by relying

on extra-foveal vision during face recognition, favoring globally-based holistic stimulus processing (Miellet et al., 2013). East Asians also show more of a reliance on extra-foveal vision than Western Caucasians when detecting low level visual stimuli (Boduroglu et al., 2009) and for change detection of complex real-world stimuli (Masuda & Nisbett, 2001), indicating that East Asians allocate their attention more broadly than Western Caucasians.

Numerous psychophysical studies have shown that the global precedence effect in typically developing individuals is mediated by low spatial frequencies (Shulman et al., 1986; Hughes et al., 1996; Robertson, 1996). Studies have also shown that stimuli presented without low spatial frequency information do not result in a global precedence effect (Badcock et al., 1990; LaGasse, 1993), but rather result in a local precedence effect (Hughes et al., 1990). Since Western Caucasians and East Asians both show a global precedence effect, it is unlikely that differences in global processing are due to an inability to process low spatial frequency information. Based on previous research showing that culture-specific tuning towards visual spatial frequency information can influence perception, we explore the notion that differences in global processing are driven by differences in the means by which low spatial frequency information is projected through the visual system.

Before visual information makes its way from visual cortex to extrastriate visual areas by the dorsal stream, which governs the visual control of action, and the ventral stream, which governs visual perception, it initially passes from the retina to the primary visual cortex via the relay station called the lateral geniculate nucleus (Hubel and Wiesel, 1972; Hendrickson et al., 1978). The lateral geniculate nucleus consists of two pathways, magnocellular and parvocellular, that operate relatively independently in early visual processing and encode contrasting information. Specifically, magnocellular pathway neurons are visual cells that are not responsive to color and are known for processing achromatic, low contrast stimuli (Maunsell et al., 1990; Merigan & Maunsell, 1993), which is critical for global processing (Hughes et al., 1990; Hughes et al., 1996). In contrast, parvocellular pathway neurons are visual cells that are highly responsive to opposing colours (red-green or blue-yellow) (Lee et al., 1988) and high spatial frequencies (Tootell et al., 1988b; Merigan et al., 1991), requiring much higher contrast (~8 % at least) when detecting achromatic stimuli (Tootell et al., 1988a). While both magnocellular and parvocellular cells are present in both dorsal and ventral processing streams (Maunsell et al., 1990; Merigan & Maunsell, 1993), magnocellular cells are primarily projected

through the dorsal stream, responsible for global processing, and parvocellular cells are primarily projected through the ventral stream, responsible for local processing.

A powerful way to gain insight into the way global information is processed in the visual system is to examine how visual information is processed through the magnocellular and parvocellular streams. For example, when stimuli are biased so that they are processed primarily through either the magnocellular or parvocellular pathway, global processing abilities differ between the two pathways in both individuals with simultanagnosia (Thomas et al., 2012) and autism spectrum disorder (Sutherland & Crewther, 2010). This biasing can be achieved by manipulating the spatial frequencies projected through the parvocellular pathway. Although an increased sensitivity for high spatial frequencies is crucial for local processing via the parvocellular pathway specifically, the parvocellular pathway's sensitivity to color information can also be selectively stimulated to act as a low-pass filter, projecting low spatial frequency information (required for global processing) when stimulated with isoluminant color stimuli (Shulman et al., 1986; Tobimatsu et al., 1996). Although the magnocellular pathway is considered the primary pathway through which global information is transmitted, biasing both pathways to project global information provides new insights into the relative contribution of these cell types to visual perception. Here we investigate the relative contribution of these two types of visual cells to the global precedence effect across Asian and Caucasian groups.

To examine the contribution of magnocellular and parvocellular cells to the global precedence effect, we used the Navon letters task (Navon, 1977) to compare global/local processing differences between Caucasian and Asian groups. Participants completed the Navon task under divided-attention conditions, indicating whether a target letter "H" was present in the hierarchical stimuli. Based on previous research (McKone et al., 2010) we expected that overall, Asians would show a stronger global advantage than Caucasians as indexed by faster reaction times, higher accuracy, and faster inverse efficiency scores when the target was presented at a global compared to a local level. We also used psychophysical techniques to examine the mechanism underlying differences in global/local processing between groups by biasing stimuli to test the indirect contribution of the dorsal and ventral pathways in mediating global and local visual processing. For each participant we first established the achromatic contrast threshold and chromatic isoluminance threshold (Kveraga et al., 2007). Next, to test global and local visual processing, we used these thresholds to dynamically generate magnocellular- and parvocellular-

biased stimuli from a set of ‘unbiased’ hierarchical letter stimuli. Considering the parvocellular system’s ability to project low spatial frequencies when stimulated with isoluminant color stimuli, both magnocellular and parvocellular systems were biased to activate in response to the same range of spatial frequencies to test the relative contributions of the dorsal and ventral pathways in mediating global visual processing in Caucasians compared to Asians. Since global processing relies on low spatial frequency information and previous research (Miellet et al., 2013) has shown that Caucasians preferentially process high spatial frequency information, which generally relies on the parvocellular system, we hypothesized that global processing in Caucasians would be more influenced by the parvocellular system than the magnocellular system when the ventral stream is biased to project low spatial frequency information via the parvocellular pathway. From this, we expected that in the parvocellular-biased condition Caucasians would process the target faster and more accurately at the global level than the local level. Similarly, since Asians have been shown to rely more on low contrast stimuli, which involves mainly the magnocellular pathway, we expected that in the magnocellular-biased condition Asians would process the target faster and more accurately at the global level than the local level.

Method

Participants

This study tested two groups: (a) 27 Caucasians (17 females) with a mean age of 23.5 years (18-36 years old) and (b) 25 Asians (15 females) with a mean age of 21.4 years (18-28 years old). The number of participants was determined based on comparable research examining cultural differences in global processing (McKone et al., 2010; Lao et al., 2013) and magnocellular functioning (Zhao et al., 2014). Based on this resulting sample size, a sensitivity analysis for the key prediction (i.e., the group x condition x level interaction) was conducted. G*Power 3.1. (Faul et al., 2007) was used to conduct an F-test for repeated measures ANOVA, specifying a within-between interaction with 2 groups (Asian, Caucasian) and 6 measurements (2 levels x 3 conditions). Assuming an error probability of .05, nonsphericity correction of 1, and power of .8, the study was 80% powered to detect an effect size $\eta_p^2 = .021$.

All participants were right-handed young adults with normal or corrected-to-normal vision. Ethnicity was determined by self-report and all participants were Introduction to

Psychology students studying at an English-language university. As such, all participants were expected to be highly fluent at identifying single English letters. Participants were excluded from the study if they failed a colorblindness test administered before the start of the experiment ($N = 7$). Participants signed an informed consent form (Appendix 1) before taking part in the study, which was approved by the Research Ethics Board (REB1) at the University of Manitoba.

General Procedure

Participants signed a consent form and completed a short demographics questionnaire. They then completed the experiment, which began with a color-blindness test, followed by a luminance contrast thresholding task of which the results were used to create the magnocellular-biased stimuli and an isoluminance task of which the results were used to create the parvocellular-biased stimuli. The final portion of the experiment involved a computerized task using the hierarchical letters task (Navon, 1977).

Psychophysical Thresholds

To determine the luminance contrast for each participant, a multiple staircase procedure was used to find the luminance threshold. Participants were shown light gray hierarchical stimuli overlaid on a dark gray background and asked if the stimuli was detected following each stimulus presentation. On 25% of the trials no stimulus was presented, which served as catch trials. Each stimulus was presented for 1500 ms, during which a response was made. If the stimulus was detected, the contrast between the stimulus and background was decreased in the next trial by modifying the luminance of the stimuli. Otherwise, the contrast was increased. A commonly used luminance threshold-finding algorithm (Kveraga et al., 2007) was used to compute the mean of the turnaround points above and below medium-gray background. A luminance ($\sim 3.5\%$ Weber contrast) value was then computed from this threshold for the grayscale stimuli and was used in the low-luminance-contrast (magnocellular-biased) condition.

For the chromatically defined stimuli in the isoluminant (parvocellular-biased) condition, the isoluminance point was found using heterochromatic flicker photometry (Siegfried et al., 1965; Livingstone & Hubel, 1987) with stimuli consisting of the same hierarchical letters from the luminance contrast task displayed in alternating colors (pure red and green). By alternating the two colors in the range of 12-20 Hz, the flicker disappears for a small range of luminance values. The color values at the point where the two colors appear to fuse together, and the

stimulus appears steady is the participant's isoluminance interval. In this task participants used the up and down arrow keys to adjust the green color to the point at which the stimulus appeared steady. Depending on the response, the output of the green color was adjusted up or down such that the participant passed over the isoluminant point many times, and the average of the values in the narrow range when the participant reported a steady stimulus was computed as the isoluminance value for that participant. This luminance contrast threshold and isoluminance value was then used to dynamically create the magnocellular- and parvocellular-biased stimuli respectively for the experiment that followed.

Stimuli and Procedure

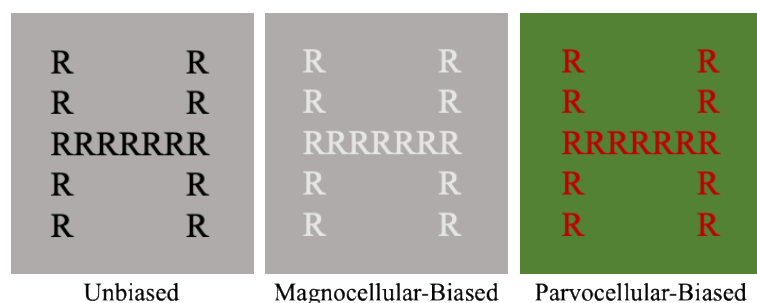
All experiments were programmed using the Python programming language (Python Software Foundation, <https://www.python.org/>). Estimation of the psychophysical thresholds and the subsequent experiments were conducted in a low-lit room with an enclosure around the monitor to ensure lighting remained consistent for all participants. Stimuli were presented on a 20-inch color monitor (resolution: 1920 x 1200 pixels; refresh rate 120 Hz) placed 50 cm in front of the participant and responses were recorded using the left and right arrow keys on a keyboard. A chin rest was used to stabilize the viewing distance and all participants made their responses with the right hand. All stimuli were presented in a pseudorandom order to ensure that identical stimuli were not presented consecutively.

Participants were instructed to indicate by key press as quickly and accurately as possible whether the target letter "H" was observed. The target could appear either as the small local letter or the large global letter (Figure 2.1), allowing the individual's implicit (i.e., uninstructed) preference for one level or the other to be assessed. The experiment began with one block of practice trials followed by the experimental trials. One third of the trials contained the target letter at the global level, one third of the trials contained the target letter at the local level, and one third of the trials served as catch trials with the target absent at both levels of processing. The stimuli were coded as Global (H made up of smaller distractor letters, either R or S), Local (H displayed as small letters forming a global S or R) and Neither (R or S made up of smaller distractor letters, either S or R respectively) for a total of 6 stimuli. The background of the hierarchical stimuli subtended 7.84° horizontally and 9.26° vertically, the global letters subtended a visual angle of $4.7^\circ \times 6.42^\circ$ and the local letters subtended $.73^\circ \times 1^\circ$, respectively. The distance between the local letters was $.2^\circ$ visual angle. Initially these stimuli were presented

as ‘unbiased’ (i.e., not biased towards the magnocellular or parvocellular pathways) hierarchical letter stimuli displayed as black letters on a grey screen. These ‘unbiased’ stimuli were converted into achromatic magnocellular-biased stimuli and red-green isoluminant parvocellular-biased stimuli using the psychophysical thresholds outlined previously, resulting in three conditions: unbiased, magnocellular-biased and parvocellular-biased. Each of the 6 stimuli were presented in each of the 3 conditions for a total of 18 stimuli.

Figure 2.1

The Three Types of Stimuli Used to Bias Processing



Note. This example shows incongruent stimuli in which the local letters (R) combine to form the global letter (H). The contrast and luminance properties of the magnocellular- and parvocellular-biased stimuli have been altered to make the stimuli are more discernible to viewers.

In the practice block, each of the six stimuli were presented twice as unbiased stimuli for a total of 12 trials. For the experimental trials, the 18 stimuli were presented 10 times for a total of 180 trials. Each trial began with a fixation cross for 1000 ms, after which the stimuli were presented until a response was indicated. Reaction time (RT) and accuracy (ACC) were collected as dependent measures, and to account for both measurements an adjusted RT measure called inverse efficiency score (IES – Bruyer and Brysbaert, 2011; Townsend and Ashby, 1978, 1983) was calculated as: $IES = RT/ACC$ and also used as a dependent measure. To determine whether there were any perceptual differences between Caucasians and Asians attributed to relative differences in global versus local distribution of attention, 2 (Group: Caucasian, Asian) x 2 (Level: Global, Local) x 3 (Condition: Magnocellular, Parvocellular, Unbiased) ANOVAs were carried out on reaction time, accuracy, and inverse efficiency score. All post-hoc pairwise comparisons were performed using Bonferroni correction and $\alpha = .05$.

Results

Reaction Time Analysis

Results of the ANOVA for reaction time showed significant main effects of level, $F(1,50) = 12.522, p = .001, \eta_p^2 = .2$, and condition, $F(2,100) = 154.638, p < .001, \eta_p^2 = .756$, and a significant level x condition interaction, $F(2,100) = 3.582, p = .031, \eta_p^2 = .067$. There was no significant main effect of group, $F(1,50) = .967, p = .330, \eta_p^2 = .019$, and no group x level x condition interaction, $F(2,100) = .174, p = .841, \eta_p^2 = .003$. Post-hoc t-tests on the level x condition interaction revealed faster identification of the target when it was presented globally compared to locally in the parvocellular condition ($p < .001$). Post-hoc tests also revealed that when the target was presented at the global level, it was identified faster in the unbiased condition compared to the magnocellular condition ($p < .001$), and in the parvocellular condition compared to the unbiased condition ($p < .001$). When the target was presented at the local level, it was identified faster in the unbiased condition compared to the parvocellular ($p < .001$) and magnocellular ($p < .001$) conditions. The target was also identified faster in the parvocellular compared to the magnocellular condition ($p < .001$).

Accuracy Analysis

Results of the ANOVA for accuracy showed significant main effects of level, $F(1,50) = 10.068, p = .003, \eta_p^2 = .168$, and condition, $F(2,100) = 22.646, p < .001, \eta_p^2 = .312$, and significant interactions between level x group, $F(1,50) = 4.889, p = .032, \eta_p^2 = .089$, level x condition, $F(2,100) = 6.553, p = .002, \eta_p^2 = .116$, and level x condition x group, $F(2, 100) = 6.160, p = .003, \eta_p^2 = .11$. There was no significant main effect of group, $F(1,50) = .166, p = .685, \eta_p^2 = .003$.

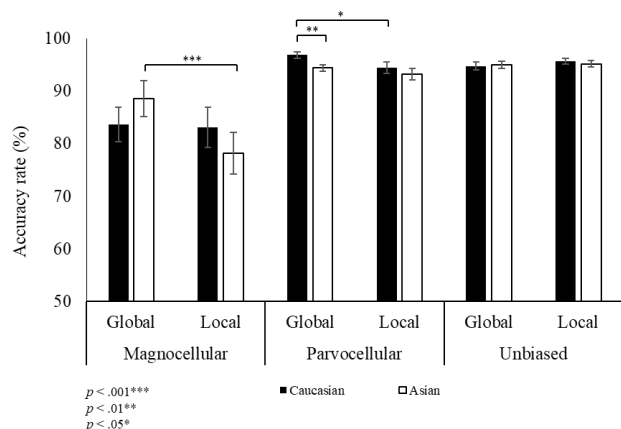
Results of the level x condition interaction revealed better accuracy when the target was presented at the global level compared to the local level in both the magnocellular ($p = .004$) and parvocellular ($p = .034$) conditions. No differences in accuracy were found in the unbiased condition. For both global and local levels, accuracy was the lowest in the magnocellular condition compared to the parvocellular (Global: $p = .001$; Local: $p < .001$) and unbiased (Global: $p = .002$; Local: $p < .001$) conditions. No accuracy differences were found between parvocellular and unbiased conditions. The level x group interaction revealed that within the

Asian group, the target at the global level was processed with more accuracy compared to when it was presented at the local level ($p < .001$).

Results of the three-way group x level x condition interaction revealed that in the parvocellular condition, when the target was presented at the global level, Caucasians responded with higher accuracy than Asians ($p = .006$; Figure 2.2). Results also showed that Caucasians responded with higher accuracy when the target was presented at the global level compared to the local level in the parvocellular condition ($p = .041$), while Asians responded with higher accuracy at the global level compared to the local level in the magnocellular condition ($p < .001$). Caucasians also showed a similar pattern of results in each condition regardless of whether the target was presented at the global or local level: accuracy was found to be lower in the magnocellular condition compared to the parvocellular (Global: $p = .001$; Local: $p = .013$) and unbiased (Global: $p = .004$; Local: $p = .005$) conditions. Individuals in the Asian group also showed this same pattern of results, but only when the target was presented at the local level. That is, accuracy was lower in the magnocellular condition compared to the parvocellular ($p = .001$) and unbiased ($p < .001$) conditions. No significant differences between conditions were found for the Asian group when the target was presented at the global level.

Figure 2.2

Accuracy Results



Note. The target was identified with higher accuracy at the global level compared to the local level in the parvocellular condition for Caucasians and in the magnocellular condition for Asians. Error bars show +/- 1 SEM.

Adjusted Reaction Time Analysis using Inverse Efficiency Score (IES)

Results of the ANOVA on IES showed significant main effects of level, $F(1,50) = 14.559, p < .001, \eta_p^2 = .226$, and condition, $F(2,100) = 72.692, p < .001, \eta_p^2 = .592$, and significant interactions between level x group, $F(1,50) = 6.101, p = .017, \eta_p^2 = .109$, condition x level, $F(2,100) = 6.996, p = .001, \eta_p^2 = .123$, and group x condition x level, $F(2,100) = 5.208, p = .007, \eta_p^2 = .094$. There was no significant main effect of group, $F(1,50) = .468, p = .497, \eta_p^2 = .009$.

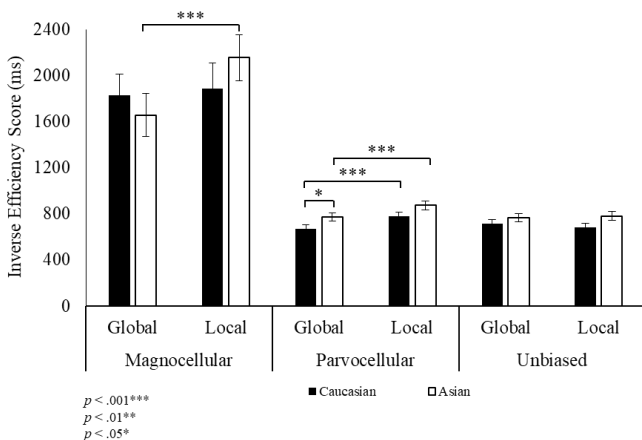
Results of the level x condition interaction revealed faster identification of the target when it was presented at the global level compared to the local level in both the magnocellular ($p = .005$) and parvocellular ($p < .001$) conditions. No differences were found in the unbiased condition. For both global and local levels the target was identified slower in the magnocellular condition compared to the parvocellular (Global: $p < .001$; Local: $p < .001$) and unbiased (Global: $p < .001$; Local: $p < .001$) conditions. A difference was also found between parvocellular and unbiased conditions at the local level ($p < .001$) but not at the global level. The level x group interaction revealed that within the Asian group, the target at the global level was processed faster than at the local level ($p < .001$). No differences were found between global and local processing for the Caucasian group.

Results of the three-way group x level x condition interaction revealed that in the parvocellular condition, when the target was presented at the global level, Caucasians responded more quickly than Asians ($p = .049$; Figure 2.3). Results also showed faster processing for Caucasians when the target was presented at the global level compared to the local level ($p < .001$) in the parvocellular condition, while Asians showed faster processing at the global compared to the local levels in both magnocellular ($p < .001$) and parvocellular ($p < .001$) conditions. Finally, at the global level Caucasians showed slower processing of the target in magnocellular compared to parvocellular ($p < .001$) and unbiased ($p < .001$) conditions and for unbiased compared to parvocellular conditions ($p = .044$). At the local level, Caucasians also showed slower processing for magnocellular compared to parvocellular ($p < .001$) and unbiased ($p < .001$) conditions and for parvocellular compared to unbiased conditions ($p < .001$). At the global level, Asians showed slower processing in the magnocellular compared to parvocellular ($p < .001$) and unbiased ($p < .001$) conditions. No significant differences were found between parvocellular and unbiased conditions. At the local level, Asians showed slower processing in

the magnocellular compared to parvocellular ($p < .001$) and unbiased ($p < .001$) conditions, as well as for parvocellular compared to unbiased conditions ($p < .001$).

Figure 2.3

Inverse Efficiency Score Results



Note. Between groups, the target was identified faster at the global level compared to the local level in the parvocellular condition for Caucasians and in both the parvocellular and magnocellular conditions for Asians. Error bars show +/- 1 SEM.

Discussion

Previous studies suggest that East Asians process scenes more globally than Western Caucasians (Lao et al., 2013; McKone et al., 2010). Perceptual differences may be driven by culture-specific tuning towards visual spatial frequency information, as demonstrated in studies showing that Western Caucasians preferentially process high spatial frequency information, while East Asians preferentially process low spatial contextual information (Miellet et al., 2013; Boduroglu et al., 2009). Within the visual system, high spatial frequency information, required for local processing, is mainly projected via the parvocellular pathway and low spatial frequency information, required for global processing, is mainly projected via the magnocellular pathway. From this, we hypothesized that perceptual differences between Caucasians and Asians might be driven by biases towards one pathway or the other. The aim of this study was to test the potential mechanism underlying these differences by examining the relative contributions of the

magnocellular and parvocellular pathways in mediating global and local visual processing in Asian and Caucasian groups.

Overall, our comparison of Caucasian and Asian groups revealed little evidence for cultural differences. In the unbiased condition, which would most closely represent the stimuli used in comparable previous studies, participants in the Caucasian group performed similarly to those of the Asian group. Even more surprising, no global bias was found within each group. The lack of robust and consistent evidence is unexpected, given the original reports of statistically significant cultural differences. However, there are several reasons that could explain these differential findings.

First, stimulus presentation may have weakened our ability to see cultural differences. McKone et al. (2010) presented their stimuli laterally rather than centrally. While location of the stimuli was not found to influence global/local response times in their study, it is possible that faster reaction times for Asians compared to Caucasians were due to a broader allocation of attention in the Asian group rather than a global processing bias (Boduroglu et al., 2009; Masuda & Nisbett, 2001). In the current study, the stimuli were always presented centrally, so it may be the case that stimulus presentation was more advantageous for Caucasians, who have been shown to preferentially process information from foveal vision (Mielliet et al., 2013). However, accuracies were high in both groups, suggesting that Asians were not that affected by the location of the stimulus.

A more plausible explanation is that differences in behavioral performance were masked by other factors such as attention. For example, if attention is viewed as a spotlight where stimuli falling within the beam of the spotlight are processed preferentially, then examining how the spotlight differs between groups may provide insight into why the two groups differ if there are characteristics that are unique to one group compared to the other, like size of the spotlight. While previous behavioral studies have shown that Asians perform better on a task requiring global processing and Caucasians perform better on a task requiring local processing (Kitayama et al., 2003), an fMRI study showed that equal levels of behavioral performance were achieved by allocating more sustained attentional effort for the local task in Asians and the global task in Caucasians (Hedden et al., 2008). As such, it is possible that Caucasians were recruiting more attentional resources to produce the same behavioral outcome as evident in the Asian group.

Future research using a combined fMRI/behavioral approach will help determine the extent to which attention influences global/local processing.

Finally, it is possible that individual biases may have influenced the extent to which global processing was observed. Previous research has shown that the degree of individual bias toward global information can vary based on stimulus parameters, such as the aspect ratio of local to global items (Kimchi, 1992; Yovel, Yovel & Levy, 2001), the overall visual angle (Kinchla & Wolfe, 1979), or the amount of time participants have to view stimuli (Paquet & Merikle, 1984). Additionally, older individuals (Lux et al., 2008), individuals induced into a state of negative affect (Gasper & Clore, 2002), individuals from remote cultures (Davidoff et al., 2008) and musicians (Stoesz et al., 2007) all tend to show a local compared to global processing bias. Conversely, individuals from collectivist cultures (McKone et al., 2010) and individuals induced into a state of positive affect (Fredrickson & Branigan, 2005) tend to show a preference for global processing. Thus, a global bias can be influenced by participant characteristics and is not absolute. As such, culture is only one of many possible influencers of global processing, and future research involving larger sample sizes in each group and controlling for a wider breadth of participant characteristics will help to untangle the relationship between culture and global/local processing.

Although no differences were observed in the unbiased condition, differences were found within the magnocellular and parvocellular conditions. A direct comparison between groups indicated higher accuracy and lower inverse efficiency scores in Caucasians compared to Asians when processing the target at the global level, compared to the local level, in the parvocellular condition specifically. Individual group differences also showed that Caucasians processed the target with higher accuracy and showed lower inverse efficiency scores at the global level compared to the local level in the parvocellular condition only, while no significant differences between global and local processing were observed in the magnocellular condition. Asians, however, processed the target with higher accuracy and showed lower inverse efficiency scores at the global level compared to the local level in the magnocellular condition. In the parvocellular condition, Asians also showed lower inverse efficiency scores at the global level compared to the local level, although there were no significant differences in accuracy. Together, this suggests that global/local processing in Caucasians is influenced more by the

parvocellular stream, and in Asians by the magnocellular stream (and to a lesser extent the parvocellular stream).

Based on our knowledge that the parvocellular pathway typically transmits high spatial frequency information and the magnocellular pathway is biased to project low spatial frequency information, we suggest that the potential mechanism underlying global/local processing in Caucasians relies more heavily on information from the parvocellular pathway, while the mechanism in Asians relies more heavily on information from the magnocellular pathway (and to a lesser extent the parvocellular pathway). This would explain why some research has found that Caucasians show a local processing bias in global/local processing tasks (see Dale & Arnell, 2010), and why Caucasians show a less robust global processing bias compared to Asians. In the current study, parvocellular stimuli were biased to also project low spatial frequency information so that global processing between the two pathways could be examined more directly. When low spatial frequency information was projected through the parvocellular pathway, Caucasians showed a significant advantage for global processing over Asians, which may not have been as evident if high spatial frequencies were not filtered out of the stimuli. However, to confirm this potential mechanism for global/local processing, future studies should examine how Caucasians process parvocellular stimuli when they are not filtered to isolate low spatial frequency information. Neuroimaging studies will also be an important contributor in verifying the extent to which these differences are observed in the brain.

A stronger influence of the magnocellular stimuli on global processing in the Asian group may also explain why these individuals show an early sensitivity to global information coding (Lao et al., 2013). Magnocellular pathway neurons, critical for global processing, transmit information much faster than parvocellular pathway neurons from the lateral geniculate nucleus to the primary visual cortex. If visual processing in Asians is more influenced by the magnocellular pathway than it is in Caucasians, this suggests that a more robust global processing bias in Asians may be driven by a stronger influence of the magnocellular pathway over the parvocellular pathway. This is also in line with previous research showing that Asians rely more on low spatial, extra foveal vision.

Visual saliency between global and local features has also been suggested as a potential explanation for why Caucasian's process scenes less globally than Asians. Lao et al. (2013) found that Caucasians were less efficient at detecting global compared to local feature changes,

while Asians performed equally well on both conditions, suggesting that the behavioral disadvantage of Caucasians in the global task stemmed from differences in visual saliency between global and local features. Their rationale was that since visual processing of global features precedes the analysis of local information (Navon, 1977), an initial preference for global processing would conflict with local information, inhibiting the ability to detect local features (Han et al., 2001; Miller & Navon, 2002; Navon 1977). Miller and Navon (2002) showed that participants identified local targets slower in the presence of a global shape, even when the global information was irrelevant. From this, Lao et al. (2013) suggest that when Caucasians are required to detect changes in local information, the presence of global features is more disruptive for them than for Asians, who seem to benefit from a top-down attention control to global features. As such, the visual saliency induced by the global feature change did not seem to disturb processing in Asians to the same extent as in Caucasians. However, our results suggest that saliency cannot fully account for this difference in processing between the two groups since Caucasians showed a global precedence in the parvocellular-biased condition using the same stimuli as was used in the unbiased and magnocellular-biased conditions. If visual saliency is the driving force behind a global processing difference, then Asians should show the same global processing advantage over Caucasians regardless of condition. It is more likely that the notion that Caucasians process scenes less globally than Asians is due to the way that visual information is projected by the two pathways. This is not to say that Caucasians do not benefit from information transmitted via the magnocellular pathway, but rather suggests that the way in which visual information is transmitted via the two streams differs between groups.

It should also be noted that while the magnocellular and parvocellular stimuli were biased in a certain way, both types of cells may have still been responding. While magnocellular and parvocellular information projected from the lateral geniculate nucleus to the primary visual cortex does remain, to some extent, functionally segregated, once this information projects beyond V1 there is a considerable amount of mixing of magnocellular and parvocellular signals. From the primary visual cortex information is still conveyed via two largely functionally distinct streams, the dorsal and ventral streams, however each stream is composed of a mixture of magnocellular and parvocellular signals (Sincich & Horton, 2005). Although information in one stream is influenced by the other, lesion studies involving the magnocellular and parvocellular pathways provide evidence for a distinct relationship between the response properties of the

magnocellular and parvocellular cells and the functions of the cortical regions along the dorsal and ventral streams. For example, lesions to the parvocellular pathway results in deficits in chromatic vision, texture perception, pattern perception, acuity and a loss in contrast sensitivity at low temporal and high spatial frequencies (Schiller et al., 1991; Merigan, 1989). Lesions to the magnocellular pathway have been found to cause deficits in flicker and motion perception (Schiller et al., 1991). Together, this demonstrates that while the dorsal and ventral streams receive input from both magnocellular and parvocellular cells, the effect these cells have on each of the two streams differs. As such, in the current study we do not assume that biasing the stimuli towards the magnocellular and parvocellular pathways only activates that individual pathway, but rather that the manipulation biases processing in one pathway over the other.

Conclusion

We have demonstrated that Caucasians can be biased to process scenes more globally than Asians as long as low spatial frequency information is projected through the parvocellular pathway. Asians also show a global precedence effect when low spatial frequency information is projected through the magnocellular pathway, and to a lesser extent through the parvocellular pathway. These findings suggest that the means by which a global processing bias is achieved depends on the subcortical pathway through which visual information is transmitted. That is, Caucasians may depend more on ventrally-based information transmitted through the parvocellular pathway in global/local processing, while Asians may depend more on dorsally-based information transmitted through the magnocellular pathway. Since the parvocellular stream projects high spatial frequency information useful for local processing when stimuli are not isoluminant, this may explain why research often finds that Asians process scenes more globally than Caucasians. These findings provide a deeper understanding of the extent to which global/local processing differences exist across cultural groups, expanding on the relationship between global/local processing, subcortical pathways, and spatial frequencies.

References

- Badcock, J.C., Whitworth, F.A., Badcock, D.R., & Lovegrove, W.J. (1990). Low-frequency filtering and the processing of local-global stimuli. *Perception, 19*, 617-629.
- Boduroglu, A., Shah, P., & Nisbett, R.E. (2009). Cultural differences in allocation of attention in visual information processing. *Journal of Cross-Cultural Psychology, 40*(3), 349–360. doi: 10.1177/0022022108331005
- Bruyer, R., & Brysbaert, M. (2011). Combining speed and accuracy in cognitive psychology: Is the inverse efficiency score (IES) a better dependent variable than the mean reaction time (RT) and the percentage of errors (PE)? *Psychologica Belgica, 51*(1), 5–13. doi: 10.5334/pb-51-1-5
- Caparos, S., Ahmed, L., Bremner, A.J., de Fockert, J.W., Linnell, K.J., & Davidoff, J. (2012). Exposure to an urban environment alters the local bias of a remote culture. *Cognition, 122*(1), 80-85. doi: 10.1016/j.cognition.2011.08.013
- Chua, H.F., Boland, J.E., & Nisbett, R.E. (2005). Cultural variation in eye movements during scene perception. *Proceedings of the National Academy of Sciences of the United States of America, 102*, 12629-12633. doi: 10.1073/pnas.0506162102
- Dale, G., & Arnell, K. M. (2010). Individual differences in dispositional focus of attention predict attentional blink magnitude. *Attention, Perception, & Psychophysics, 72*, 602–606. doi:10.3758/APP.72.3.602
- Davidoff, J., Fonteneau, E., & Fagot, J. (2008a). Local and global processing: Observations from a remote culture. *Cognition, 108*, 702-709. doi: 10.1016/j.cognition.2008.06.004
- Evans, K., Rotello, C.M., Li, X., & Rayner, K. (2009). Scene perception and memory revealed by eye movements and receiver-operating characteristic analyses: Does a cultural difference truly exist? *The Quarterly Journal of Experimental Psychology, 62*, 276-285. doi: 10.1080/17470210802373720
- Fabre-Thorpe, M., Delorme, A., Marlot, C., & Thorpe, S. (2001). A limit to the speed of processing in ultra-rapid visual categorization of novel natural scenes. *Journal of Cognitive Neuroscience, 13*(2), 1-10. doi: 10.1162/089892901564234
- Faul, F., Erdfelder, E., Lang, A., & Buchner, A. (2007). G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods, 39*(2), 175-191.

- Fredrickson, B. L., & Branigan, C. (2005). Positive emotions broaden the scope and attention and thought-action repertoires. *Cognition and Emotion, 19*, 313–332. doi:10.1080/02699930441000238
- Gaspar, K., & Clore, G. L. (2002). Attending to the big picture: Mood and global versus local processing of visual information. *Psychological Science, 13*, 34–40. doi:10.1111/1467-9280.00406
- Han, S., He, X., Yund, E.W., & Woods, D.L. (2001). Attentional selection in the processing of hierarchical patterns: An ERP study. *Biological Psychology, 56*(2), 113–130. doi: 10.1016/s0301-0511(01)00073-4
- Hedden, T., Ketay, S., Aron, A., Markus, H.R. & Gabrieli, J.D.E. (2008). Cultural influences on neural substrates of attentional control. *Psychological Science, 19*, 12-17. doi: 10.1111/j.1467-9280.2008.02038.x
- Hendrickson, A.E., Wilson, J.R., & Ogren, M.P. (1978). The neuroanatomical organization of pathways between the dorsal lateral geniculate nucleus and visual cortex in the old world and new world primates. *J Comp Neurol, 182*, 123–136.
- Hubel, D.H., & Wiesel, T.N. (1972). Laminar and columnar distribution of geniculo-cortical fibers in the macaque monkey. *J Comp Neurol, 146*, 421–450.
- Hughes, H.C., Fendrich, R., & Reuter-Lorenz, P.A. (1990). Global versus local processing in the absence of low spatial frequencies. *Journal of Cognitive Neuroscience, 2*, 272-282. doi: 10.1162/jocn.1990.2.3.272
- Hughes, H.C., Nozawa, G., & Kitterle, F. (1996). Global precedence, spatial frequency channels, and the statistics of natural images. *Journal of Cognitive Neuroscience, 8*, 197-230. doi: 10.1162/jocn.1996.8.3.197
- Kimchi, R. (1992). Primacy of wholistic processing and global/local paradigm: A critical review. *Psychological Bulletin, 112*, 24–38. doi:10.1037/0033-2909.112.1.24
- Kinchla, R. A., & Wolfe, J. M. (1979). The order of visual processing: “Top-down”, “bottom-up”, or “middle-out”. *Perception & Psychophysics, 25*, 225–231. doi:10.3758/BF0320299
- Kitayama, S., Duffy, S., Kawamura, T., & Larsen, J.T. (2003). Perceiving an object and its context in different cultures: A cultural look at new look. *Psychological Science, 14*, 201-206. doi: 10.1111/1467-9280.02432

- Kveraga, K., Bosyan, J., & Bar, M. (2007). Magnocellular projections as the trigger of top-down facilitation in recognition. *Journal of Neuroscience*, *27*, 13232-13240. doi: 10.1523/JNEUROSCI.3481-07.2007
- LaGasse, L.L. (1993). Effects of good form and spatial frequency on global precedence. *Attention, Perception & Psychophysics*, *53*, 89-105.
- Lao, J., Vizioli, L., & Caldara, R. (2013). Culture modulates the temporal dynamics of global/local processing. *Culture and Brain*, *1*(2-4), 158-174. doi: 10.1007/s40167-013-0012-2
- Lee, B., Martin, P., & Valberg, A. (1988). The physiological basis of heterochromatic flicker photometry demonstrated in the ganglion cells of the macaque retina. *Journal of Physiology*, *404*, 323-347. doi: 10.1113/jphysiol.1988.sp017292
- Livingstone, M.S. & Hubel, D.H. (1984). Anatomy and physiology of a color system in the primate visual cortex. *Journal of Neuroscience*, *4*, 309-356. doi: 10.1523/JNEUROSCI.04-01-00309.1984
- Lux, S., Marshall, J. C., Thimm, M., & Fink, G. R. (2008). Differential processing of hierarchical visual stimuli in young and older healthy adults: Implications for pathology. *Cortex*, *44*, 21–28. doi:10.1016/j.cortex.2005.08.001
- Masuda, T., & Nisbett, R.E. (2001). Attending holistically versus analytically: Comparing the context sensitivity of Japanese and Americans. *Journal of Personality and Social Psychology*, *81*, 922-934. doi: 10.1037//0022-3514.81.5.922
- Masuda, T., & Nisbett, R.E. (2006). Culture and change blindness. *Cognitive Science*, *30*, 381-399. doi: 10.1207/s15516709cog0000_63
- Maunsell, J.H., Nealey, T.A., & DePriest, D.D. (1990). Magnocellular and parvocellular contributions to responses in the middle temporal visual area (MT) of the macaque monkey. *Journal of Neuroscience*, *10*, 3323-34. doi: 10.1523/JNEUROSCI.10-10-03323.1990
- McKone, E., Davies, A.A., Fernando, D., Aalders, R., Leung, H., Wickramariyaratne, T., & Platow, M.J. (2010). Asia has the global advantage: Race and visual attention. *Vision Research*, *50*, 1540-1549. doi:10.1016/j.visres.2010.05.010
- Merigan, W.H., (1989). Chromatic and achromatic vision of macaques: Role of the P pathway. *Journal of Neuroscience*, *9*, 776-783.

- Merigan, W.H. & Maunsell, J.H.R. (1993). How parallel are the primate visual pathways? *Annual Review of Neuroscience*, *16*, 369-402. doi: 10.1146/annurev.ne.16.030193.002101
- Merigan, W.H., Katz, L.M., & Maunsell, J.H. (1991). The effects of parvocellular lateral geniculate lesions on the acuity and contrast sensitivity of macaque monkeys. *Journal of Neuroscience*, *11*, 994-1001. doi: 10.1523/JNEUROSCI.11-04-00994.1991
- Miellet, S., Vizioli, L., He, L., Zhou, X., & Caldara, R. (2013). Mapping face recognition information use across cultures. *Frontiers in psychology*, *4*(34), 1-12. doi: 10.3389/fpsyg.2013.00034
- Miellet, S., Zhou, X., He, L., Rodger, H., & Caldara, R. (2010). Investigating cultural diversity for extrafoveal information use in visual scenes. *Journal of Vision*, *10*(6), 21. doi: 10.1167/10.6.21
- Miller, J., & Navon, D. (2002). Global precedence and response activation: Evidence from LRPs. *The Quarterly Journal of Experimental Psychology*, *55*(1), 289–310. doi: 10.1080/02724980143000280
- Navon, D. (1977). Forest before trees: The precedence of global features in visual perception. *Cognitive Psychology*, *9*, 353-383. doi: 10.1016/0010-0285(77)90012-3
- Nisbett, R.E., & Masuda, T. (2003). Culture and point of view. *Proceedings of the National Academy of Sciences*, *100*(19), 11163–11170. doi: 10.1073/pnas.1934527100
- Paquet, L., & Merikle, P. M. (1984). Global precedence: The effect of exposure duration. *Canadian Journal of Psychology*, *38*, 45–53. doi:10.1037/h0080783
- Rayner, K., Li, X., Williams, C.C., Cave, K.R., & Well, A.D. (2007). Eye movements during information processing tasks: Individual differences and cultural effects. *Vision Research*, *47*, 2714-2726. doi: 10.1016/j.visres.2007.05.007
- Robertson, L.C. (1996). Attentional persistence for features of hierarchical patterns. *Journal of Experimental Psychology: General*, *125*, 227-249.
- Schiller, P.H., Logothetis, N.K., & Charles, E.R. (1991). Parallel pathways in the visual system: Their role in perception at isoluminance. *Neuropsychologia*, *29*, 433-441.
- Shulman, G., Sullivan, M.A., Gish, K., & Sakoda, W.J. (1986). The role of spatial frequency channels in the perception of local and global structure. *Perception*, *15*, 259-279. doi: 10.1068/p150259

- Siegfried, J.B., Tepas, D.I., Sperling, H.G., & Hiss, R.H. (1965). Evoked brain potential correlates of psychophysical responses: Heterochromatic flicker photometry. *Science*, *149*, 321-323. doi: 10.1126/science.149.3681.321
- Sincich, L.C., & Horton, J.C. (2005). The circuitry of V1 and V2: Integration of color, form, and motion. *Annual Reviews Neuroscience*, *28*, 303-326.
- Stoesz, B. M., Jakobson, L. S., Kilgour, A. R., & Lewycky, S. T. (2007). Local processing advantage in musicians: Evidence from disembedding and constructional tasks. *Music Perception*, *25*, 153–165. doi:10.1525/mp.2007.25.2
- Sutherland, A., & Crewther, D.P. (2010). Magnocellular visual evoked potential delay with high autism spectrum quotient yields a neural mechanism for altered perception. *Brain*, *133*, 2089-2097. doi:10.1093/brain/awq122
- Thomas, C., Kveraga, K., Huberle, E., Karnath, H.-O., & Bar, M. (2012). Enabling global processing in simultanagnosia by psychophysical biasing of visual pathways. *Brain*, *135*, 1578-1585. doi: 10.1093/brain/aws066
- Tobimatsu, S., Tomoda, H., & Kato, M. (1996). Human VEPs to isoluminant chromatic and achromatic sinusoidal gratings: Separation of parvocellular components. *Brain Topography*, *8*, 241–243. doi: 10.1007/BF01184777
- Tootell, R.B., Hamilton, S.L., & Switkes, E. (1988a). Functional anatomy of macaque striate cortex: IV. Contrast and magno-parvo streams. *Journal of Neuroscience*, *8*, 1594-609. doi: 10.1523/JNEUROSCI.08-05-01594.1988
- Tootell, R.B., Silverman, M.S., Hamilton, S.L., Switkes, E., & De Valois, R.L. (1988b). Functional anatomy of macaque striate cortex: V. Spatial frequency. *Journal of Neuroscience*, *8*, 1610-1624. doi: 10.1523/JNEUROSCI.08-05-01610.1988
- Torralba, A., Aude, O., Castelhana, M. S., Henderson, J. M. (2006). Contextual guidance of eye movements and attention in real-world scenes: The role of global features in object search. *Psychological Review*, *113*(4), 766-786. doi: 10.1037/0033-295X.113.4.766
- Townsend, J.T., & Ashby, F.G. (1978). Methods of modeling capacity in simple processing systems. *Cognitive Theory*, *3*, 200–239.
- Townsend, J.T., & Ashby, F.G. (1983). *The stochastic modeling of elementary psychological processes*. Cambridge: CUP Archive.

- Yovel, G., Yovel, I., & Levy, J. (2001). Hemispheric asymmetries for global and local visual perception: Effects of stimulus and task factors. *Journal of Experimental Psychology. Human Perception and Performance*, 27, 1369–1385. doi:10.1037/0096-1523.27.6.1369
- Zhao, J., Qian, Y., Bi, H-Y., & Coltheart, M. (2014). The visual magnocellular-dorsal dysfunction in Chinese children with developmental dyslexia impedes Chinese character recognition. *Scientific Reports*, 4, 1-7. doi: 10.1038/srep07068
- Zhou, J., Gotch, C., Zhou, Y., & Liu, Z. (2008). Perceiving an object in its context – Is the context cultural or perceptual? *Journal of Vision*, 8, 1-5. doi: 10.1167/8.12.2

CHAPTER III: PERCEPTION AND ATTENTION

Study 2: Neural Correlates of Perceptual Grouping Under Conditions of Inattention and Divided-Attention

In order to make sense of the visual scenes we encounter, meaningful perception relies on our ability to quickly and efficiently organize visual information. The visual system groups elements using principles first introduced by Gestalt psychologists, including similarity, proximity and closure (Wertheimer, 1923). This allows incoming information to be organized and integrated from meaningless and fragmented input into coherent, whole objects and backgrounds. Behavioral research has demonstrated that visual object representations not only occur in situations in which such objects are attended or task-relevant, but also take place when they are unattended and task-irrelevant (Moore & Egeth, 1997; Russell & Driver, 2005; Lamy, Segal, & Ruderman, 2006; Müller et al., 2010). Previous research using visual illusions, in which susceptibility depends on grouping incoming information together, as well as grouped patterns, has established that individuals are susceptible to grouping even when they are unable to explicitly report the elements being grouped [Moore & Egeth, 1997; Russell & Driver, 2005; Lamy et al., 2006; Driver, Davis, Russell, Turatto, & Freeman, 2001; Kimchi & Peterson, 2008; Kimchi & Razpurker-Apfeld, 2004; Carther-Krone, Shomstein, & Marotta, 2016; Shomstein, Kimchi, Hammer, & Behrmann, 2010). This suggests that perceptual grouping may occur relatively automatically and independently of top-down attentional selection. This is further supported by studies involving patients with neurological disabilities such as hemispatial neglect (Russell & Driver, 2005; Shomstein et al., 2010; Vuilleumier & Landis, 1998; Vuilleumier, Valenza & Landis, 2001) and simultanagnosia (Huberle & Karnath, 2006; Karnath, Ferber, Rorden & Driver, 2000), who show an ability to implicitly group elements despite difficulties explicitly reporting the global configurations. However, it is unclear which brain regions are responsible for grouping unattended stimuli, and whether access to a visual stimulus, even if unattended, activates the same regions.

While previous research has established that perceptual grouping can occur without focused attention, there is little research examining the neural mechanisms underlying grouping in this context and how it might differ from grouping under conditions of explicit attention. Of the research that exists, much of it focuses on grouping under varying conditions of attention, pointing to areas V1 and V2 of the visual cortex (Ross, Grossberg & Mingolla, 2000), the

inferior parietal cortex, middle temporal gyrus and prefrontal cortex (Seymour, Karnath, & Himmelbach, 2008) as regions responsible for grouped compared to ungrouped visual information. Furthermore, research has suggested that different Gestalt properties rely on different neural mechanisms (Han, Song, Ding, Yund & Woods, 2001; Han, Jiang, Mao, Humphreys & Gu, 2005; Vidal, Chaumon, O'Regan & Tallon-Baudry, 2006), and that these properties may be driven differentially by local and global processing strategies (Han et al., 2001; Prieto, Mayas, & Ballesteros, 2014). As a result, there is a considerable divergence of findings regarding perceptual grouping, and most research on perceptual grouping has explicitly involved the recruitment of attentional mechanisms to some extent. Neuroimaging research examining grouping without attention has focused mainly on comparing grouped to ungrouped stimuli. One line of work has examined the visual suppression that occurs between simultaneously presented proximal visual elements to show that these competitive interactions appear to occur automatically, without attention, in the early visual cortex (Kastner, De Weerd, Desimone, & Ungerleider, 1998; Reynolds, Chelazzi & Desimone, 1999). Another study comparing grouped to ungrouped visual information pointed to the inferior parietal lobe as important in perceptual grouping when grouping was task-irrelevant and participants were unaware of the stimuli to be grouped (Xu & Chun, 2007). Although the limited amount of research examining perceptual grouping without attention points to the early visual cortex and inferior parietal lobe as an important marker of grouping under conditions of inattention, there has to date been no within studies comparisons of the neural correlates activated in response to perceptual grouping under conditions of inattention compared to when attentional processes are recruited.

To determine whether distinct brain regions are recruited for perceptual grouping without attention compared to grouping under conditions of divided-attention, an fMRI investigation was conducted in which we utilized a version of the Ponzo illusion (Ponzo, 1910) that superimposed two horizontal lines over a background of black and white dots. When the black dots were grouped, they formed the two converging lines of the Ponzo illusion (Moore & Egeth, 1997). Inattentive processing was examined by requiring participants to determine which of two horizontal lines was longer after a brief presentation of the illusion. If participants consistently judged the line placed at the converging end of the illusion as longer, this would indicate that they were processing the illusion without attention. Following the inattention trials, divided-

attention was investigated by instructing participants to attend to the background while performing the same line judgement task as previously administered in the inattention condition.

If grouping without attention and under conditions of divided-attention result in similar brain regions being activated, then these overlapping regions would suggest a general processing mechanism is responsible for perceptual grouping regardless of whether or not it is perceived. However, if distinct regions of activation are found for grouping stimuli without attention, then this would suggest that input that is not explicitly reported is driven by those regions, and that attention may serve as a modulating factor in differentiating between implicit and explicit grouping.

Here we report novel findings comparing brain regions activated during perceptual grouping without attention and under conditions of divided-attention. While previous research has examined the brain regions activated in response to perceptual grouping in general, the extent to which attention modulates these regions has mainly focused on paradigms requiring divided- or selective-attention. The current study not only examined the brain regions involved in perceptual grouping under conditions of inattention, but also provides a direct comparison of grouping under inattention and divided-attention conditions in the same study. While activity related to perceptual grouping was found within previously reported regions of the occipital lobes, frontal lobes and left parietal lobe, activation was also observed in the right supramarginal gyrus for grouping specifically in the inattention condition. This inferior parietal activation is consistent with previous research (Xu & Chun, 2007), but further demonstrates that it is unique to grouping under conditions of inattention by comparing grouping mechanisms to those resulting when attention is explicitly recruited, in which this activation is no longer found. The specific activation of the right supramarginal gyrus under conditions of inattention suggests that this region is directly involved in grouping only when we do not explicitly attend to a stimulus.

Method

Participants

The study protocol was approved by the Psychology/Sociology Human Research Ethics Board (PSREB) at the University of Manitoba and Thunder Bay Regional Health Sciences Center Ethics Board. The number of participants was pre-set to 20-25 based on comparable recent research using fMRI to study visual illusions (Selles et al., 2014; He, Mo, Wang, & Fang, 2015; Mikellidou et al., 2016) and attention (Kok, Bains, van Mourik, Norris, & de Lange, 2016;

Salo, Salmela, Salmi, Numminen, & Alho, 2017; Santangelo, Fagioli, & Macaluso, 2010). Twenty-eight typically developing individuals were recruited and provided written informed consent (Appendix 2). Inclusion criteria included normal or corrected-to-normal vision and no preclusions for MRI. Participants received \$25.00 to compensate them for any expenses related to the study participation. There were several sources of data attrition: one participant could not be tested due to technical difficulties with the MRI and was excluded without data collection, data from one participant was discarded due to problems with the MRI in acquiring the T1-weighted anatomical scan, three participants were discarded due to excess (greater than 2mm in any direction) head motion, and behavioral data from one participant was discarded due to problems acquiring responses using the MRI compatible trackball. Thus, the final sample consisted of twenty-two right-handed participants (13 females) aged 31 ± 6.85 (mean \pm 1 SD).

Apparatus and Stimuli

Stimuli were generated on a 12.7" Dell Tablet using E-Prime software (Psychology Software Tools, Pittsburgh, PA) and projected onto a screen that was viewed by subjects via a mirror measuring 13 cm x 8 cm ($50^\circ \times 32^\circ$ in visual angle) mounted on the head coil. The approximate distance from the participants eye to the screen was 14 cm (depending on individual head size and position in the head coil). The spatial resolution of the computer was 1024 x 768 pixels, and the refresh rate was 60 frames per second.

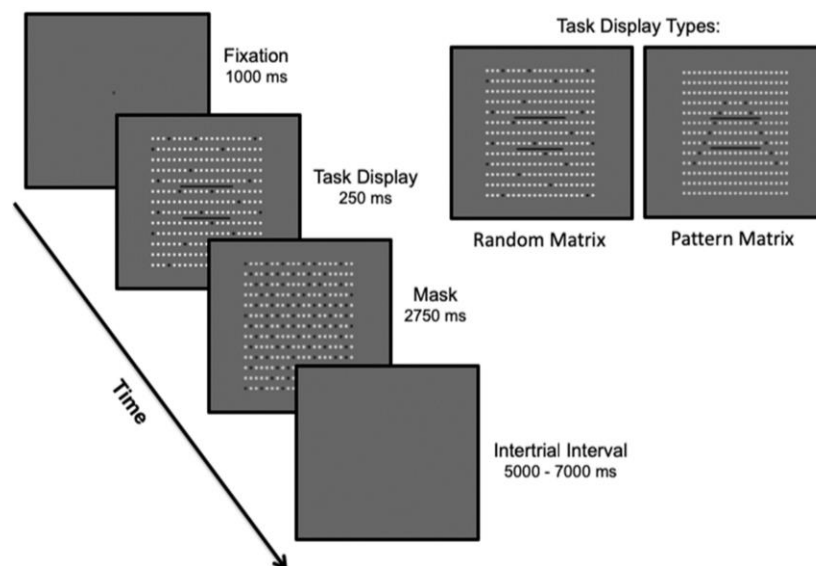
Each trial began with a black $.8^\circ \times 1^\circ$ fixation cross presented in the center of a grey background (luminance: 106 cm/m^2). Trial displays consisted of a matrix of 21 columns and 13 rows of black and white dots subtending approximately $18.4^\circ \times 19.2^\circ$, centered on the grey background, with two horizontal black line segments superimposed over the dot matrix. Each dot had a diameter of $.6^\circ$. Dots within a row were separated by 1° (center to center), and those within a column were separated by 1.5° (center to center). The line segments were $.4^\circ$ wide. Line segments were centered horizontally within the matrix and positioned approximately one third of the way down from the top of the matrix (between the 5th and 6th rows of dots) and one third of the way up from the bottom of the matrix (between the 8th and 9th rows of the dots).

Trials consisted of either random matrix or pattern matrix trials. Random matrix trials consisted of dot matrices in which a random 8% of the dots were black and the rest were white. The line segments superimposed over the matrix were presented so that one line segment was slightly longer than the other, and the lengths were randomly chosen from three short-long pairs:

(8.3° , 7.3°), (8.7° , 7.7°), (9.3° , 8.3°). In these trials, the longer line segment was presented equally often in the top and bottom positions (Figure 3.1). Pattern matrix trials consisted of dot matrices in which the dots formed a pattern based on grouping by similarity. In these trials, the line segments were equal in length (9.1°). Each trial was immediately followed by a mask consisting of a dot matrix in which a random 30% of the dots were black and the rest were white.

Figure 3.1

Stimulus Backgrounds and Time Course of Trial Events



Procedure

Each participant was tested individually in one session lasting approximately one hour. The length of the line discrimination task was approximately 20 minutes, with the rest of the time allocated to preparing and informing the participant for the MRI (i.e., filling out the consent and demographics forms), MRI safety prescreening, ensuring comfort of the participant in the scanner, and acquiring anatomical scans.

Before going into the scanner, participants were given instructions about the line discrimination task. They were told that each trial would begin with a fixation cross, followed by the brief presentation of a dot matrix with two horizontal line segments superimposed on it. Participants were instructed to indicate whether they thought the top or bottom line was longer by making their response using the MRI compatible trackball, where a left click indicated that

the top line was longer and a right click indicated that the bottom line was longer. Participants were asked to take a best guess if they were unsure which line was longer.

Once participants were comfortable with the task instructions, they were given an opportunity to perform 10 random matrix practice trials on a computer outside the scanner to ensure they were able to see the two line segments. Following these practice trials, participants completed the experimental trials in the MRI.

For the experimental trials, each participant completed the task four times (four runs), with each run starting with a 4000 ms grey screen (Figure 3.1). Subsequently, the first trial began with a fixation cross shown for 1000 ms, followed by a trial display for 250 ms, which was immediately replaced by a mask display that remained on the screen for 2750 ms, allowing participants to indicate their response. A jittered intertrial interval (ITI) ranging from 5000 to 7000 ms in intervals of 250 ms with an average of 6000 ms followed, appearing as a grey background, after which the next trial was presented. In each run 36 trials were randomly presented (18 pattern, 18 random). The ITI was jittered to increase variance for blood-oxygen-level dependent (BOLD) deconvolution analysis.

Each run ended with a random matrix trial, and following the last trial of the second run, participants were presented with two surprise questions (direct query and forced choice) regarding the background pattern. For the direct query question, participants were asked, “Did you notice a pattern in the background of dots on any of the preceding trials?” Following the direct query participants were shown two versions of the Ponzo illusion (converging lines towards the top of the screen and converging lines towards the bottom of the screen) and asked to indicate the pattern they observed, taking a best guess if no pattern was seen. Participants were always shown the illusion with the lines converging towards the top of the screen so they could be queried about the background over the whole block of trials rather than only the last pattern trial preceding the direct query and forced choice questions. These questions served the purpose of examining whether participants were viewing the stimuli without attending the background. Trials from these first two runs were classified together as the inattention condition. Following these two questions, participants were asked to complete two more runs of the same task but were instructed to also observe the background pattern while carrying out the line discrimination task. After the last pattern matrix trial of the final run, participants were once again asked the same two questions. Consistent with previous research (Moore & Egeth, 1997),

participants were able to see and identify the background pattern, indicating that participants were completing the task under divided-attention. As such, trials from these last two runs were classified together as the divided-attention condition.

fMRI Image Acquisition

Imaging was performed on a 3 Tesla Philips Achieva MRI scanner (Philips, Best, Netherlands) equipped with an eight-channel Sensitivity Encoding (SENSE) head coil (Philips, Best, Netherlands). Participants were positioned in a supine position on the scanner bed with their right index and middle fingers positioned on the appropriate response buttons of a response box. Stimuli were back projected onto a screen mounted at the rear end of the scanner and participants viewed the display via a mirror attached on the head coil. To minimize head motion, the head was fitted with memory foam cushions. Whole-brain functional images were acquired using a T2*-weighted single-shot two-dimensional gradient echo, echo planar imaging pulse sequence (179 volumes, 30 slices, slice thickness = 4 mm, FOV = 240 x 240 mm², voxel size = 3.75 x 3.75 x 4.0 mm³, TR/TE = 2000/30 ms, flip angle = 90°) while participants performed the task. The fMRI scans were repeated four times (one for each run of the task). After functional imaging, structural data were acquired for each participant using a T1-weighted MPRAGE sequence for detailed reconstruction of anatomy with isotropic voxels (1.00 mm x 1.00 mm x 1.00 mm) in a 256 mm² field of view (256 x 256 matrix, 160 slices, TR = 8.1 ms, TE = 3.7 ms).

fMRI Data Preprocessing

Brain image preprocessing and statistical analyses were performed using BrainVoyager 2.8 (Brain Innovation, Maastricht, The Netherlands; (Goebel, Esposito, & Formisano, 2006)). The first two volumes of each fMRI scan were discarded to allow the MRI signal to reach a steady state. Images from each functional run were slice time corrected, motion corrected, and then temporally high-pass filtered using a general linear model with Fourier basis set to remove low frequency noise in the functional time series. All anatomical images were interpolated into 1 mm isotropic voxels and corrected for inhomogeneity, and then co-registered to the mean functional image and transformed into the standardized Talairach and Tournoux atlas space using an AC/PC transform (Talairach & Tournoux, 1988). These images were then spatially smoothed with a Gaussian kernel with a full width half maximum (FWHM) of 6 mm and the 6 motion predictors from each functional run were z-transformed and added into the general linear model as predictors.

Behavioral Data Analysis

In this study, perceptual grouping abilities under conditions of inattention (runs 1 & 2) and divided-attention (runs 3 & 4) were examined by assessing participants' susceptibility to the Ponzo illusion in the perceptual grouping task. Random and pattern matrix trials were analyzed separately in each attentional condition by first calculating the percentage of correct responses for each participant across the trials in each condition and then averaging these results across all participants to obtain the mean percentage of correct responses for each trial type in each attentional condition. The random matrix trials served to ensure that the participants could make perceptual judgments based on line lengths, and a "correct" line judgment was coded when participants chose the longer line in the random matrix trials (i.e., the line that was physically longer) or indicated an illusion-based response in the pattern matrix trials (i.e., chose a physically identical line that was consistent with the illusory percept). Perceptual grouping abilities were assessed by comparing illusion susceptibility to a chance level (50%) for the pattern matrix condition. Similarly, line discrimination abilities were assessed by comparing accuracy in the random matrix trials (i.e., the percentage of trials in which participants successfully chose the longer of the two lines) to a chance level (50%). All analyses were carried out using $\alpha = .05$.

GLM First-level Analysis

Data were analyzed for each subject using the general linear model (GLM). A contrast was applied to examine regions of statistically greater activation for the pattern matrix condition in comparison to the random matrix condition. The random matrix condition included all of the components of the pattern matrix condition except for the requirement of grouping the black dots together to perceive the illusion. Thus, the subtraction of the random matrix condition from the pattern matrix condition should reveal areas actively involved with perceptual grouping. Statistical analysis at the first level involved generating within-subject parametric activation maps for this contrast in both inattention and divided-attention conditions and modeling stimulus onsets using the hemodynamic response function.

GLM Group Analysis

Random-effects general linear models were performed at the group level to determine regions significantly activated in association with perceptual grouping in both inattention and divided-attention conditions. Group-wise statistical maps were determined using the random-effects general linear model and cluster threshold estimation was calculated for each cluster of

voxels ($p_{uncorr} < .01$) to correct for multiple comparisons and eliminate false positives. This correction method incorporates the observation that neighboring voxels activate in clusters and calculates the likelihood of obtaining different cluster sizes (Forman et al., 1995). Main effects were calculated first by contrasting pattern matrix trials with random matrix trials across both attentional conditions (Grouping type), as well as contrasting pattern and random matrix trials in the inattention condition with pattern and random matrix trials in the divided-attention condition (Attentional type). The interaction was also examined to test whether any brain regions related to perceptual grouping were activated specifically in each attentional condition. Finally, simple effects analyses involved two separate ANOVAs contrasting pattern to random matrix trials for each attentional condition, as well as a 2 (Trial Type: Pattern, Random) x 2 (Attentional Condition: Inattention, Divided-Attention) ANOVA to determine how much activation in response to pattern compared to random matrix trials differed between attentional conditions. Significant areas of activation in each condition were localized using the Talairach atlas.

Results

Behavioral Results

In this study, a line discrimination task was performed in which two horizontal lines were superimposed on a background of black and white dots organized so that, on occasion, the black dots induced the Ponzo Illusion if perceptually grouped together. Trials in which the background dots were randomly configured confirmed that participants were able to make perceptual judgments based on the line lengths. A “correct” line judgment was coded when participants chose the longer line in the random matrix trials (i.e., the line that was physically longer) or indicated an illusion-based response in the pattern matrix trials (i.e., chose a physically identical line that was consistent with the illusory percept). Perceptual grouping abilities were examined both under conditions of inattention (i.e., before participants were aware of the illusion inducing elements in the background) and under conditions of divided-attention (i.e., when participants had their attention directed to both the background elements and the line judgment task).

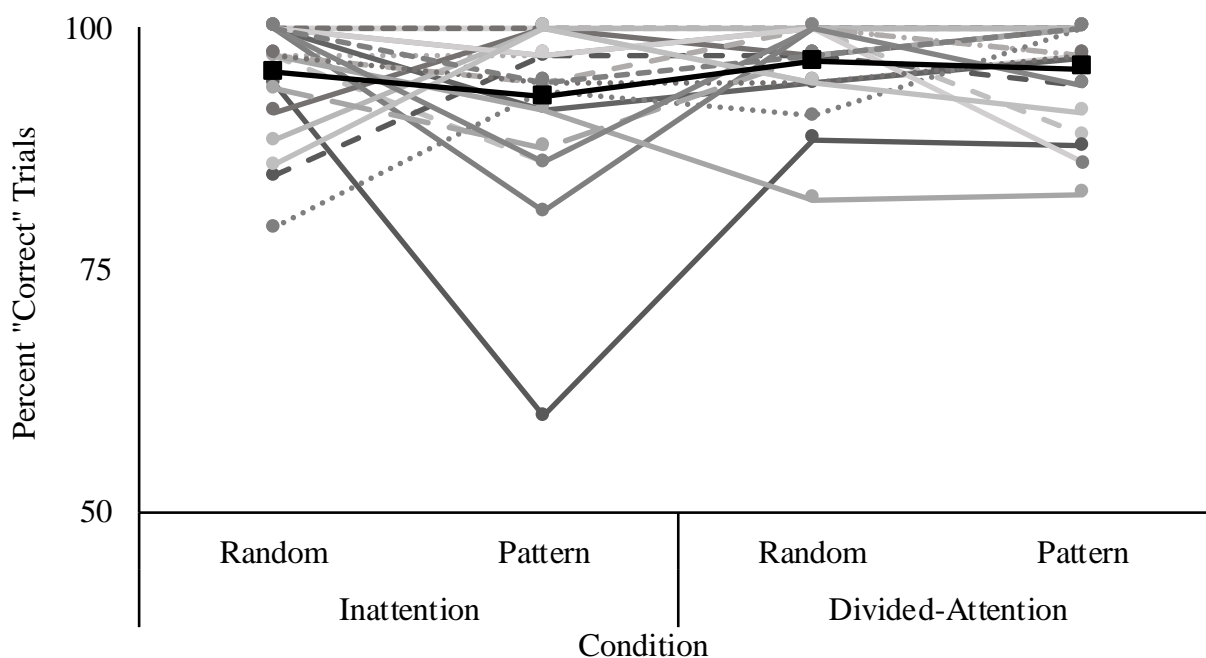
Participants showed high accuracy in line discrimination ability in the random matrix trials in both inattention and divided-attention conditions (Figure 3.2), identifying the longer line segment on 95.6% ($\pm 6.02\%$) of the trials in the inattention condition and 96.48% ($\pm 4.59\%$) of the trials in the divided-attention condition, both of which differed significantly from a 50% chance result, $t(21) = 74.074$, $p < .001$, Cohen’s $d = 2.93$ and $t(21) = 98.021$, $p < .001$, Cohen’s d

= 8.74, respectively (Values of the form $x \pm y$ refer to a 95% confidence interval of y , surrounding a mean of x). The results from the pattern matrix trials were consistent with previous research (Moore & Egeth, 1997; Carther-Krone et al., 2016), showing that participants were influenced by the background pattern in both inattention and divided-attention conditions, reporting the line toward the converging end of the patterned lines on 90.21% ($\pm 15.31\%$) of the trials in the inattention condition and 95.57% ($\pm 5.27\%$) of the trials in the divided-attention condition, both of which differed significantly from a 50% chance result, $t(21) = 27.479$, $p < .001$, Cohen's $d = 1.72$ and $t(21) = 84.591$, $p < .001$, Cohen's $d = 8.59$, respectively.

Furthermore, a 2 (Attentional Condition: Inattention, Divided-Attention) \times 2 (Trial Type: Pattern, Random) repeated measures ANOVA revealed that there were no significant main effects of attentional condition, $F = 4.14$, $p = .06$, trial type, $F = 2.404$, $p = .136$, or interaction between the two, $F = 1.494$, $p = .235$. Taken together, these findings demonstrate that participants were able to complete the line judgment task with high accuracy regardless of trial type or attentional condition. Thus, it is highly unlikely that any brain activations in response to perceptual grouping in either attention condition is due to differences in performing the grouping task.

Direct Query and Forced Choice Results

For the direct query, 50% of the participants (11 out of 22 participants) reported noticing a pattern after the inattention trials. However, over 80% of participants (18 out of 22 participants) reported seeing the pattern after the divided-attention trials. In the forced choice measure, of the participants who reported seeing the pattern after the inattention trials, 55% of them (6 out of 11 participants) were able to accurately identify the pattern, which did not differ significantly from a chance finding, $t(10) = .289$, $p = .779$. Of the total sample, 36% of participants (8 out of 22 participants) were able to accurately identify the pattern, which also did not differ significantly from a chance finding, $t(21) = -1.299$, $p = .208$. Of the participants who reported seeing the pattern after the divided-attention trials, all of them were able to accurately identify the pattern. There were four participants who reported not being able to see the pattern in response to the direct query question following the divided-attention trials, however, of these four participants, three of them were still able to correctly identify the pattern.

Figure 3.2*Behavioral Results of the Perceptual Grouping Task*

Note. The percent “correct” trials indicate the percentage of trials that each participant correctly chose the longer line in the random matrix trials (i.e., the line that was physically longer) and the percentage of trials that each participant indicated an illusion-based response in the pattern matrix trials (i.e., chose a physically identical line that was consistent with the illusory percept). Each line represents one participant’s data ($N = 22$), and due to the distributional characteristics of the data being very similar amongst most participants some of the lines overlap. Participants showed high accuracy in their ability to complete the behavioral task, further emphasized by the mean for each condition (represented by the black square).

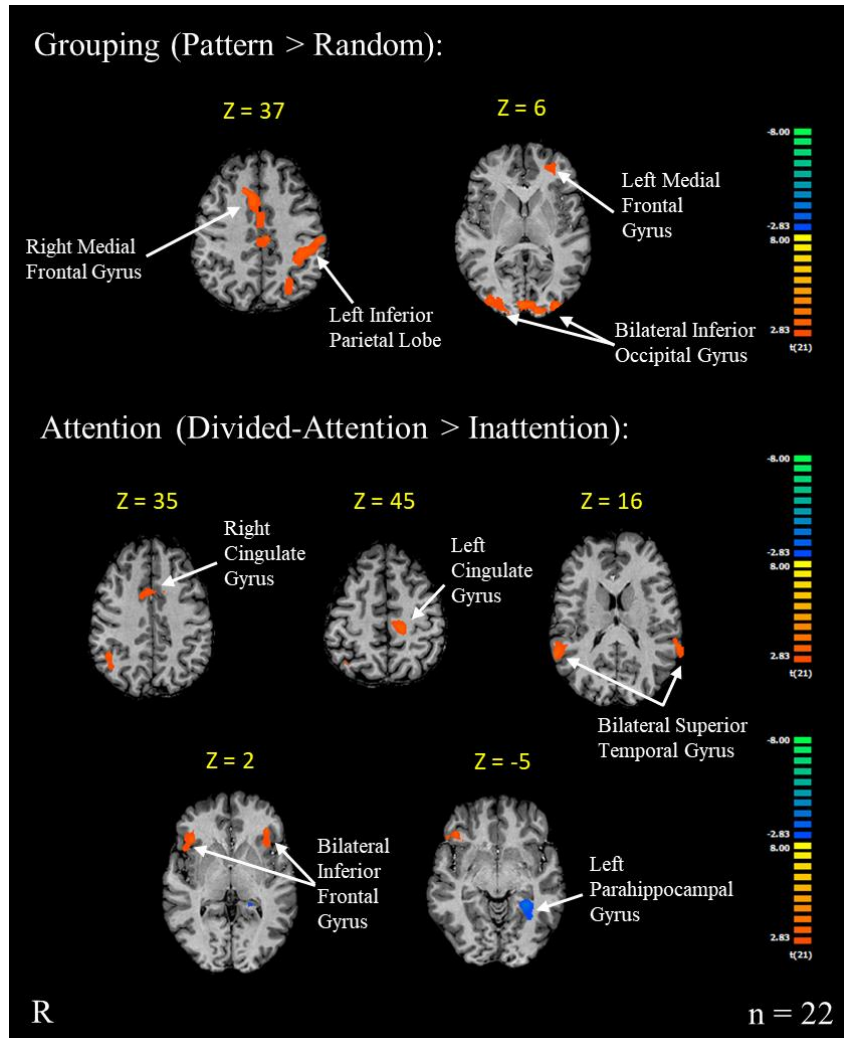
Correlation between Forced Choice Responses and Illusion Susceptibility

For all participants, a point-biserial correlation was calculated between the accuracy of the forced-choice response (0 = incorrect; 1 = correct) and the percentage of pattern matrix trials in which a response consistent with the illusion was reported (i.e., reporting the line at the converging end of the illusion as longer) for both inattention and divided-attention trials. A significant positive correlation would suggest that a high percentage of illusion-based responses

may have been due to those participants who happened to notice the pattern on the illusion-based trials. The results showed that the correlation did not differ significantly from zero for both inattention, $r = .163$, $p = .403$, and divided-attention, $r = -.188$, $p = .403$, trials. A second point-biserial correlation was also calculated between the accuracy of the direct query response and the percentage of pattern matrix trials in which a response consistent with the illusion was reported for both inattention and divided-attention trials. Again, the correlation did not differ significantly from zero for both inattention, $r = -.302$, $p = .172$, and divided-attention, $r = -.144$, $p = .524$, trials. Together, these results suggest that the high percentage of illusion susceptibility was not due to those participants who happened to notice the pattern during the inattention trials, which is further verified by a similar non-significant correlation in the divided-attention trials.

fMRI Results

A whole-brain analysis examining the brain regions involved in perceptual grouping was performed by testing the main effects of grouping and attention as well as the interaction between the two variables, using follow up post-hoc analyses of the simple effects to determine when attention influences grouping. First, pattern matrix trials were contrasted with random matrix trials (pattern > random) across both attentional conditions (Grouping Type). Activation in response to pattern matrix trials was found within the inferior gyrus of the left occipital lobe, middle frontal gyrus of the left frontal lobe, inferior region of the left parietal lobe and cingulate gyrus of the right limbic lobe (Figure 3.3). Next, pattern and random matrix trials in the inattention condition were contrasted with pattern and random matrix trials in the divided-attention condition (Attentional Type). Activation specific to pattern and random matrix trials in the inattention condition was found in the parahippocampal gyrus of the left limbic lobe, while activation specific to these trials in the divided-attention condition was found bilaterally in the superior temporal gyrus, inferior frontal gyrus of the frontal lobe, and cingulate gyrus of the limbic lobe (Figure 3.3).

Figure 3.3*Main Effects Analysis*

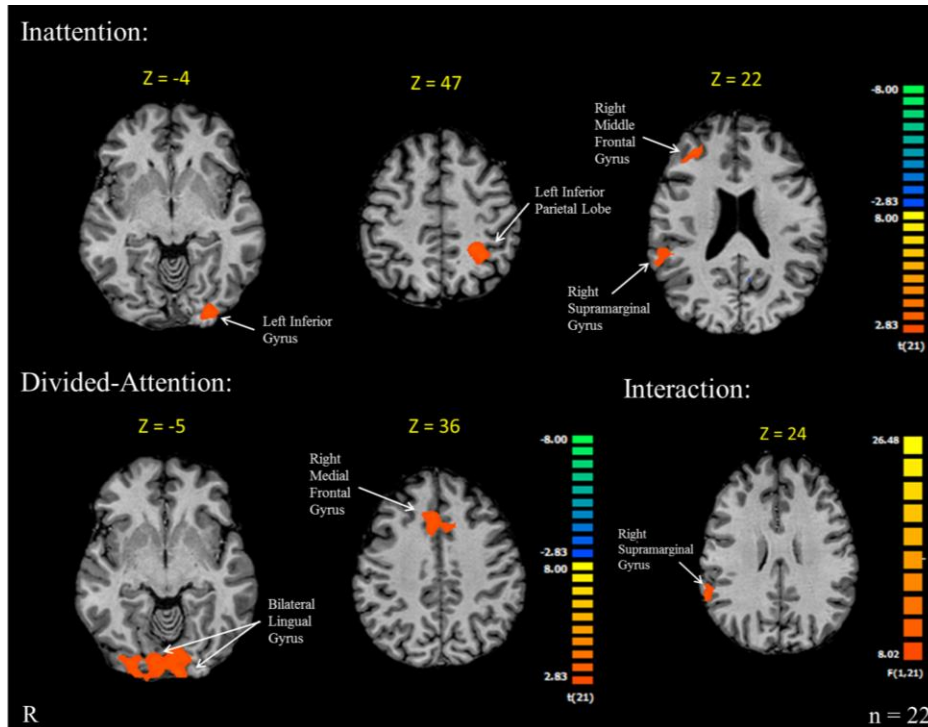
Note. Images presented in radiological orientation. Whole brain axial slices of the average activation from all participants ($n = 22$) are shown. Multiple comparisons were corrected using cluster threshold estimation ($p_{uncorr} = .01$). Activations in the grouping condition are the result of contrasting pattern (+) trials with random (-) trials across both attention conditions. Activations in the attention condition are the result of contrasting pattern and random matrix trials in the divided-attention (+) condition with pattern and random matrix trials in the inattention (-) condition. In testing the main effect of attention, orange activations represent stronger activation in the divided-attention trials, while blue activations represent stronger activation in the inattention trials.

Following tests of the main effects, the interaction between grouping and attention was examined in order to test whether any brain regions related to perceptual grouping were activated specifically in each attentional condition. A 2 (Trial Type: Random, Pattern) x 2 (Attentional Condition: Inattention, Divided-Attention) ANOVA revealed a significant interaction in the supramarginal gyrus of the right parietal lobe, $F(1,21) = 12.689$, $p = .002$ (Figure 3.4). Post-hoc comparisons involving the beta values (Figure 3.5) revealed significantly stronger activation for pattern matrix trials in the inattention compared to divided-attention conditions, $p = .021$.

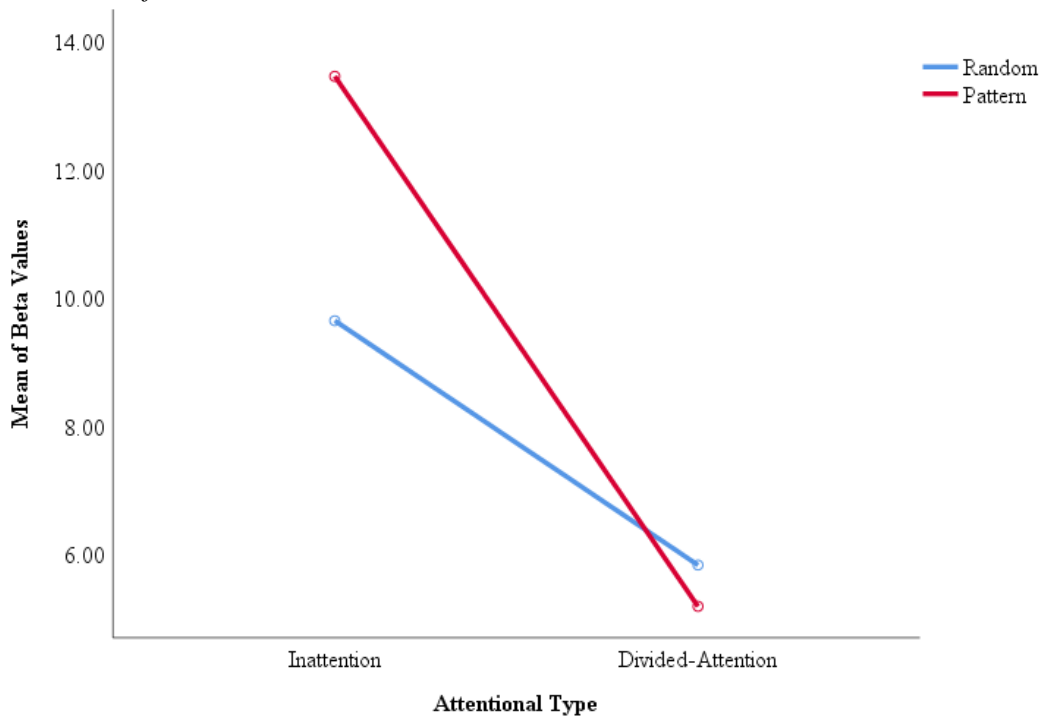
Finally, a simple effects analysis was performed involving two separate 2 (Grouping Type: Pattern, Random) x 2 (Attentional Condition: Inattention, Divided-Attention) ANOVAs contrasting pattern to random matrix trials for each attentional condition. Activation in response to perceptual grouping in the inattention condition revealed activation within the inferior gyrus of the left occipital lobe, middle frontal gyrus of the right frontal lobe, inferior region of the left parietal lobe and supramarginal gyrus of the right parietal lobe. Activation in response to perceptual grouping in the divided-attention condition revealed activation in the right medial frontal gyrus and in the lingual gyrus of the occipital cortex bilaterally (Figure 3.4). The peak location and cluster sizes for the main effects, interaction and post-hoc analyses are summarized in Table 3.1. Significant areas of activation in each condition were localized using the Talairach atlas.

Figure 3.4

Interaction and Simple Effects



Note. Images presented in radiological orientation. Whole brain axial slices of the average activation from all participants ($n = 22$) are shown. Multiple comparisons were corrected using cluster threshold estimation ($p_{uncorr} = .01$). Activations are the result of GLM predictor contrast of the random (-) and pattern (+) conditions during perceptual grouping under conditions of inattention, divided-attention and the interaction between trial type (random (-) and pattern (+)) and attentional type (inattention (+), divided-attention (-)).

Figure 3.5*Beta Values from Interaction*

Note. Post-hoc tests from the repeated measures ANOVA performed on the beta values exported from BrainVoyager revealed significantly higher activation for pattern matrix trials compared to random matrix trials in the inattention condition, but not the divided-attention condition.

Table 3.1*Activation Regions for Grouping in Inattention and Divided-Attention Conditions*

Location	Side	Brodmann Area	TAL Coordinates			Voxels (1x1x1 mm)
			x	y	z	
Main Effects:						
Stimulus (Pattern vs. Random)						
Inferior Occipital Gyrus (Occipital Lobe)	L	18	-27	-88	-8	29600
Cingulate gyrus (Limbic Lobe)	R	24	3	-10	31	6202
Inferior Parietal Lobe (Parietal Lobe)	L	40	-39	-31	46	9953
Medial Frontal Gyrus (Frontal Lobe)	L	9	-24	44	10	1794
Attention (Inattention > Divided-Attention)						
Parahippocampal Gyrus (Limbic Lobe)	L	36	-27	-40	-5	1541
Attention (Divided-Attention > Inattention)						
Superior Temporal Gyrus (Temporal Lobe)	R	22	60	-46	19	4450
Inferior Frontal Gyrus (Frontal Lobe)	R	44	48	17	10	3483
Cingulate Gyrus (Limbic Lobe)	R	24	6	8	37	1350
Cingulate Gyrus (Limbic Lobe)	L	31	-15	-25	43	1477
Inferior Frontal Gyrus (Frontal Lobe)	L	45	-36	29	7	1569
Superior Temporal Gyrus (Temporal Lobe)	L	22	-54	-49	10	1627
Interaction:						
Supramarginal Gyrus (Parietal Lobe)	R	40	61	-49	25	587
Simple Effects:						
Inattention Condition:						
Supramarginal Gyrus (Parietal Lobe)	R	40	60	-49	29	1488
Middle Frontal Gyrus (Frontal Lobe)	R	46	39	36	19	1238
Inferior Occipital Gyrus (Occipital Lobe)	L	18	-30	-88	-8	1630
Inferior Parietal Lobe (Parietal Lobe)	L	40	-24	-43	52	2991
Divided-Attention Condition:						
Bilateral Lingual Gyrus (Occipital Lobe)	L/R	17	3	-88	7	20505
Medial Frontal Gyrus (Frontal Lobe)	R	32	6	14	40	2878

Note: The number of voxels refers to the size of the cluster following application of the cluster-level statistical threshold estimator. TAL coordinates refer to the peak voxel (the voxel with the most significant activation).

Discussion

The aim of the present experiment was to explore and further clarify the neural areas affected by perceptual grouping using a line discrimination task that allowed us to directly compare grouping ability under conditions of inattention to grouping ability under conditions of divided-attention. The behavioral data clearly indicated that participants perceived the Ponzo illusion during fMRI scanning: they perceived the horizontal line at the converging end of the illusion as longer than the horizontal line at the diverging end. This effect did not occur when no illusion was presented in the background, and in this case, participants were able to accurately identify the longer of the two different horizontal lines.

Perceptual Grouping and Attention

Our findings revealed activation in the frontal, parietal and occipital regions of the brain in response to grouping in general, consistent with previous research involving perceptual grouping (Ross et al., 2000; Seymour et al., 2008). Furthermore, activation in the bilateral frontal, temporal and cingulate gyrus in response to divided-attention trials compared to inattention trials is consistent with the increased cognitive demands resulting from carrying out the line discrimination task while attending to the background (Herath, Klingberg, Young, Amunts & Roland, 2001; Fink, Halligan, Marshall, Frith, Frackowiak & Dolan, 1996), as well as mechanisms related to encoding and retrieving (Anderson, Iidaka, Cabeza, Kapur, McIntosh & Craik, 2000). Activation in the parahippocampal gyrus in response to inattention trials compared to divided-attention trials may also be involved in mechanisms related to encoding (Kensinger, Clarke & Corkin, 2003). While these results related to perceptual grouping and attention are supported by previous research, this study further extends these findings by providing a direct comparison of perceptual grouping mechanisms under varying levels of attention. Results indicated that the right supramarginal gyrus is involved in perceptual grouping specifically under conditions of inattention. Together, the results of this study replicate previous behavioral studies in which the Ponzo illusion was elicited under conditions of inattention (Moore & Egeth, 1997; Carther-Krone et al., 2016) and extend them to include the underlying neural mechanisms. Given that much of the visual world at any moment is not represented in conscious perception, these findings provide crucial information about how we make sense of visual scenes in the real world.

Grouped vs. Ungrouped Stimuli

When pattern matrix trials were contrasted with random matrix trials across attentional conditions, our analysis revealed activations in the inferior parietal cortex, medial frontal gyrus, inferior occipital gyrus and cingulate gyrus. This is consistent with previous research demonstrating that the early visual cortex (Ross, Grossberg & Mingolla, 2000) as well as inferior parietal cortex and prefrontal cortex (Seymour et al., 2008) are involved in attending to grouped vs. ungrouped stimuli. Neuroimaging studies point to the inferior parietal cortex as an important region underlying perceptual grouping, namely in integrating local features into a global percept, which is supported by studies showing that damage to the inferior parietal cortex leads to difficulties integrating local elements into a global whole (Karnarth et al., 2000; Huberle & Karnarth, 2006). In addition to the inferior parietal cortex, activation was also found in the frontal region of the cortex, which has been commonly implicated with visual processes succeeding local feature integration, such as perceiving and recognizing objects (Logothetis, 1998). Activation in the early visual cortex of the occipital lobe has been shown to be involved in maintaining sensitivity to the contrasts and spatial organization of cues involved in perceptual grouping (Ross, Grossberg & Mingolla, 2000) and is important in extracting bottom-up information required to perceive the grouped stimuli. Finally, activation in the cingulate gyrus has been shown to be involved in encoding and retrieving information (Anderson et al., 2000), which is likely activated in response to instructing participants to recall information about the background in divided-attention conditions. Together these findings demonstrate that the inferior parietal, middle frontal, early occipital and cingulate regions are involved in gestalt perception in general. This is supported by previous research, and provides evidence that grouping mechanisms were successfully activated using our stimulus involving a visual illusion.

Divided-Attention vs. Inattention Conditions

When divided-attention trials were contrasted with inattention trials, our analysis showed activation in the bilateral frontal, temporal and cingulate gyrus. This is consistent with previous research demonstrating that the frontal and temporal regions of the brain are recruited as the cognitive load required to perform a task increases (Johnson & Zatorre, 2006; Herath et al., 2001; Fink et al., 1996), as well as the importance of the cingulate cortex in encoding and retrieving (Anderson et al., 2000). Previous research has shown cingulate and prefrontal cortex activation in response to a linguistic dual task paradigm (Benedict et al., 1998), and prefrontal

activation has been shown to be involved in top-down attentional control (Corbetta & Shulman, 2002). Prior research has also shown that the cingulate cortex is activated in response to increased task difficulty in a working memory task, while the prefrontal cortex responds to increased working memory load (Barch et al., 1997). Since participants in this study had to perform the line discrimination task while attending to the background in the divided-attention condition, activation in the cingulate cortex likely represents an increase in task difficulty compared to the inattention trials, while prefrontal activation likely represents an increase in working memory load and executive functioning (Loose, Kaufmann, Auer, & Lange, 2003).

Increased activation was also found bilaterally in the superior temporal gyrus at the region of the temporoparietal junction (TPJ). While this region has been implicated in detection of salient distractors and cognitive control more generally (Chang et al., 2013; Geng and Mangun, 2011), more specifically this region appears to be robustly activated in response to detecting behaviorally relevant stimuli (Corbetta, Patel & Shulman, 2008; Serences et al., 2005). As a result, the TPJ is a possible brain region responsible for the integration of top-down and bottom-up processes. In the current study, the divided-attention condition required increased cognitive control compared to the inattention condition due to the increased task demands, with participants tasked to detect behaviorally relevant stimuli (i.e., the background patterns) while carrying out the line discrimination task. Although participants were instructed to perform the line discrimination task while attending to the background dot patterns, since these patterns did not occur on every trial it is possible that the random occurrence of these patterns provided enough saliency to capture attention in a bottom-up fashion initially, bringing patterns into awareness for later recollection. This would suggest that TPJ has a role in integrating bottom-up and top-down attentional processes.

When inattention trials were contrasted with divided-attention trials, activation was only found in the left parahippocampal gyrus. While it is unclear how this region may be specifically involved in inattention *per se*, this region has been shown in prior research to be involved in the successful encoding of stimuli in a relatively easy divided-attention task when compared to a more cognitively demanding divided-attention task (Kensinger et al., 2003). While further research is necessary to uncover the extent to which activation in this region is specific to implicit grouping, this activation nonetheless suggests that encoding occurs to some extent, likely involving the horizontal lines to which attention is pointed in the inattention condition.

Brain Activity Related to the Interaction Between Grouping and Attention

Activation in the right supramarginal gyrus of the parietal lobe was characterized by a significant interaction between grouping and attention. Our interpretation of this interaction was guided by a simple effects analysis examining brain regions activated for pattern compared to random matrix trials at each attentional condition separately, demonstrating significant activation of the right supramarginal gyrus for pattern matrix trials compared to random matrix trials in the inattention condition.

While parietal activation was found generally in response to grouped stimuli, the distinct region activated in response to inattention suggests the importance of this region in perceptual grouping even before attentional mechanisms are recruited. The region of the supramarginal gyrus is located in the inferior parietal cortex, which has been established as important in forming object representations, a process important in grouping perceptual information together. Since inattention trials required participants to indicate the longer of the two horizontal lines while implicitly grouping the background stimuli together to form the illusion, and divided-attention trials required participants to indicate the longer of the two lines while explicitly attending to the background stimuli, this would suggest that activation in the parietal lobe in the inattention condition is involved in implicitly grouping the black dots together to form the illusory percept. This is supported by previous research showing differing activation in the inferior parietal lobe in response to grouped shapes compared to ungrouped shapes when observers report being unaware of the groupings (Xu & Chun, 2007).

While activation in the inferior parietal lobe in response to perceptual grouping and the ability to group visual information under conditions of inattention has been previously and well established as separate entities, the importance of this finding is that it shows the inferior parietal lobe as a region responsible for perceptual grouping even when participants are not able to explicitly report on the grouped information. Prior studies tend to focus on low-level brain regions such as the early visual cortex as areas implicated in implicit grouping, and findings from this study suggest that processing in higher regions are modulating grouping effects even when attention is not specifically directed at them.

Possible Limitations

A possible concern that should be acknowledged in the divided-attention runs is the difference in instructions for this study compared to similar studies that have used this paradigm

in the past. While previous studies of inattention probe participants about the irrelevant background stimuli and then ask them to continue performing the same task again, with the assumption being that drawing their attention to the background will lead to a division of attention from that point forward, in this study we explicitly asked participants to attend to the irrelevant stimuli while performing the discrimination trials after we had probed them about the background following the inattention trials. This difference in task instruction may result in a limitation of the generalizability of results in the divided-attention runs, but was modified in order to ensure that participants were really motivated to divide their attention. Another modification of this study from prior similar studies is the presentation of the background illusion with the lines always converging towards the top of the screen, which allowed us to query participants about the background over the whole block of trials as opposed to a single trial. While it is possible that this may have introduced a response bias, a prior version of this experiment (Carther-Krone, Shomstein, Marotta, 2016) where participants were shown the illusion with the lines converging towards the top and bottom of the screen showed that participants accurately identified the perceived longer line as that at the converging end, whether the lines converged towards the top or bottom of the screen, supporting our claim that participants are in fact influenced by the Ponzo illusion.

In referring to the divided-attention condition, it should also be acknowledged that while increased task demands are most likely driving activation found in the frontal lobe, the manipulation of the attentional condition may be confounded by eye movements. Since participants are instructed to attend to the background as well as the horizontal lines, increased eye movement may be more likely in the divided-attention condition, which may also explain the frontal activation in this attentional condition. Future research involving eye tracking is suggested to remove eye movement as a potential confound in these types of studies.

A final concern involves the inclusion of all participants in our study. Of the 22 participants in this study, 11 participants noted seeing the pattern when probed following the inattention trials. However, of these 11 participants only 6 were able to accurately identify the pattern. Since consciously perceiving the pattern based on awareness measures involves explicitly stating the pattern was seen as well as accurately identifying it, our sample included 6 participants who fit this criterion. While removing these participants may be viewed as the optimal solution to ensuring a more representative “inattention” condition, we would argue that

this is not the case since exclusion procedures suffer from regression-to-the-mean effects (Shanks, 2017). As such we have chosen to include all the participants in our analysis to avoid this statistical error, as well as to strengthen the power of our sample. However, during publication at the request of one of the reviewers we also ran the analysis with the exclusion of those participants who reported seeing the pattern at the query stage and found similar results¹. Namely, many of the regions of interest discussed in this study were the same whether or not all participants were included. As such, we have full confidence that our findings represent the question asked in this study.

Conclusion

In summary, the present findings suggest that the right supramarginal gyrus is an important region for implicit perceptual grouping. While previous research has demonstrated this region to be responsible for object representation, most research has focused on grouping under conditions of divided-attention or selective-attention, often using multiple sensory modalities to support their claims. Of the research that examines grouping under conditions of inattention, findings tend to be limited to low-level brain regions, demonstrating involvement of early visual cortex in grouping information when attentional processes are limited. Here we not only examined perceptual grouping under two varying conditions of attention, but we provided a direct comparison between regions activated in response to grouped vs. ungrouped stimuli in each attentional condition. Our findings converge with previous studies showing similar regions of activation for both perceptual grouping and divided-attention in general, emphasizing that the stimuli used in our study was able to replicate previous findings. This provided the support required to perform the direct comparison, which indicated the importance of the right supramarginal gyrus in grouping under conditions of inattention. This demonstrates that even under conditions of inattention, more complex visual processing is occurring. Future research involving multiple types of Gestalt processing under varying conditions of attention will serve to strengthen this finding. However, our current findings clearly demonstrate that visual information below the level of explicit awareness can influence perception of the visual world, and that the neural mechanisms driving perception are modulated by attentional allocation.

¹ Analysis of only the participants who were able to consciously perceive the pattern based on awareness measures following the inattention block (N = 16) showed similar activations to those in Table 3.1. Activation was no longer found in the left frontal, temporal and bilateral cingulate gyrus for inattention vs. divided-attention trials or right frontal gyrus for perceptual grouping in inattention trials.

References

- Anderson, N. D., Idaka, T., Cabeza, R., Kapur, S., McIntosh, A. R., & Craik, F. I. (2000). The effects of divided attention on encoding-and retrieval-related brain activity: A PET study of younger and older adults. *Journal of cognitive neuroscience*, *12*(5), 775-792.
- Barch, D. M., Braver, T. S., Nystrom, L. E., Forman, S. D., Noll, D. C., & Cohen, J. D. (1997). Dissociating working memory from task difficulty in human prefrontal cortex. *Neuropsychologia*, *35*(10), 1373-1380.
- Benedict, R. H., Lockwood, A. H., Shucard, J. L., Shucard, D. W., Wack, D., & Murphy, B. W. (1998). Functional neuroimaging of attention in the auditory modality. *Neuroreport*, *9*(1), 121-126.
- Carther-Krone, T. A., Shomstein, S., & Marotta, J. J. (2016). Looking without perceiving: Impaired preattentive perceptual grouping in Autism Spectrum Disorder. *PLoS One*, *11*(6), e0158566. <https://doi.org/10.1371/journal.pone.0158566>
- Chang, C. F., Hsu, T. Y., Tseng, P., Liang, W. K., Tzeng, O. J., Hung, D. L., & Juan, C. H. (2013). Right temporoparietal junction and attentional reorienting. *Human Brain Mapping*, *34*(4), 869-877.
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature reviews neuroscience*, *3*(3), 201.
- Corbetta, M., Patel, G., & Shulman, G. L. (2008). The reorienting system of the human brain: from environment to theory of mind. *Neuron*, *58*(3), 306-324.
- Driver, J., Davis, G., Russell, C., Turatto, M., & Freeman, E. (2001). Segmentation, attention and phenomenal visual objects. *Cognition*, *80*(1-2), 61-95. [https://doi.org/10.1016/S0010-0277\(00\)00151-7](https://doi.org/10.1016/S0010-0277(00)00151-7)
- Fink, G. R., Halligan, P. W., Marshall, J. C., Frith, C. D., Frackowiak, R. S. J., & Dolan, R. J. (1996). Where in the brain does visual attention select the forest and the trees?. *Nature*, *382*(6592), 626.
- Forman, S. D., Cohen, J. D., Fitzgerald, M., Eddy, W. F., Mintun, M. A., & Noll, D. C. (1995). Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): Use of a cluster-size threshold. *Magn Reson Med.*, *33*(5), 636-47. <https://doi.org/10.1002/mrm.1910330508>

- Geng, J. J., & Mangun, G. R. (2011). Right temporoparietal junction activation by a salient contextual cue facilitates target discrimination. *Neuroimage*, *54*(1), 594-601.
- Goebel, R., Esposito, F., & Formisano, E. (2006). Analysis of functional image analysis contest (FIAC) data with brainvoyager QX: From single-subject to cortically aligned group general linear model analysis and self-organizing group independent component analysis. *Hum Brain Mapp.*, *27*(5), 392-401. <https://doi.org/10.1002/hbm.20249>
- Han, S., Jiang, Y., Mao, L., Humphreys, G. W., & Gu, H. (2005). Attentional modulation of perceptual grouping in human visual cortex: Functional MRI studies. *Hum Brain Mapp.*, *25*(4), 424-32. <https://doi.org/10.1002/hbm.20119>
- Han, S., Jiang, Y., Mao, L., Humphreys, G. W., & Qin, J. (2005). Attentional modulation of perceptual grouping in human visual cortex: ERP studies. *Hum Brain Mapp.*, *26*(3), 199-209. <https://doi.org/10.1002/hbm.20157>
- Han, S., Song, Y., Ding, Y., Yund, E. W., & Woods, D. L. (2001). Neural substrates for visual perceptual grouping in humans. *Psychophysiology*, *38*(6), 926-35. <https://doi.org/10.1111/1469-8986.3860926>
- He, D., Mo, C., Wang, Y., & Fang, F. (2015). Position shifts of fMRI-based population receptive fields in human visual cortex induced by Ponzo illusion. *Exp Brain Res.*, *233*(12), 3535-41. <https://doi.org/10.1007/s00221-015-4425-3>
- Herath, P., Klingberg, T., Young, J., Amunts, K., & Roland, P. (2001). Neural correlates of dual task interference can be dissociated from those of divided attention: an fMRI study. *Cerebral cortex*, *11*(9), 796-805.
- Huberle, E., & Karnath, H. O. (2006). Global shape recognition is modulated by the spatial distance of local elements--evidence from simultanagnosia. *Neuropsychologia*, *44*(6), 905-11. <https://doi.org/10.1016/j.neuropsychologia.2005.08.013>
- Johnson, J. A., & Zatorre, R. J. (2006). Neural substrates for dividing and focusing attention between simultaneous auditory and visual events. *Neuroimage*, *31*(4), 1673-1681.
- Karnath, H., Ferber, S., Rorden, C., & Driver, J. (2000). The fate of global information in dorsal simultanagnosia. *Neurocase*, *6*, 295-306. <https://doi.org/10.1080/13554790008402778>
- Kastner, S., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1998). Mechanisms of directed attention in the human extrastriate cortex as revealed by functional MRI. *Science*, *282*(5386), 108-11. <https://doi.org/10.1126/science.282.5386.108>

- Kensinger, E. A., Clarke, R. J., & Corkin, S. (2003). What neural correlates underline successful encoding and retrieval? A functional magnetic resonance imaging study using a divided attention paradigm. *Journal of Neuroscience*, *23*(6), 2407-2415.
- Kimchi, R., & Peterson, M. A. (2008). Fig-ground segmentation can occur without attention. *Psychol Sci*, *19*(7), 660-8. <https://doi.org/10.1111/j.1467-9280.2008.02140.x>
- Kimchi, R., & Razpurker-Apfeld, I. (2004). Perceptual grouping and attention: Not all groupings are equal. *Psychon Bull Rev*, *11*(4), 687-96. <https://doi.org/10.3758/BF03196621>
- Kok, P., Bains, L. J., van Mourik, T., Norris, D. G., & de Lange, F. P. (2016). Selective activation of the deep layers of the human primary visual cortex by top-down feedback. *Curr Biol.*, *26*(3), 371-6. <https://doi.org/10.1016/j.cub.2015.12.038>
- Lamy, D., Segal, H., & Ruderman, L. (2006). Grouping does not require attention. *Percept Psychophys*, *68*(1), 17-31. <https://doi.org/10.3758/BF03193652>
- Lo, S. Y., & Yeh, S. L. (2011). Independence between implicit and explicit processing as revealed by the Simon effect. *Conscious Cogn.*, *20*(3), 523-33. <https://doi.org/10.1016/j.concog.2010.11.007>
- Logethetis, N. (1998). Object vision and visual awareness. *Current opinion in neurobiology*, *8*(4), 536-544.
- Loose, R., Kaufmann, C., Auer, D. P., & Lange, K. W. (2003). Human prefrontal and sensory cortical activity during divided attention tasks. *Human brain mapping*, *18*(4), 249-259.
- Mikellidou, K., Gouws, A. D., Clawson, H., Thompson, P., Morland, A. B., & Keefe, B. D. (2016). An orientation dependent size illusion is underpinned by processing in the extrastriate visual area, LO1. *Iperception*, *7*(5), 2041669516667628. <https://doi.org/10.1177/2041669516667628>
- Moore, C. M., & Egeth, H. (1997). Perception without attention: Evidence of grouping under conditions of inattention. *J Exp Psychol Hum Percept Perform*, *23*(2), 339-52. <https://doi.org/10.1037/0096-1523.23.2.339>
- Müller, D., Winkler, I., Roeber, U., Schaffer, S., Czigler, I., & Schröger, E. (2010). Visual object representations can be formed outside the focus of voluntary attention: Evidence from event-related brain potentials. *J Cogn Neurosci.*, *22*(6), 1179-88. <https://doi.org/10.1162/jocn.2009.21271>

- Ponzo, M. (1910). Intorno ad alcune illusioni nel campo delle sensazioni tattili, sull'illusione di Aristotele efenomeni analoghi [On some tactile illusions, Aristotle's illusion, and similar phenomena]. *Archiv für die Gesamte Psychologie.*, 16, 307-45.
- Prieto, A., Mayas, J., & Ballesteros, S. (2014). Time course of grouping by proximity and similarity in a haptic speeded orientation task. *LNCS, Haptics: Neuroscience, Devices, Modeling, and Applications*, 8618(PartI), 379-385. https://doi.org/10.1007/978-3-662-44193-0_47
- Reynolds, J. H., Chelazzi, L., & Desimone, R. (1999). Competitive mechanisms subserve attention in macaque areas V2 and V4. *J Neurosci.*, 19(5), 1736-53. <https://doi.org/10.1523/JNEUROSCI.19-05-01736.1999>
- Ross, W. D., Grossberg, S., & Mingolla, E. (2000). Visual cortical mechanisms of perceptual grouping: Interacting layers, networks, columns, and maps. *Neural Netw.*, 13(6), 571-88. [https://doi.org/10.1016/S0893-6080\(00\)00040-X](https://doi.org/10.1016/S0893-6080(00)00040-X)
- Russell, C., & Driver, J. (2005). New indirect measures of "inattentive" visual grouping in a change-detection task. *Percept Psychophys*, 67(4), 606-23. <https://doi.org/10.3758/BF03193518>
- Salo, E., Salmela, V., Salmi, J., Numminen, J., & Alho, K. (2017). Brain activity associated with selective attention, divided attention and distraction. *Brain Res.*, 1664, 25-36. <https://doi.org/10.1016/j.brainres.2017.03.021>
- Santangelo, V., Fagioli, S., & Macaluso, E. (2010). The costs of monitoring simultaneously two sensory modalities decrease when dividing attention in space. *Neuroimage*, 49(3), 2717-27. <https://doi.org/10.1016/j.neuroimage.2009.10.061>
- Selles, R. W., Michielsen, M. E., Bussmann, J. B., Stam, H. J., Hurkmans, H. L., Heijnen, I., ... Ribbers, G. M. (2014). Effects of a mirror-induced visual illusion on a reaching task in stroke patients: Implications for mirror therapy training. *Neurorehabil Neural Repair*, 28(7), 652-9. <https://doi.org/10.1177/1545968314521005>
- Serences, J. T., Shomstein, S., Leber, A. B., Golay, X., Egeth, H. E., & Yantis, S. (2005). Coordination of voluntary and stimulus-driven attentional control in human cortex. *Psychological science*, 16(2), 114-122.

- Seymour, K., Karnath, H. O., & Himmelbach, M. (2008). Perceptual grouping in the human brain: Common processing of different cues. *Neuroreport*, *19*(18), 1769-72. <https://doi.org/10.1097/WNR.0b013e328318ed82>
- Shanks, D. R. (2017). Regressive research: The pitfalls of post hoc data selection in the study of unconscious mental processes. *Psychonomic Bulletin & Review*, *24*(3), 752-775.
- Shomstein, S., Kimchi, R., Hammer, M., & Behrmann, M. (2010). Perceptual grouping operates independently of attentional selection: Evidence from hemispatial neglect. *Atten Percept Psychophys*, *72*(3), 607-18. <https://doi.org/10.3758/APP.72.3.607>
- Talairach, J., & Tournoux, P. (1988). Co-planar stereotaxic atlas of the human brain. New York: Thieme.
- Vidal, J. R., Chaumon, M., O'Regan, J. K., & Tallon-Baudry, C. (2006). Visual grouping and the focusing of attention induce gamma-band oscillations at different frequencies in human magnetoencephalogram signals. *J Cogn Neurosci.*, *18*(11), 1850-62. <https://doi.org/10.1162/jocn.2006.18.11.1850>
- Vuilleumier, P., & Landis, T. (1998). Illusory contours and spatial neglect. *Neuroreport*, *9*(11), 2481-4. <https://doi.org/10.1097/00001756-199808030-00010>
- Vuilleumier, P., Valenza, N., & Landis, T. (2001). Explicit and implicit perception of illusory contours in unilateral spatial neglect: Behavioural and anatomical correlates of preattentive grouping mechanisms. *Neuropsychologia*, *39*(6), 597-610. [https://doi.org/10.1016/S0028-3932\(00\)00148-2](https://doi.org/10.1016/S0028-3932(00)00148-2)
- Wertheimer, M. (1923). Untersuchungen zur Lehre von der Gestalt II. *Psychologische Forschung*, *4*, 301-50. <https://doi.org/10.1007/BF00410640>
- Xu, Y., & Chun, M. M. (2007). Visual grouping in human parietal cortex. *Proc Natl Acad Sci U S A.*, *104*(47), 18766-71. <https://doi.org/10.1073/pnas.0705618104>

CHAPTER IV: PERCEPTION AND VISUAL FEEDBACK

Study 3: The Influence of the Sander Parallelogram Illusion and Early, Middle and Late Vision on Goal-Directed Reaching and Grasping

Over the last couple of decades there has been considerable controversy regarding how the visual system uses incoming visual information to complete various perceptual and motor tasks. Arguably the most influential position has been Milner and Goodale's Two Visual Systems Hypothesis (TVSH), which suggests a dissociation between 'vision-for-action' and 'vision-for-perception' (Goodale and Milner 1992; Milner and Goodale 1995). The basis of the TVSH is that perceptual judgments are associated with a ventral visual pathway that travels from the primary visual cortex to the inferior temporal region of the brain, while goal-directed action movements rely on a dorsal visual pathway originating in the primary visual cortex and extending to the superior parietal area of the brain. Although much of the support for the TVSH comes from animal studies and clinical studies of humans with brain deficits (Milner and Goodale 1995), studies using visual illusions such as the Ebbinghaus and Müller-Lyer illusions have also been used to investigate this dissociation in intact humans.

Since the seminal work of Aglioti, DeSouza and Goodale (1995), in which they showed that grip apertures were relatively immune to the effects of the Ebbinghaus Illusion, some of the most informative and controversial evidence for the TVSH has come to light from studies involving visual illusions. Studies supporting the TVSH have shown that perceptual judgements are affected by the visual context associated with the illusory configurations, while goal-directed action movements tend to be immune to these perceptual biases. Typically, a grasping or aiming movement towards a target presented in the context of a visual illusion where full vision is available throughout the entirety of the movement will show that grasping and aiming movements are unaffected or less affected by the illusion compared to perceptual judgements about the same stimuli (eg. Bridgeman, Kirch, and Spearling 1981; Mack, Heuer, Villardi, and Chambers 1985; Aglioti, DeSouza, and Goodale 1995; Brenner and Smeets 1996; Daprati and Gentilucci 1997; Gentilucci, Chieffi, Daprati, Saetti, and Toni 1996; Haffenden and Goodale 1998). This notion that the ventral stream is affected by illusory visual context while the dorsal stream remains immune is thought to rely on the way each of the streams code visual-spatial information. Specifically, the ventral stream is involved with the allocentric coding of space, incorporating visual information about the target's relationship to its surroundings, while the

dorsal stream is involved with the egocentric coding of space, relying on a body-based frame of reference (Haffenden and Goodale 1998).

However, other studies have shown that actions are not immune to illusory context. When vision is withdrawn before movement onset, the outcome reflects the perceptual bias of the illusion, showing shorter aiming movements in pointing studies (Elliott and Lee, 1995) and peak grip apertures consistent with the perceived size of the illusion in reaching and grasping studies (Bruno and Franz 2009; Franz, Hesse, and Kollath 2009; Westwood & Goodale, 2003; Whitwell et al., 2018). These differences in illusory susceptibility suggest that object-directed action operates under two systems of control: an ‘offline’ (memory-guided) system that depends on ventrally-based perceptual mechanisms, and an ‘online’ (real-time) system that does not (Goodale, Jakobson & Keillor, 1994; Milner et al., 2001). As such, perceptual mechanisms have been argued as critical for controlling memory-guided actions because the visuomotor mechanisms underlying the dorsal stream require direct visual input and, as a result, only have a brief memory (Goodale et al., 1994). Visual information processed by the dorsal stream generates a precise and accurate movement program when the target is first viewed, which is based on factors such as the surrounding environment and the goals of the viewer, but if the target is subsequently occluded, the program decays quickly. In the case of memory-guided tasks, the motor system relies on the stored representation of the target to generate a new movement program, and this less accurate representation is maintained by the perceptual mechanisms in the ventral stream (Westwood & Goodale, 2003). This assumes that the dorsal stream is engaged when the target is identified. However, previous research by Westwood and Goodale (2003) demonstrates that real-time, visuomotor mechanisms are not recruited for the control of action unless the target is visible when the response is cued. When participants were shown a target in the context of a size-contrast illusion and then cued by an auditory tone to grasp the target, they found that peak grip aperture was not affected by the illusion when the target was visible between the response cue and movement onset. But, when the target was occluded once the response was cued, peak grip aperture was more consistent with the illusion suggesting that dorsal mechanisms are not engaged until an action is required (i.e., at the response cue) – and only if the target is visible at the same time. Since the egocentric position of a target can change quickly and in an unpredictable way, it is more efficient for the dorsal stream to generate a movement plan once an action is required as opposed to when the target is first identified,

which would ultimately result in the continuous updating of the plan in response to egocentric position changes. Taken together, these studies suggest that visually-guided, object-directed actions are largely unaffected by scene-based perceptual information extracted by the ventral stream, but rather relies heavily on the absolute metrics of the target, which are extracted in real-time from the dorsal stream to guide the fingers, hands, and limbs.

Contradictory evidence for the dissociation between ‘vision-for-perception’ and ‘vision-for-action’ stems from the notion that comparisons of grasping and perceptual judgments are confounded by differences in attention, sensory feedback, obstacle avoidance, metric sensitivity and priming. However, a recent study by Whitwell et al. (2018) addressed and eliminated each of these issues using the Sander Parallelogram Illusion. Participants either reached out to grasp three-dimensional target bars placed on a two-dimensional picture of the Sander Parallelogram illusion or made explicit estimates of the length of the target bars. Grasps were performed without visual feedback, and participants could grasp the targets after making their size-estimates in order to reduce illusory error with haptic feedback. Consistent with previous research, the Sander Parallelogram illusion influenced both perception and grasps performed without visual feedback. More importantly, their results showed that illusion effects were more robust for perceptual judgments than grasps, supporting the notion that human vision is comprised of functionally and anatomically dissociable systems.

While it has been well established that there is a clear dissociation between ‘vision-for-action’ and ‘vision-for-perception’, recent studies have proposed that there are multiple processes involved in visual online control. Specifically, Elliott et al. (2010) proposed that there are two processes involved in visual online regulation: a process early in the movement concerned with comparisons between actual and expected sensory consequences, and another process late in the movement involved in providing information about the relative positions of the limb and target. Although this notion is supported by previous studies (Grierson and Elliott 2009; Kennedy, Bhattacharjee, Hansen, Reid and Tremblay 2015; Roberts et al. 2013), they are limited to pointing and aiming tasks to examine the overall functioning of these underlying visuomotor processes and as such it is unclear how online control may differ when the outcome diverges from pointing to, for example, grasping the target. Regardless, this divergence from a dichotomous set of visual coding processes emphasizes an emerging issue in the study of

perception and visuomotor control related to the time course in which the visuomotor system is affected by perceptual information.

To better understand how online visual processes are influenced by visual context, this study builds off of previous research using aiming tasks in the context of the Müller-Lyer illusion by examining the processes involved in online regulation using a reaching and grasping task involving the remarkably powerful Sander Parallelogram illusion. Similar to previous studies involving aiming tasks (Elliott et al. 2010; Grierson and Elliott 2009; Kennedy et al. 2015; Roberts et al. 2013), we manipulated the presence and absence of visual feedback over the entire movement as well as occluded vision during various points along the movement trajectory. While previous studies have focused on the early and late portions of the movement trajectory (Elliott et al. 2010; Grierson and Elliott 2009; Roberts et al. 2013) as well as limb velocity to designate time course windows (Kennedy et al. 2015), here we isolated early, middle and late portions of the movement trajectory using predefined time windows based on each participants own natural movements to gain a better understanding of how online control is influenced by the context in which the target is presented. Since illusion susceptibility relies on allocentric cues from the ventral stream of visual processing, we expected to see more pronounced perceptual biases in the early vision condition compared to conditions in which visual information was only available in the latter parts of the reach or during the full duration of the reach. We also expected that providing vision during the middle or late window would yield reach characteristics reflective of uncertainty within the reach, specifically, lower maximum velocities and longer reach durations, time to maximum grip aperture and wrist deceleration periods compared to conditions in which vision is available for the full or early parts of the reach. To ensure illusion susceptibility, and to test the extent to which participants were susceptible to the illusion, we also included a perceptual task in which participants were asked to manually estimate the length of the target bar and a grasping condition in which vision was only available until the movement was cued by an auditory tone (occluded vision condition). Consistent with previous research (i.e., Whitwell et al., 2018; Westwood and Goodale, 2003), we expected participants to show susceptibility to the illusion in both conditions, albeit to a lesser extent in the occluded vision condition compared to the manual estimation condition, supporting the notion that there is a clear dissociation between ‘vision-for-action’ and ‘vision-for-perception’.

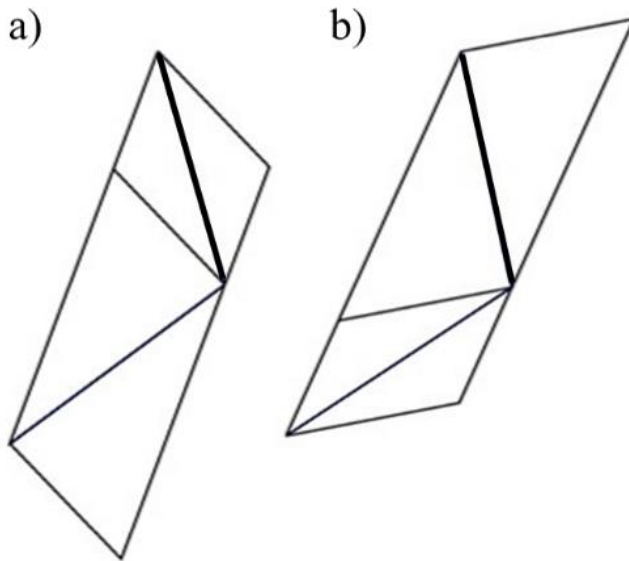
Method

Participants

Thirty-five undergraduate psychology students were recruited for this study and received research credits for their participation. Of these participants, three were excluded from data analysis due to an inability to properly perform the study tasks, two were excluded due to technical difficulties, and five were excluded due to reach durations that exceeded the time window required to perform the reach as determined prior to the experimental trials. In total, twenty-five participants (8 males) between ages 18 to 35 ($M = 22.92$, $SD = 4.84$) were included in the study. All participants had normal or corrected-to-normal vision and were right-hand dominant, as determined by a modified version of the Edinburgh Handedness Questionnaire (Oldfield 1971). This experiment was approved by the Psychology/Sociology Research Ethics Board (PSREB) of the University of Manitoba.

Materials/Apparatus

The Sander Parallelogram illusion was used to examine illusory effects on reaching and grasping when visual information is only available at certain points along the reach trajectory. The illusion underlying the Sander Parallelogram is that the diagonal line bisecting the larger parallelogram appears to be considerably longer than the line bisecting the smaller parallelogram, even though both lines are the same length. Each trial consisted of a single two-dimensional Sander Parallelogram, printed in black on a white background. The target was a three-dimensional black rectangular bar made of aluminum that was physically placed on top of the two-dimensional display by the experimenter such that it either bisected the perceived smaller (Figure 4.1a) or perceived longer (Figure 4.1b) configurations of the illusion. The target bar was 6 cm x 0.3 cm x 0.3 cm and a single target was placed within one of the parallelograms on each trial. The illusion was rotated so that participants could grasp the block comfortably, and to ensure that participants were reaching and viewing the block at the same angle and distance for each trial.

Figure 4.1*Sander Parallelogram Illusion*

Note. The bold line in a) denotes the perceptually shorter of the two diagonal lines, while the bold line in b) denotes the perceptually longer of the two diagonal lines. Blocks were laid along these bold lines to ensure comfortable grasping and similar placement of the blocks on each trial.

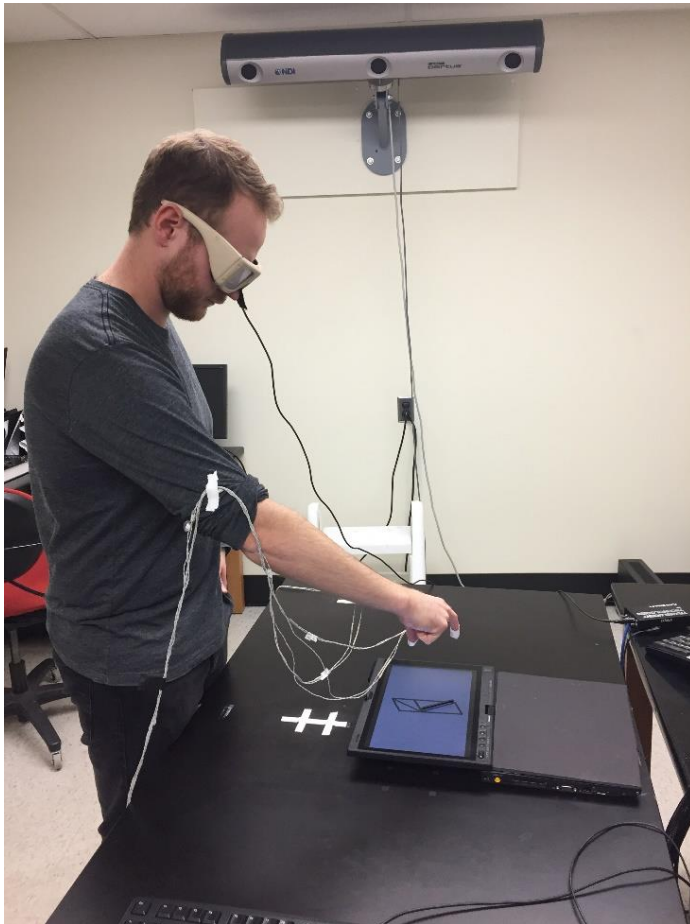
PLATO goggles (Translucent Technologies, Toronto, ON, Canada) were worn by participants to ensure that they were not able to see the stimuli before the trial began and to vary the amount of vision provided to the participant over the time course of the reach. Six infrared light-emitting diodes (IREDs) were placed on the participant's right hand (2 IREDs on each index finger, thumb and wrist), which were situated in the 'starting position' on the desk in front of them. The three-dimensional positions of the IREDs were recorded using an Optotrak Certus 3D motion tracking system (130 Hz sampling rate, spatial accuracy up to .01 mm; Northern digital Inc., Waterloo, Ontario, Canada). MotionMonitor software (Innovative Sports Training Inc., Chicago, IL, USA) was also used to control the time intervals at which the PLATO shutter goggles became transparent or opaque, as well as to generate the auditory tone (350 Hz) that served as a response cue for the participants to perform the grasping or estimation tasks. This software was run on an Inspiron 545 Dell computer (Duo Core 3.16 GHz).

Procedure

All participants performed a manual estimation task and a reaching and grasping task. These tasks were presented in separate blocks of trials and were counterbalanced across participants. After completion of the consent (Appendix 3) and demographics forms, participants were outfitted with IREDS on their right hand and asked to wear the PLATO goggles for the duration of the experiment. Participants stood in front of a tabletop on which the illusory display and target stimuli were always centered at the same position along the individual's sagittal plane. Participants were asked to rest their index finger and thumb together in a pinched position at a designated starting spot located 10 cm from the edge of the table and 30 cm from the stimulus display (Figure 4.2).

Figure 4.2

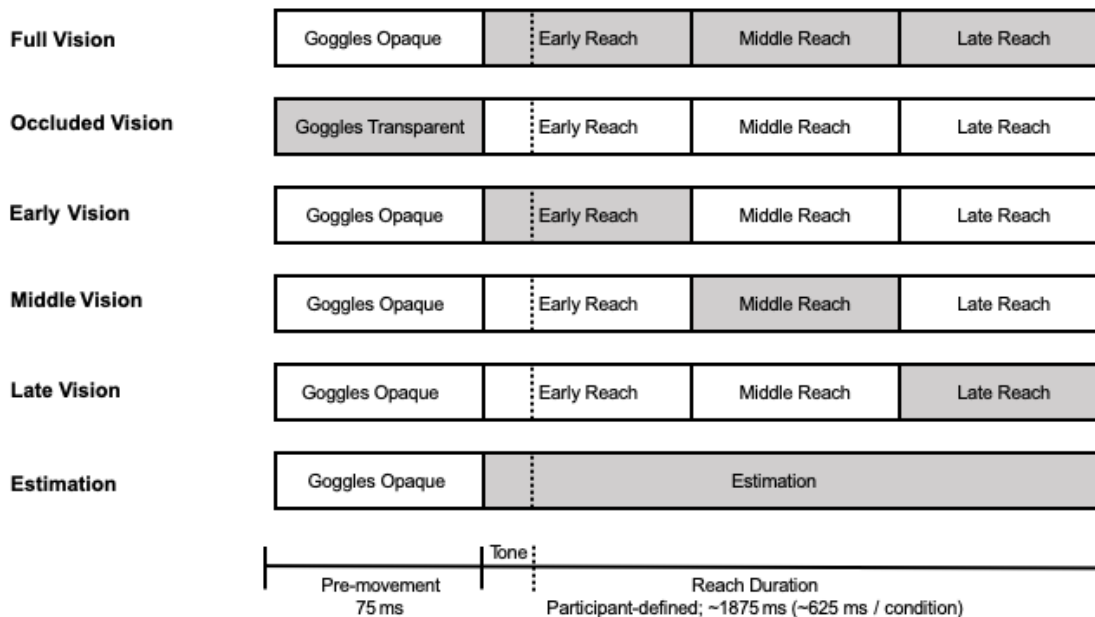
Experimental Set Up



At the start of each trial, the goggles cleared to permit the participant a full view of the display. Participants were instructed to keep their thumb and index finger pinched together at the start location, and an auditory tone (350 Hz) indicated to participants to begin the estimation or reaching and grasping task. In the manual estimation task, participants were instructed to look at the target bar and adjust their thumb and index finger to match the perceived length of the bar. They were also instructed to keep their hand on the table at the location of the start position to minimize any movement towards the target. Once participants were satisfied with their estimation they gave a verbal “ok” to the experimenter, who then ended the trial and the participant resumed the start position. All manual estimation trials were completed with full vision available to the participant for two main reasons. First, we wanted participants to have enough time to be confident and satisfied with their estimates. Second, since manual estimation is driven by the perceptual system, this condition served as a control to ensure that participants were susceptible to the illusion at a perceptual level. As such, we wanted the illusion effect to be as strong as possible, and it has been well established in previous studies that the most robust effects of illusion susceptibility are found when participants are provided with visual feedback for the duration of the estimation (Fabre and Vishton 2003).

In the reaching and grasping task, following the auditory tone, participants were instructed to reach out and pick up the target bar along its length using their right index finger and thumb. Participants were told at the beginning of the block of trials that on some trials vision would be available for the full duration of the reach, while on others the goggles would close during certain portions of the ongoing movement such that vision would only be available for the early, middle or late parts of the reach or not at all. In all, there were five visual conditions: full vision, early vision, middle vision, late vision and occluded vision (Figure 4.3). In each condition, except for the occluded vision condition, participants were cued to the beginning of the trial with a short beep from the computer. During this time, the goggles remained opaque, and after approximately 75 ms, an auditory tone cued the participant to begin the reach (the response cue). For the occluded vision trials, visual feedback was available for the 75 ms before the tone in order to ensure participants had some visual context of where to reach their hand, which was particularly important given the size of the small target bar and the precision required to grasp it. Following the auditory tone vision was either made available for the full duration of the reach (full vision condition), the first “third” of the reach (early vision

condition), the second “third” of the reach (middle vision condition) or the last “third” of the reach (late vision condition). For each participant early, middle, and late time windows were determined based on a series of 12 reaching trials performed by each participant prior to the experimental phase. In these trials, participants were asked to reach out and grasp the target bar in the exact same context as the experimental trials, but without the two-dimensional illusory background. Reach duration was then averaged for these 12 trials and divided by three to determine early, middle and late time windows based on the participants own natural reach rather than using standardized time windows or limb velocity as has been reported in previous studies (Roberts et al. 2013; Kennedy et al. 2015). Since the manipulation of vision was based on each individual’s average reach time, it was important to only include participants who were close to achieving their average movement time criterion. To this end, we removed participants ($N = 5$) failing to reach a mean movement time within 120 ms of their average movement time, a boundary that was based on the visual feedback processing time window (see Carlton 1992 for a review). On average, vision was provided for 1875 ms in the full vision condition, and 625 ms for each of the early, middle and late vision conditions.

Figure 4.3*Procedural Timing Used in the Experiment*

Note. The grey color refers to when vision of the target was made available. At the beginning of each trial the goggles were either opaque (full, early, middle & late conditions and estimation trials) or transparent (occluded vision condition) for 75 ms. A brief, 350 Hz tone indicated participants to begin the reach, and vision was manipulated such that it was either available for the full duration of the reach, early, middle or late part of the reach, or not available at all. The amount of time vision was available in each of the early, middle and late conditions was defined for each participant based on a set of 12 reaching trials performed before the experiment itself, and each participants' average reach time was divided by three to determine the amount of time the goggles would be transparent in each condition. In order to ensure participants were able to make contact with the target in late trials, visual feedback was available until wrist movement was slowed to 5 cm/s, even if it meant vision was available for longer in the late condition. On average, the reach duration was 1875 ms, with approximately 625 ms allotted to each of the early, middle and late conditions.

In total, each participant performed 84 trials. Before the experimental trials, participants completed the 12 trials used to determine the early, middle and late time windows. Participants then completed the experimental trials. The experimental block for grasping consisted of 5 exposure conditions (occluded vision, early, middle, late vision and full vision) and 2 background conditions presented in two-dimensions (looks smaller and looks larger) for a total of 10 conditions. Each condition was repeated 6 times, for a total of 60 trials of reaching and grasping. The experimental block for perceptual estimation was completed with full vision and the same 2 background conditions for a total of 2 conditions. Each condition was repeated 6 times, for a total of 12 trials of manual estimation.

Data Analysis

The primary dependent measure for the manual estimation trials was the final grip aperture (FGA). As per the experimenter's instructions, the final grip aperture represented the participant's perceptual estimation of the target block as measured by the distance between the IREDs on the thumb and index finger at the final frame of the trial. The primary dependent measure for the reaching and grasping task was the maximum grip aperture (MGA). This measure was extracted using a velocity-based search window, where only frames during which the hand was moving towards the target were included in the analysis. Reaching movement onset and offset were defined as the first frame that the wrist IRED exceeded 5 cm/s or fell below 5 cm/s. The MGA was defined as the maximum vector distance between the IREDs on the thumb and index fingers within this search window. Other variables analyzed to characterize the reach included time to MGA, movement time (MT), wrist deceleration period (WDP) and maximum velocity (MV). Time to MGA was defined as the duration of time from movement onset until MGA. MT was defined as the time from movement onset until movement offset (ie: the velocity-based search window). MV was defined as the frame at which velocity peaked during the velocity-based search window and served as an indicator of the effect of the illusion on pre-movement planning, and WDP was defined as the duration of time from MV until movement offset, allowing for inferences to be made regarding uncertainties in the grasping movement.

Condition means were computed for each participant and for each of the dependent measures. Using the FGA means from the manual estimation trials and the MGA means from the grasping trials the unadjusted effect of the illusion was also calculated for each participant by

subtracting their mean measure from the responses directed at the illusory “short” conditions from their mean measure from responses directed at the illusory “long” conditions. Thus, positive values are consistent with the direction of the illusion. The unadjusted effect of the illusion was tested using one-sample t-tests against zero to determine which conditions participants were actually susceptible to the illusion as well as paired-sample t-tests to determine whether conditions differed from each other. A grip aperture analysis was also conducted using a repeated-measures ANOVA with Condition (Estimation (Est), Grasp – full vision (GFV), Grasp – occluded vision (GNV), Grasp-early vision (GEV), Grasp – middle vision (GMV), Grasp – late vision (GLV)) and Illusion (perceived “long”, perceived “short”) as the factors to further dissociate the differences between conditions found in the one-sample t-tests. The remainder of the variables representing the reach kinematics (time to MGA, MT, RT, MV, WDP) were analyzed using separate 2 (Illusion: perceived “long”, perceived “short”) x 5 (Condition: Est, GFV, GNV, GEV, GMV, GLV) repeated-measure ANOVAs. All analyses were carried out using $\alpha = .05$ and post-hoc analyses were performed using Bonferroni correction.

Results

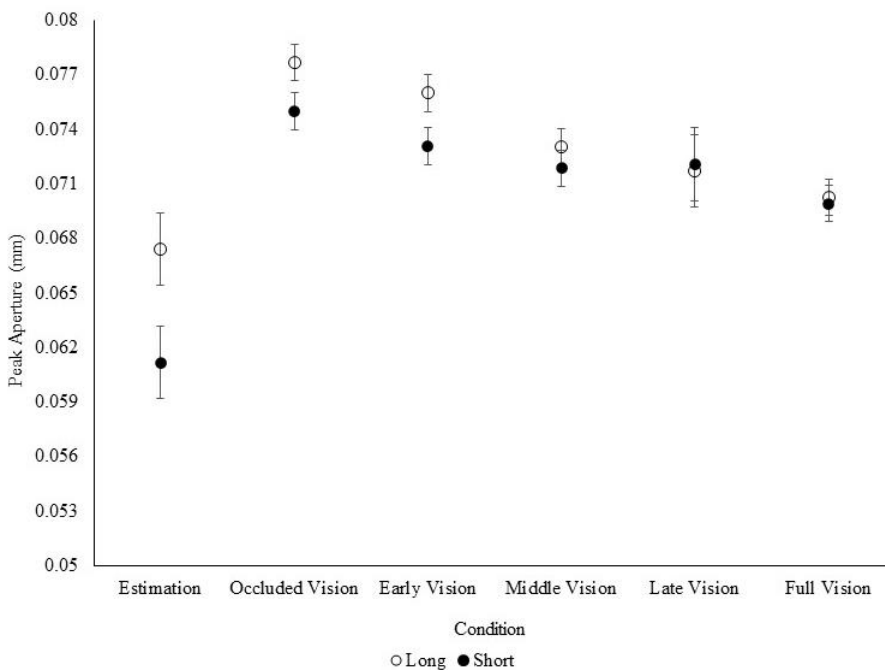
Grip Aperture Analysis

The Sander Parallelogram illusion showed a significant influence on manual estimations, as well as grasps, when no visual feedback was available during reaching or visual feedback was allowed only for the early part of the reach (Table 4.1). A significant main effect of Condition, $F(5, 100) = 10.87, p < .001, \eta_p^2 = .352$, showed that manual estimations resulted in significantly smaller final grip apertures (6.4 cm) than the maximum grip apertures produced in conditions where participants had occluded vision (7.6 cm, $p = .009$), or early vision (7.4 cm, $p = .037$), of the block. Significantly larger peak apertures were found in the occluded vision condition than the middle (7.2 cm, $p = .012$), late (7.2 cm, $p = .003$) or full (7 cm, $p < .001$) vision conditions. The full vision condition also resulted in smaller peak apertures than early ($p < .001$) or middle ($p = .012$) conditions. A significant main effect of Illusion, $F(1, 20) = 23.656, p < .001, \eta_p^2 = .542$, showed that peak apertures were larger in the “long” condition (7.3 cm) than the “short” condition (7 cm, $p < .001$). The Condition x Illusion interaction was also significant, $F(5, 100) = 7.627, p < .001, \eta_p^2 = .276$, showing an effect of the illusion in manual estimation, occluded vision and early vision conditions (Figure 4.4), consistent with the results in Table 4.1.

Table 4.1*Unadjusted Effects of the Illusion (in cm)*

Task	N	Mean	SEM	Tests against zero
Manual estimation	25	0.6252	0.107	$t^* = 5.867, p < .001$
Early vision	25	0.2912	0.076	$t^* = 3.812, p = .001$
Middle vision	25	0.1183	0.092	$t = 1.293, p = .208$
Late vision	25	-0.0377	0.078	$t = -.481, p = .635$
Full vision	25	0.0343	0.0699	$t = .490, p = .629$
Occluded vision	21	0.2759	0.1	$t^* = 2.759, p = .012$

Note. As the table shows, the mean slopes for manual estimation, occluded vision and early vision conditions differed significantly from zero. The asterisk (*) denotes significant tests using the Holm (1979) multiple comparisons procedure.

Figure 4.4*Mean Peak Aperture*

Note. Mean peak aperture for each of the illusion conditions (long = perceived longer; short = perceived shorter) across the manual estimation task and the 5 visual conditions of the grasping task. Error bars show standard errors.

To examine the extent to which there was a dissociation between ‘vision-for-perception’ and ‘vision-for-action’, paired sample t-tests were performed to assess whether illusory effects found in grasping conditions differed significantly from those of the estimation condition. Results showed a stronger illusion effect in the estimation condition compared to all grasping conditions, even if the grasping condition also showed a significant effect of the illusion (Table 4.2). Crucially, the early and occluded vision conditions, in which a significant effect of the illusion was found, both differed significantly from the estimation condition. Within the grasping conditions, only the early vision condition differed significantly from the late vision condition, suggesting that there are multiple processes involved in online visuomotor control.

Table 4.2

Paired Sample T-Tests on the Illusion Effects Across Visual Conditions (in cm)

Pairwise Comparisons	Mean	SEM	Paired Samples Test
Estimation - Full	0.475	0.111	$t^* = 4.265, p < .001$
Estimation - Occluded	0.333	0.139	$t^* = 2.391, p = .003$
Estimation - Early	0.297	0.104	$t^* = 2.864, p = .001$
Estimation - Middle	0.406	0.150	$t^* = 2.705, p = .004$
Estimation - Late	0.586	0.120	$t^* = 4.896, p < .001$
Full - Occluded	-0.151	0.142	$t = -1.061, p = .305$
Full - Early	-0.178	0.112	$t = -1.588, p = .129$
Full - Middle	-0.069	0.128	$t = -.541, p = .595$
Full - Late	0.110	0.122	$t = .907, p = .376$
Occluded - Early	-0.019	0.134	$t = -.145, p = .887$
Occluded - Middle	0.134	0.147	$t = .914, p = .375$
Occluded - Late	0.256	0.148	$t = 1.730, p = .103$
Early - Middle	0.108	0.104	$t = 1.043, p = .310$
Early - Late	0.288	0.088	$t^* = 3.294, p = .004$
Middle - Late	0.180	0.113	$t = 1.597, p = .127$

Note. As the table shows, significant differences were found between manual estimations and all grasping conditions, as well as between early vision and late vision conditions. The asterisk (*) denotes significant tests using the Holm (1979) multiple comparisons procedure.

Time to Maximum Grip Aperture

A significant main effect of Condition, $F(4, 80) = 14.657, p < .001, \eta_p^2 = .423$, revealed that the time to maximum grip aperture was longer in the late condition (1268.144 ms) than in the early (1053.291 ms, $p < .001$), middle (1073.764 ms, $p < .001$), full vision (1046.453 ms, $p < .001$) or occluded vision (1074.957 ms, $p = .003$) conditions (Figure 4.5a). The main effect of Illusion, $F(1, 20) = .802, p = .381, \eta_p^2 = .039$, and the Condition x Illusion interaction, $F(4, 80) = .992, p = .417, \eta_p^2 = .047$, were null.

Movement Time Analysis

A significant main effect of Condition, $F(4, 80) = 23.787, p < .001, \eta_p^2 = .543$, showed that participants completed the reach significantly slower in the late condition (1565.592 ms) than the early (1323.309 ms, $p < .001$), middle (1343.022 ms, $p < .001$), full vision (1290.632 ms, $p < .001$) or occluded vision (1338.071 ms, $p = .006$) conditions (Figure 4.5b). The main effect of Illusion, $F(1, 20) = .022, p = .883, \eta_p^2 = .001$, and the Condition x Illusion interaction, $F(4, 80) = 2.154, p = .082, \eta_p^2 = .097$, were null. Thus, the time it took for participants to reach out and grasp the block was primarily influenced by the point at which they received vision to perform the reach.

Maximum Velocity and Wrist Deceleration Period

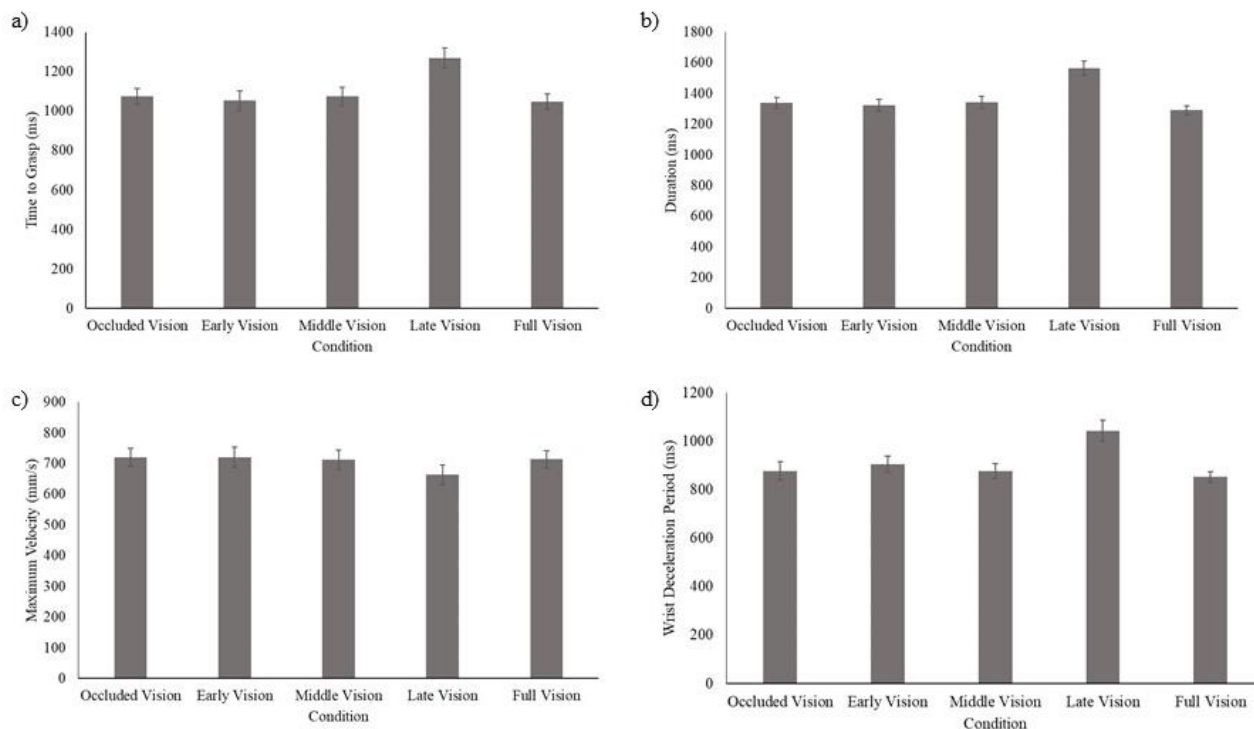
For maximum velocity a significant main effect of Condition, $F(4, 80) = 5.219, p = .001, \eta_p^2 = .207$, and the Condition x Illusion interaction, $F(4, 80) = 2.626, p = .041, \eta_p^2 = .116$, were found (Figure 4.5c). The main effect of Illusion, $F(1, 20) = 1.697, p = .208, \eta_p^2 = .078$, was null. Follow-up tests showed that maximum velocity was significantly lower for the late condition (663.089 mm/s) than the early (720.326 mm/s, $p = .03$), full vision (714.041 mm/s, $p = .031$) or occluded vision (720.248 mm/s, $p = .026$) conditions. There was no significant difference between the late condition and the middle (712.678 mm/s, $p = .140$) condition. For the interaction, it was found that maximum velocity was lower for trials in which the stimuli was perceived as longer (697.160 mm/s) than shorter (743.337 mm/s) in the occluded vision condition, $p = .026$.

As with maximum velocity, analysis of the wrist deceleration period revealed a significant main effect of Condition, $F(4, 80) = 15.850, p < .001, \eta_p^2 = .442$ (Figure 4.5d). The main effect of Illusion, $F(1, 20) = .376, p = .547, \eta_p^2 = .018$, and the Condition x Illusion interaction, $F(4, 80) = .802, p = .528, \eta_p^2 = .039$, were also null. Follow-up tests showed that

wrist deceleration period was significantly longer for the late condition (1042.292 ms) than it was for the early (906.078 ms, $p = .002$), middle (876.981 ms, $p < .001$), occluded vision (877.299 ms, $p = .003$) or full vision (852.981 ms, $p < .001$) conditions.

Figure 4.5

Overall Effect of Condition



Note. The main effect of Condition in each analysis showed a longer time to reach MGA (A), longer overall reach duration (B), lower maximum velocity (C) and a longer wrist deceleration period (D) in the late condition compared to the other conditions. All bars represent condition means, and error bars represent standard errors.

Discussion

The purpose of this study was to examine how online visuomotor processing is influenced by the surrounding context in which a target is presented when vision is manipulated at varying points along the movement trajectory. Extending prior research using the Müller-Lyer illusion and aiming tasks (Elliott et al. 2010; Grierson and Elliott 2009; Kennedy et al. 2015; Roberts et al. 2013), participants performed a perception-based manual estimation task and an

action-based reaching and grasping task in the context of the Sander Parallelogram illusion. Our results showed a robust illusion effect in the manual estimation condition, confirming that participants were susceptible to the illusion and ruling out this methodological consideration as a potential confound to the results of the grasping analysis. Results of the grasping analysis showed that when grasps were performed with visual feedback (closed loop), the illusion did not influence maximum grip aperture (MGA), consistent with previous research (Aglioti et al. 1995; Gentilucci et al. 1996). Grasps performed without visual feedback for the duration of the reaching movement (open loop) showed that MGA reflected a susceptibility to the illusion, also consistent with previous literature (Westwood and Goodale, 2003; Gentilucci et al. 1996; Haffenden and Goodale 1998). Interestingly, grasps were also influenced by the illusion when visual information was only available for the early part of the reach, similar to results of the manual estimation task albeit less robust. No bias towards the illusion was found when vision was provided for the middle or late parts of the reach. From these results two major points emerge. First, the Sander Parallelogram illusion was found to influence both manual estimations and grasps performed when vision was occluded for the duration of the reach or with vision only available for the early part of the reach. Second, compared to the manual estimations, pairwise comparisons showed that grasps were influenced significantly less by the illusion (Whitwell, Goodale, Merritt, and Enns 2018; Aglioti et al. 1995; Gentilucci et al. 1996; Haffenden and Goodale 1998). As such, these results are consistent with Milner and Goodale's (1992) TVSH that action and perception are part of two dissociable streams, while also supporting the notion that goal-directed movement involves multiple processes.

Previous research has established that the extent to which actions are immune to illusions is partially reliant on the amount of visual information available to the participants before movement onset. In the current study, our occluded vision condition was designed such that participants were able to view the target until the auditory tone (response cue), after which vision was occluded for the duration of the reach. Importantly, no visual feedback was available between the response cue and movement onset, which prior research has shown leads to a reduction in the illusory response (Westwood & Goodale, 2003). MGAs were found to be consistent with an illusion-based response, suggesting that ventrally-driven information was used to influence the outcome, and in line with previous research supports the argument that dorsal visuomotor mechanisms are only engaged when the response is cued *and* the target is visible

(Westwood and Goodale, 2003; Elliott and Lee 1995; Bruno and Franz 2009; Franz et al. 2009; Haffenden and Goodale 1998). In the full vision condition, there were no illusion-based differences, suggesting that dorsally-driven information was used to process the outcome. That is, the availability of vision during the whole duration of the reach allowed the visual system to correct for errors resulting in unbiased hand position by the end of the reach. However, when vision was only available during early, middle, or late parts of the reach, results showed that only middle and late vision conditions showed MGAs consistent with those of the full vision condition. When vision was presented at the beginning of the reach, the MGA was consistent with the illusion such that participants had larger grip apertures for stimuli perceived as longer than shorter. Critically, pairwise comparisons revealed that illusion effects in the early vision condition differed significantly from those of the late vision condition, suggesting that visuomotor processing includes two online control processes, consistent with the notion that goal-directed movement involves multiple processes (Elliott et al. 2010).

Although MGA in the early vision condition was influenced by the illusion, it is important to note that the illusory configuration did not influence movement time, time to MGA, maximum velocity, or wrist deceleration period for any of the five visual conditions. However, these reach kinematics were impacted by the point at which visual feedback was provided, showing differences for the late condition compared to the other conditions. While participants were able to complete the reaching and grasping task successfully and within their pre-defined average movement time window regardless of the point at which they received visual feedback, movement duration in the late condition still took significantly longer than the other conditions overall. Longer movement durations in the late condition are likely a byproduct of the lower maximum velocity and longer wrist deceleration period also found in this condition (Handlovsky et al. 2004), which is typically associated with error-reducing online processes as a result of a speed/accuracy trade-off. This notion of a speed/accuracy trade-off is consistent with Elliott et al.'s (2010) multiple-process model of limb control, which suggests that aimed movements function under the guidance of two visually dependent modes of online control: a process of impulse regulation and a process of late discrete control. Specifically, impulse control early in the movement is more involved in bringing the limb as close to the target area as possible without overshooting it, while late discrete control involves error estimation and small submovements designed to correct any aiming error (Elliott, Helsen & Chua, 2001; Meyer,

Abrams, Kornblum, Wright, Smith, 1988). In the current study, when vision was only provided for the early part of the reach, a quick ballistic movement would have propelled the limb towards the target, but with vision occluded for the latter part of the movement there would be no opportunity for error correction. That is, MGA must reflect the initial motor plan associated with the perceived size of the target block. However, when vision was available for the late part of the reach, corrective processes were available to reduce discrepancies between limb and target position. Vision was also provided in the late condition until target contact to ensure that trials in this condition were accurately reflecting the kinematics associated with the latter part of the reach.

One of the limitations to this design is that while participants were instructed to naturally reach out to grasp the block as they did in the pre-experimental trials used to derive their movement time window, they may have become aware that vision was available in late trials until the movement was completed and inadvertently taken longer to complete the trial once vision came online. However, time to MGA, which involves the duration from movement onset until MGA, was also longer for late trials. Since MGA occurs during the latter part of the reach and time to MGA includes the early and middle parts of the reach when vision was not available, longer durations in the late condition likely also reflect a degree of uncertainty associated with starting the reach without any visual feedback. As such, longer reach durations in the late condition may be due to participants inadvertently moving their hand more slowly than expected by the participants standard reach profile, resulting in more time to correctly grasp the target and a decrease in illusion susceptibility. Yet, the anomalous movement time in the late condition is not enough to explain why participants did not fall for the illusion in this condition since a reduced effect of the illusion was found on grasps overall, and a similarly null effect of the illusion was found in middle vision and full vision conditions, both of which had durations that did not differ significantly from the participants standard reach profile. It is likely, then, that decreased illusion susceptibility in the late condition is due to the recruitment of corrective processes and the availability of online, real-time visual feedback until target contact to make corrections as opposed to a longer duration of time to complete the reach in this condition.

Another limitation concerns the sensitivity of different responses to target-size. Due to the number of conditions tested in this study we only included one target size, which has the potential to lead to biased estimates in both manual estimation and grasping conditions (Franz,

Fahle, Bühlhoff, & Gegenfurtner, 2001, Whitwell et al., 2018). However, since our study design follows closely with that of Whitwell et al., (2018), who found that task-differences in response-sensitivity to a difference in the length of the target stimuli did not affect their overall findings, it is unlikely that an adjustment in the current study would end up equating the effect of the illusion on the manual estimates and grip apertures in the grasping conditions.

While results from this study suggest that there are two types of processing involved in visuomotor control, the mechanisms by which the early part of the reach operates under remains unclear. Elliott et al. (2010) posit that before a movement is initiated, both motor and sensory representations of the expected consequences of the movement are formed. This motor representation, or efferent copy, provides a reference against which incoming visual and proprioceptive feedback can be compared. It should follow then, that in the occluded vision condition in which visual information was only available before the response was cued the efferent copy reflects the perceived size of the target block since the recruitment of dorsal mechanisms requires the response to be cued *and* vision of the target. Without visual feedback, there is nothing to compare to the efferent copy to, and without vision to facilitate online corrective processes in the latter part of the reach, resulting MGAs should reflect the perceived size of the target bar. In the full vision condition, the efferent copy would have been formed at the beginning of the reach once the response was cued and the target became visible. Visual and proprioceptive feedback would have then been compared to this efferent copy, and corrective processes applied in the latter part of the reach producing MGAs unbiased by the illusion. Results showing that MGA's in the early vision condition were susceptible to the illusion just as they were in the occluded vision condition suggests that the initial efferent copy represents the perceived size of the target. However, since the response cue occurred at the same time the target became visible, this would suggest that dorsal visuomotor mechanisms were engaged at the beginning of the reach. Since dorsal mechanisms rely on online, real-time information, it is likely that the movement plan generated at the beginning of the movement decayed once vision was occluded, resulting in more of a reliance on stored internal representations coming from the ventral stream. While this could likely be elaborated on in future studies using eye-tracking technology, our current results suggest that perceptual mechanisms are easily accessible when dorsal mechanisms are taken 'offline', supporting the notion that visuomotor control involves multiple online control processes.

Conclusion

People typically organize their reaching and grasping movements to achieve a precise, efficient movement while optimizing movement speed. When unexpected changes to the visual environment occur, people are quite adept at making adjustments to their movement trajectories to accommodate the new visual constraints. In the current study, we showed that part of this accommodation process may be due to the recruitment of multiple processes during the reaching movement. The results indicated that grasps were influenced by the Sander Parallelogram illusion in occluded vision and early vision conditions, indicating that the perceptual system influences online motor control to some extent. Late vision conditions were characterized by longer movement durations, time to MGA, wrist deceleration period and lower maximum velocities compared to other vision conditions, indicating a temporal cost associated with online trajectory amendments. While these results point to the idea of multiple online control processes involved in voluntary movement, it is also important to note that manual estimations were more robustly affected by the illusion compared to grasps, supporting Milner and Goodale's (1992, 1995) important work on the differential roles of ventral and dorsal stream processing. As such, the current study moves beyond a single dichotomous model to examine the extent to which visuomotor control involves multiple online processes, providing support for a two component model: an initial movement impulse that relies heavily on perceptual processes and a late feedback-based control process that provides online corrections consistent with a traditional view of dorsal processing in action.

References

- Aglioti S, DeSouza JFX, Goodale MA (1995) Size-contrast illusions deceive the eye but not the hand. *Curr Biol* 5:679-685. doi:10.1016/S0960-9822(95)00133-3
- Brenner E, Smeets JBJ (1996) Size illusion influences how we lift but not how we grasp an object. *Exp Brain Res* 111:473-476. doi:10.1007/BF00228737
- Bridgeman B, Kirch M, Sperling A (1981) Segregation of cognitive and motor aspects of visual functioning in induced motion. *Percept Psychophys* 29:336-342. doi:10.3758/bf03207342
- Bruno N, Franz VH (2009) When is grasping affected by the Müller-Lyer illusion?: A quantitative review. *Neuropsychol* 47(6):1421-1433. doi:10.1016/j.neuropsychologia.2008.10.031
- Carlton LG (1992) Visual processing time and the control of movement. In: *Advances in psychology*. North-Holland, Vol. 85, pp. 3-31.
- Daprati E, Gentilucci M (1997) Grasping an illusion. *Neuropsychol* 35(12):1577–1582. doi:10.1016/S0028-3932(97)00061-4
- Elliott D, Lee TD (1995) The role of target information on manual-aiming bias. *Psychol Res*, 58:2-9. doi:10.1007/BF00447084
- Elliott D, Helsen WF, Chua R (2001) A century later: Woodworth's (1899) two-component model of goal-directed aiming. *Psychol bull* 127(3):342-357. doi:10.1037/0033-2909.127.3.342
- Elliott D, Hansen S, Grierson LE, Lyons J, Bennett SJ, Hayes SJ (2010) Goal-directed aiming: Two components but multiple processes. *Psychol bull* 136(6):1023-1044. doi:10.1037//0033-2909.127.3.342
- Fabre E, Vishton P (2003) Effects of the Ebbinghaus illusion on different behaviors: One-and two-handed grasping; one-and two-handed manual estimation; metric and comparative judgment. *Spat Vis* 16(3):377-392. doi:10.1163/156856803322467590
- Franz VH, Fahle M, Bühlhoff HH, Gegenfurtner KR (2001) Effects of visual illusions on grasping. *J Exp Psychol Hum Percept Perform* 27(5):1224-1244 doi:10.1037/0096-1523.27.5.1124
- Franz VH, Hesse C, Kollath S (2009) Visual illusions, delayed grasping, and memory: No shift from dorsal to ventral control. *Neuropsychol* 47(6):1518-1531. doi:10.1016/j.neuropsychologia.2008.08.029

- Gentilucci M, Chieffi S, Deprati E, Saetti MC, Toni I (1996) Visual illusion and action. *Neuropsychol* 34:369-376. doi:10.1016/0028-3932(95)00128-X
- Goodale MA, Milner AD (1992) Separate visual pathways for perception and action. *Trends Neurosci* 15:20–25. doi:10.1016/0166-2236(92)90344-8
- Goodale MA, Jakobson LS, Keillor JM (1994) Differences in the visual control of pantomimed and natural grasping movements. *Neuropsych* 32:1159-1178. doi: 10.1016/0028-3932(94)90100-7
- Grierson LE., Elliott D (2009) Goal-directed aiming and the relative contribution of two online control processes. *Am J Psychol* 309-324.
- Haffenden AM, Goodale MA (1998) The effect of pictorial illusion on prehension and perception. *J Cogn Neurosci* 10:122-136. doi:10.1162/089892998563824
- Handlovsky I, Hansen S, Lee TD, Elliott D (2004) The Ebbinghaus illusion affects on-line movement control. *Neurosci Lett* 366(3):308-311. doi:10.1016/j.neulet.2004.05.056
- Holm S. (1979) A simple sequentially rejective multiple test procedure. *Scand J Stat*, 6:65-70.
- Kennedy A, Bhattacharjee A, Hansen S, Reid C, Tremblay L (2015) Online vision as a function of real-time limb velocity: Another case for optimal windows. *J Mot Behav*, 47(6):465-475. doi:10.1080/00222895.2015.1012579
- Mack A, Heuer F, Villardi K, Chambers D (1985) The dissociation of position and extent in Müller-Lyer figures. *Percept Psychophys* 37(4):335–344. doi:10.3758/bf03211356
- Meyer DE, Abrams RA, Kornblum S, Wright CE, Smith JE (1988) Optimality in human motor performance: Ideal control of rapid aimed movements. *Psychol Rev* 95(3):340-370. doi:10.1037/0033-295x.95.3.340
- Milner AD, Dijkerman HC, Pisella L, McIntosh RD, Tilikete C, Vighetto A, Rosetti Y (2001) Grasping the past: Delay can improve visuomotor performance. *Curr Biol* 11:1896-1901. doi:10.1016/s0960-9822(01)00591-7
- Milner AD, Goodale MA (1995) *The visual brain in action*. Oxford University Press.
- Oldfield R (1971) The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychol* 9(1):97–113. doi:10.1016/0028-3932(71)90067-4
- Roberts J, Burkitt JJ, Willems B, Ludzki A, Lyons J, Elliott D, Grierson LE (2013) The influence of target context and early and late vision on goal-directed reaching. *Exp Brain Res* 229(4):525-532. doi:10.1007/s00221-013-3614-1

Westwood DA, Goodale MA (2003) Perceptual illusion and the real-time control of action. *Spat Vis* 16:243-254. doi: 10.1163/156856803322467518

Whitwell RL, Goodale MA, Merritt KE, Enns JT (2018) The Sander parallelogram illusion dissociates action and perception despite control for the litany of past confounds. *Cortex* 98:163-176. doi:10.1016/j.cortex.2017.09.013

CHAPTER V: GENERAL DISCUSSION

Our ability to see is not merely a result of light patterns falling on the retina but is rather a complex and impressive process undertaken by the visual system. The studies outlined in this dissertation explore how the way we perceive and interact with our surroundings is influenced by factors such as culture (Study 1), attention (Study 2) and visual feedback (Study 3). The findings from Study 1 suggest that the global processing bias found in both Caucasians and Asians is dependent on the subcortical pathway through which visual information is transmitted. That is, Caucasians processed perceptual stimuli more globally than Asians when low-spatial frequency information was made available to the ventral pathway via parvocellular-biased stimuli, while Asians showed a global processing advantage when low-spatial frequency information was made available to the dorsal pathway via magnocellular-biased stimuli, and to a lesser extent to the ventral pathway. In Study 2, when the perceptual system was manipulated under conditions of inattention and divided-attention to examine the brain regions responsible for accessing visual stimuli, results showed involvement of the right supramarginal gyrus in grouping under conditions of inattention, suggesting that complex processing occurs even when we are unaware of the visual stimuli we are “seeing” in our environment. Finally, Study 3 examined how visual feedback impacts the way our perceptual system influences our ability to interact with objects in our environment. Consistent with previous research, the perceptual system had more of an influence on grasp kinematics when vision was restricted to the early part of the reach or when vision was not available during the reaching movement. Since the perceptual system influenced the grasp kinematics less during the latter parts of the movement when vision was available, these findings suggest that early visuomotor control involves multiple online control processes that are influenced by our perceptual system. Together these studies demonstrate that perception is influenced by many factors. Our cultural identity, the way we orient our attention and the amount of visual feedback available when viewing a visual environment all have the potential to influence the way we perceive a visual scene, which explains why two people viewing the same visual scene can perceive it in two completely different ways.

Limitations and Future Directions

Study 1: Perception and Culture

Traditionally, studies investigating visual perception and attention rarely collect demographic information related to a participants’ cultural identity. However, over the last 15

years the concept of cultural psychology has emerged, emphasizing that psychological functioning cannot be separated from the culture in which it takes place. In this perspective, cognitive processes such as perception are inseparable from culture, and as such many studies have begun to discover the significant impact that culture can have on psychological processes. One of the main themes in cultural psychology that has come to light has been an “East” versus “West” comparison, placing more emphasis on holism, collectivism, spatial orientation and interdependence in Eastern cultures and analysis, verbal formulations, individualism and independence in Western cultures (Triandis, 1995; Markus & Kitayama, 1991; Kitayama & Uskul, 2011; Nisbett, 2004). Consistent with this notion, Study 1 showed that visual perception is influenced by culture. While this finding emphasizes the importance of controlling for culture when examining even the most fundamental psychological processes, it is only a starting point for the more expansive research required for future studies. A difference in global processing based on whether stimuli were more magnocellular- or parvocellular-biased suggests an underlying mechanism responsible for global processing based on culture but does not offer an explanation about the evolution of such a difference in the first place. Perhaps the difference is driven by a heritable genetic contribution or a broader degree of visual complexity based on physical environment. Some studies have suggested that differences may be due to the way babies’ attention is directed during infancy, such that being raised by a culturally Asian mother produces more of a bias towards global attention while being raised by a native-English speaking mother results in a relative bias towards local attention (Fernald & Morikawa, 1993; Tardif et al., 1999; McKone et al., 2010). A more plausible explanation is that this difference is not driven by only one factor but rather a combination of factors that interact. In this same regard, future studies should also consider how findings extend to immigrant families (i.e., individuals who are physically Asian but born and raised in a culturally Western country) as well as how findings are influenced by language (i.e., potential differences due to primarily speaking or reading an Asian language vs. English language). In the current study, participants were simply asked to self-report on their ethnicity and whether they spoke English as their first language, and as a result the effect of the potential factors listed above cannot be considered without collecting more extensive data in the future. Regardless, Study 1 emphasizes the importance of controlling for cultural differences in cognitive psychology studies to ensure that important differences are not missed if study samples are too small, or the demographic distribution is skewed. As such,

future studies should explicitly report cultural identity along with other relevant demographic information and depending on the purpose of the study being conducted, should even go so far as to prospectively control for cultural identity the same way that one might control for other common demographics like age and biological sex.

Study 2: Perception and Attention

To date, there has been little research on the brain regions involved in accessing visual stimuli under inattention conditions. While behavioral research has consistently shown that even visual information we are unaware of can still influence our perception of the world around us (Moore & Egeth, 1997), the extent to which the neural mechanisms underlying attention and perception overlap are less clear. In Study 2, many similar brain regions were found regardless of whether perceptual processes were engaged in inattention or divided-attention conditions, suggesting that similar neural mechanisms are responsible for perception under both levels of attention. However, under inattention conditions specifically results showed that the right supramarginal gyrus was important for implicit perceptual grouping, emphasizing that complex processing occurs very early on in visual processing. While the result is novel, it is limited to Gestalt grouping by similarity across divided-attention and inattention conditions. Future research incorporating multiple types of Gestalt processing under varying conditions of attention will provide additional strength to these results. It would also be useful to supplement these findings with eye-tracking research. Understanding how attention influences the way we move our eyes around a visual environment may provide additional insights into how we group elements of our environment together to provide a coherent representation of our visual world. Nonetheless, Study 2 clearly demonstrates that visual information below the level of explicit awareness can influence perception of our visual world and that to some extent the neural mechanisms driving perception are modulated by attentional allocation.

Study 3: Comparison to Existing Models of Motor Control

While the initial argument for the TVSH focused on the dissociation between ‘vision-for-action’ and ‘vision-for-perception’, more recent research has emphasized the way the two streams interact to transform sensory information into purposeful acts (Milner & Goodale, 1995; see Milner, 2017 for a review). Results from Study 3 are consistent with the TVSH as demonstrated by a stronger illusion effect on manual estimations (a perceptual task) compared to grasping (a motor act), as well as an interaction between the two visual streams based on the

finding that a smaller illusion effect was also observed in the occluded vision and early vision grasping conditions.

While studies conducted with full visual feedback have shown that actions are less susceptible to illusory context (Aglioti et al., 1995; Gentilucci, Chieffi, Daprati, Saetti, & Toni, 1996; Haffenden & Goodale, 1998), other studies in which vision is only available before movement onset have shown that actions are influenced by the perceptual bias of the illusion (Elliott & Lee, 1995; Bruno and Franz 2009; Franz, Hesse, and Kollath 2009; Haffenden and Goodale 1998). This has been the driving force behind Glover and Dixon's (2001, 2002) Planning-Control Model, which suggests that movement planning is controlled by a different process than movement execution. Results of Study 3 support this model to an extent, as an effect of the illusion was observed on grasping trials in which vision was only available before movement onset (the occluded vision condition), however results also showed an effect of the illusion on grasping trials in which vision was available for the early part of the movement execution phase, which is not consistent with Glover and Dixon's model.

What we can glean from these findings, though, is that there appears to be a dichotomous set of visual coding processes involved in visual online regulation. This is consistent with Elliott et al.'s (2010) multiple-process model of limb control, which posits that there are multiple processes involved in visual online control. More specifically, Elliott et al. (2010) posits that there are two processes involved in visual online regulation: a process early in the movement execution phase that is concerned with comparisons between actual and expected consequences, and a second process later on in the movement execution phase involved in providing information about the relative positions of the limb and target. Under the premise that the first part of the movement relates to impulse regulation and the second part relates to limb-target regulation, it is possible that the reason grasps were more consistent with the illusion in the early and occluded vision conditions is that there was not enough time to engage limb-target regulation processes, leading to grasps more consistent with the perceived length of the target as opposed to the actual length of the target. While the temporal timeline related to this model was not outlined in Elliott's model, Tremblay et al. (2013) addressed this in their study examining the optimal window for online vision.

In Tremblay et al. (2013), vision was manipulated as a function of limb velocity in order to assess when impulse-regulation and limb-target regulation processes take place during a

reaching movement. They found that vision provided between .8 and .9 m/s improved impulse regulation processes, while vision provided up to 1.1 m/s increased limb-target regulation processes. These findings together demonstrated that the two control phases of movement put forth by Elliott et al. (2010) can take place at different velocities during a movement. However, the limitation to this study was that vision was available to a large portion of the movement. This was addressed in a later study by Kennedy et al. (2015), in which shorter visual windows or velocity ranges were constructed to examine online control of reaching movements. In this study the entire velocity profile of a reaching movement was parsed into three windows such that an early (.8 – 1.4 m/s), middle (above 1.4 m/s), and late (1.4 - .8 m/s) segment were selected based on the results of Tremblay et al. (2013). They hypothesized that the early segment would contribute the most to endpoint precision and online correction measures since the early segment included the velocity ranges found to be important for Elliott et al.'s (2010) multiple process model. Results showed that endpoint consistency was comparable to full vision trials when using vision from early and middle windows, although the middle window also involved a temporal cost as denoted by a longer deceleration phase. The late window was not useful to implement online trajectory amendments. These results suggest that early visuomotor control involves multiple online control processes during voluntary movement. While results of Study 3 showed grasp formations consistent with the actual length of the block in middle, late and full vision trials, trials in which vision was only available for the early part of the reach or occluded at movement onset showed grasp formations consistent with the perceived length of the block (i.e., illusion susceptibility). Since perception influenced the grasp when vision was available for the first part of the reach but not the middle or late parts of the reach, these findings suggest that early visuomotor control, and in turn the multiple control processes that occur during this phase of the movement, are also influenced by perception. As such, future studies examining when vision is most useful to optimally engage visuomotor processes during an action will also need to consider how the ventral stream may be interacting with the dorsal stream, particularly early on in movement execution.

Another factor that warrants further investigation is the influence that attention towards non-target stimuli has on goal-directed actions. Action-centered theories and models of attention suggest that the capture of attention by a stimulus automatically activates an action plan designed to interact with that stimulus. Tipper et al. (1992) found that stimuli appearing between the

hands' starting point and the target causes more interference than stimuli appearing beyond the target, suggesting that stimuli not related to the target itself activates a competing motor response alongside the target-directed response. In the context of visual illusion research, this suggests that attention directed towards nontarget stimuli (i.e., the perceptually grouped components of the illusion) may also influence how the target is processed, particularly when visual stimuli is placed between the hand starting position and the target. While it is possible that alternating between illusion configurations in Study 3 may have increased/decreased the amount of distracting information presented to the participant during the reach, since illusion susceptibility requires grouping all of the visual information into a whole, it is assumed that the participant is viewing the stimuli holistically such that the parts of the illusion between the hand and the target are part of the target-directed response and not a competing motor response. Nonetheless, future studies involving illusion configurations in which there is no visual stimuli between the hand and the target could help address the extent to which this might be an issue.

Significance

Perceptual grouping seems like a simple concept to define. The visual system determines which regions and parts of a visual scene belong together, and those elements are grouped to form the overall gist of how we see the world around us. Yet, the studies presented here demonstrate that this process is anything but simple and is highly influenced by many factors. Before information even reaches the visual cortex, complex processing related to perception occurs, and this processing appears to differ based on cultural identity. Although magno cells have traditionally been characteristic of global processing and parvo cells have been attributed to local processing, results from Study 1 suggests that the relative contribution of these two types of visual cells differs across cultures, influencing the extent to which global processing occurs in different populations. In other words, what we see is dependent to some extent on our cultural identity. Similarly, what we see is influenced by attention. Study 2 demonstrated that attention influences our perception of the world even before we are explicitly aware of how we are directing out attention. Results showed processing in higher brain regions even when information was grouped implicitly, emphasizing that the way we orient our attention has a powerful influence on how we see the world around us. Finally, Study 3 showed that what we see is influenced by the amount of visual feedback available to us, which in turn influences how we interact with the world around us. So, while perception and action can largely be distinguished from one another,

there is a significant amount of interaction that also occurs between the two visual streams. These findings together are an important step forward in developing a more specified and detailed model of perceptual grouping that not only provides critical insights into the functional architecture of this important processing mechanism but has applications for the development of robotics and artificial intelligence (AI) devices.

As robotics and AI devices become more integrated into our day-to-day lives, it becomes more critical than ever to understand how we perceive the world around us if we are to develop technologies that can compete with the human brain. In our lifetime we have already seen the development of robots that can facilitate and optimize flow in the workplace, talk like a human (hey Siri!), and even walk on the surface of Mars. Yet, it is only lately that we are beginning to see robots that can make a decent cup of coffee. The ability to perceive and understand the world around us is critical for carrying out habitual and streamlined tasks, such as what is required when making a cup of coffee – turning on the machine, pouring the beans, finding the milk in the fridge and the sugar somewhere in the pantry. These perceptual abilities, while seemingly effortless to humans are still largely a mystery when it comes to machine technology.

Conclusion

Collectively these studies have emphasized that perception is not a stand-alone event, but rather a process that is heavily influenced by external factors. The ability for our perceptual system to group discrete elements is crucial for forming a meaningful understanding of our visual environment. However, forming a coherent representation of our visual environment is more complex than simply recognizing and grouping individual features together. Perception is modulated by a myriad of factors including culture and attention, and in turn the way we perceive the world around us influences how we interact with it. Cultural perceptual biases characterize cognitive processing in Caucasian and Asian populations, demonstrating the importance of controlling for demographic variables such as cultural identity when administering cognitive psychology studies. Attentional allocation also influences perceptual processing, and more importantly, even information we cannot explicitly report on still influences the way we perceive the world around us. At the same time that our perceptual system is influenced by factors such as culture and attention, it is also influencing the way we interact with the world around us. This is largely due to the way the two visual streams interact, and factors such as visual feedback facilitate this crosstalk between the two streams with perceptual processes

influencing visuomotor behavior when vision is limited during the action. Taken together, it is clear that the human visual system is complex and relies on many different cortical and subcortical brain regions varying in the extent to which they act together and independently. By examining how visual perception influences our visuomotor system and is influenced by information projected to it from the retina, as well as by examining the neural mechanisms underlying visual perceptual grouping, a better understanding of how the visual system is organized and the processes that lead to meaningful interaction with our environment is established.

References

- Aglioti, S., DeSouza, J.F.X., & Goodale, M.A. (1995). Size-contrast illusions deceive the eye but not the hand. *Current Biology*, *5*, 679-685.
- Bruno, N., & Franz, V.H. (2009). When is grasping affected by the Müller-Lyer illusion?: A quantitative review. *Neuropsychologia*, *47*(6):1421-1433.
doi:10.1016/j.neuropsychologia.2008.10.031
- Elliott, D., & Lee, T.D. (1995). The role of target information on manual-aiming bias. *Psychological Research*, *58*, 2-9. doi:10.1007/BF00447084
- Elliott, D., Hansen, S., Grierson, L.E., Lyons, J., Bennett, S.J., & Hayes, S.J. (2010). Goal-directed aiming: Two components but multiple processes. *Psychological Bulletin*, *136*(6), 1023-1044. doi:10.1037//0033-2909.127.3.342
- Fernald, A., & Morikawa, H. (1993). Common themes and cultural variations in Japanese and American mothers' speech to infants. *Child development*, *64*(3), 637-656.
- Franz, V.H., Hesse, C., & Kollath, S. (2009). Visual illusions, delayed grasping, and memory: No shift from dorsal to ventral control. *Neuropsychologia*, *47*(6), 1518-1531.
doi:10.1016/j.neuropsychologia.2008.08.029
- Gentilucci, M., Chieffi, S., Deprati, E., Saetti, M. C., & Toni, I. (1996). Visual illusion and action. *Neuropsychologica*, *34*, 369-376.
- Glover, S.R., & Dixon, P. (2001). Dynamic illusion effects in a reaching task: evidence for separate visual representations in the planning and control of reaching. *Journal of Experimental Psychology: Human Perception and Performance*, *27*(3), 560-572.
doi:10.1037/0096-1523.27.3.560
- Glover, S.R., & Dixon, P. (2002). Dynamic effects of the Ebbinghaus illusion in grasping: Support for a planning/control model of action. *Perception & Psychophysics*, *64*(2), 266-278. doi:10.3758/BF03195791
- Haffenden, A.M. & Goodale, M.A. (1998). The effect of pictorial illusion on prehension and perception. *Journal of Cognitive Neuroscience*, *10*, 122-136.
- Kennedy, A., Bhattacharjee, A., Hansen, S., Reid, C., & Tremblay, L. (2015). Online vision as a function of real-time limb velocity: another case for optimal windows. *Journal of motor behavior*, *47*(6), 465-475. doi:10.1080/00222895.2015.1012579

- Kitayama, S., & Uskul, A. K. (2011). Culture, mind, and the brain: Current evidence and future directions. *Annual review of psychology*, *62*, 419-449.
- Markus, H.R., & Kitayama, S. (1991). Culture and the self: Implications for cognition, emotion, and motivation. *Psychological review*, *98*(2), 224.
- McKone, E., Davies, A.A., Fernando, D., Aalders, R., Leung, H., Wickramariyaratne, T., & Platow, M.J. (2010). Asia has the global advantage: Race and visual attention. *Vision Research*, *50*, 1540-1549. doi:10.1016/j.visres.2010.05.010
- Milner, A.D., & Goodale, M.A. (1995). Oxford psychology series, No. 27. The visual brain in action.
- Milner, A.D. (2017). How do the two visual streams interact with each other?. *Experimental brain research*, *235*(5), 1297-1308.
- Moore, C.M. & Egeth, H. (1997). Perception without attention: Evidence of grouping under conditions of inattention. *Journal of Experimental Psychology: Human Perception and Performance*, *23*(2), 339-352.
- Nisbett, R. (2004). *The geography of thought: How Asians and Westerners think differently... and why*. Simon and Schuster.
- Tardif, T., Gelman, S.A., & Xu, F. (1999). Putting the “noun bias” in context: A comparison of English and Mandarin. *Child Development*, *70*(3), 620-635.
- Tipper, S.P., Lortie, C., & Baylis, G.C. (1992). Selective reaching: Evidence for action-centered attention. *Journal of Experimental Psychology: Human Perception and Performance*, *18*(4), 891-905. doi:org/10.1037/0096-1523.18.4.891
- Tremblay, L., Hansen, S., Kennedy, A., & Cheng, D.T. (2013). The utility of vision during action: Multiple visuomotor processes?. *Journal of Motor Behavior*, *45*(2), 91-99.
- Triandis, H.C. (2018). *Individualism and collectivism*. Routledge.

APPENDIX 1: CONSENT FORM FOR STUDY 1



Department of Psychology

190 Dysart Road
Winnipeg, Manitoba
Canada R3T 2N2
Telephone (204) 474-9338
Fax (204) 474-7599

INFORMED CONSENT FORM

**PRINCIPAL
INVESTIGATORS:**

Dr. Jonathan Marotta
University of Manitoba
(204) 474-7057

Tiffany Carther-Krone
University of Manitoba
(204) 480-1248

This consent form, a copy of which will be left with you for your records and reference, is only part of the process of informed consent. It should give you the basic idea of what the research is about and what your participation will involve. If you would like more detail about something mentioned here, or information not included here, you should feel free to ask. Please take the time to read this carefully and to understand any accompanying information.

PURPOSE: We are interested in how individuals with and without high functioning forms of autism spectrum disorders process visual information. The way visual information is processed is important because it allows us to identify and attach meaning to our surroundings.

DESCRIPTION: This experiment will take place over one 1-hour session in the University of Manitoba *Perception and Action lab* (P241 Duff Roblin Building). You will first be asked to fill out a short questionnaire about your general health. You will then be asked to complete a short questionnaire inquiring about social and communication skills, imagination, and attention. Following this survey, you will complete two short computerized tasks that will help us to create the stimuli for the experimental part of the study, which will consist of three parts. First, you will be shown stimuli in which a large letter is made up of smaller letters and asked to identify which letter you see first. Next, you will be shown similar stimuli and asked to determine whether or not it contains the letter 'A'. Finally, you will be asked to attend to either the large letter or the smaller letters making up the large letter and identify it as quickly and accurately as you are able.

RISKS AND BENEFITS: There are no evident risks inherent in the tasks you will perform but some of the tests may be difficult. While this may be frustrating to you, there will always be an investigator with you to assist you and support you.

COSTS AND PAYMENTS: Participants who are not enrolled in Introductory to Psychology will be reimbursed for any travel expenses (e.g. parking or bus tickets), and participants enrolled in Introductory to Psychology will be awarded 2 participation credits.

CONFIDENTIALITY: Your information will be kept confidential. You will be referred to by a code number. All files containing identifying information will be stored in a locked cabinet separate from data with your code number. Your files will only be accessible by the investigators and will be destroyed 5 years after the completion of the study. All papers containing personal information will be shredded. All electronic files will be deleted. Results from this study will be disseminated through conference presentations and refereed publications. Participant confidentiality will not be jeopardized.

VOLUNTARY CONSENT: Your signature on this form indicates that you have understood to your satisfaction the information regarding participation in the research project and agree to participate as a subject. In no way does this waive your legal rights nor release the researchers, sponsors, or involved institutions from their legal and professional responsibilities. You are free to withdraw from the study at any time (participation is completely voluntary), and /or refrain from answering any questions you prefer to omit, without prejudice or consequence. Your continued participation should be as informed as your initial consent, so you should feel free to ask for clarification or new information throughout your participation.

This research has been approved by the Psychology/Sociology Research Ethics Board of the University of Manitoba. If you have any concerns or complaints about this project you may contact any of the above-named persons or the Human Ethics Coordinator (HEC) at 204.474.7122. A copy of this consent form has been given to you to keep for your records and reference. If you would like to receive a general summary, please indicate your contact information in the space provided below.

Signature of the Participant

Date

Signature of Investigator

Date

If you would like to receive general summary of the results from this study when it is completed (anticipated completion date: January 2020), please complete your email or mailing address below:

Email or Mailing Address: _____

Thank you for your participation!



APPENDIX 2: CONSENT FORM FOR STUDY 2

RESEARCH SUMMARY AND INFORMED CONSENT

Title of Research Project:

Neural Mechanisms Involved in Gestalt Grouping During Preattentive Visual Processing

PRINCIPAL INVESTIGATORS:

Dr. Jane Lawrence-Dewar

Miss. Andrea Pepe

Thunder Bay Regional Research Institute
(807) 684-7289

Dr. Jonathan Marotta

Miss. Tiffany Lazar

University of Manitoba
(204) 474-7057

SPONSORSHIP: This research is supported by the University of Manitoba and TBRRI.

FUNDING SOURCES: Funding for this research has been awarded to Dr. Jonathan Marotta by the Natural Sciences and Engineering Research Council

This document contains information regarding the purpose of the study, the methods involved, and the risks and benefits of participating. If you find any of the provided information unclear or have further questions, or after taking time to review this information you wish to make an appointment, please contact Jane Lawrence-Dewar at (807) 684-7289.

If you have any concerns regarding your rights as a research participant, or wish to speak to someone other than a research team member about this research project, you are welcome to contact the:

Chair, Research Ethics Board

Thunder Bay Regional Health Sciences Centre
980 Oliver Road, Thunder Bay, Ontario P7B 6V4
phone: 807-684-6422 fax: 807- 684-5904
email: ResearchEthics_Chair@tbh.net

As this study involves researchers from the University of Manitoba, it has been reviewed and approved by the University of Manitoba Psychology/Sociology Research Ethics Board (PSREB)

If you would like to speak with someone outside of the research team at the University of Manitoba, please contact:

Margaret Bowman

Coordinator – Human Ethics

CTC Building

208 – 194 Dafoe Road, Winnipeg, Manitoba

phone: 204-474-7122 fax: 204-269-7173

email: Margaret.Bowman@umanitoba.ca



WHAT IS THE RESEARCH ABOUT?

Every day our brains take in more information than we can process. By the time we see what is around us, our brains have already gone through and organized large amounts of information, deciding on which parts of our environment that we should focus. A failure to organize this information can lead to a meaningless and confusing view of the world. One important part of this organization is being able to “see the big picture” by combining the single parts of our environment together into a whole. Although research has shown that we can combine and group this information before we are even aware of it, the parts of the brain that cause this grouping to happen are unclear. The goal of this research is to look at which parts of the brain are used for grouping parts of our environment together before we are even aware that it is happening, so that we can make sense of the world around us. This study will use procedures to look at the brain while a task is being completed.

AM I ELIGIBLE TO PARTICIPATE?

All participants who participate in this research study must be right-handed, healthy individuals, between 18 and 45 years of age and must pass a prescreening check to be completed by the investigator prior to scheduling the study appointment as well as by the MR technologist at the study appointment. This study involves entering a high magnetic field which may not be safe for all individuals. It is important that you identify any implants that you may have in your body to the investigator and MR technologist. An MRI information sheet is included in your participant package to help answer any questions you may have.

You may not participate in the study if you:

1. Have a history of neurological injury or disease
2. Have a physical impairment or affliction that limits use of your right hand
3. Have a medical condition that could be made worse by stress or are claustrophobic
4. Are or may be pregnant
5. Weigh more than 330 pounds

This study is purely voluntary. You may decide not to participate in this study or you may withdraw from the study at any time.

WHAT WILL I HAVE TO DO?

When you call to make an appointment, you will be asked a series of questions to confirm you are eligible. These will include several questions to make sure that there are no metal objects in your body so that it is safe for you to have an MRI done. A copy of the detailed prescreening form with the questions that Dr. Jane Lawrence-Dewar will ask you when you make an appointment is enclosed for you to review.



You will make one visit to the Thunder Bay Regional Health Sciences Centre where you will have a MRI of your brain using the research dedicated MRI system. The scan itself will take about 60 minutes, but allow a total of 2 hours for the visit.

At your appointment the investigator will explain all of the details of the experiment and review this consent form with you and answer any questions you may have. You should make sure that all your questions are answered and that you agree to participate in the study before signing the consent form. An MR technologist will go through the MR Safety Screening Form with you. Before entering the magnet room, you will be asked to change into a hospital gown and to remove all metal objects, such as keys, coins, since they could be attracted to the MRI scanner with great force. You will be provided with a space to securely store your belongings. A pregnancy test will be available for your use if you think there is a chance you could be pregnant.

For the MRI scan, you will be positioned comfortably on your back and provided with soft earplugs to reduce the noise from the MRI scanner (the sound it produces is a loud knocking noise). A special receiver will be placed around your head. A mirror attached to this receiver will allow you see a projection screen placed at the back of the MRI scanner. You will then be slid into the large, tunnel-shaped scanner until your head is at the center of the magnet. The tunnel approximately 2 feet wide and is open at both ends.

During the scan, the MR operator or researcher will talk with you regularly through a two-way intercom to let you know what to do. During the study, you will be asked to judge the length of two parallel lines, which will be displayed on a background of randomly patterned dots on a computer screen.

After the scan has been completed and you have left the magnet room, we will ask you to fill out a questionnaire about how the study went for you. We will also ask if you would like remain on our potential participant list for future studies you may be eligible for of if you would like us to erase your contact information from our database. You can ask to have your name and information removed from our list at any time.

WHAT ARE THE POSSIBLE HARMS OR BENEFITS?

The risk of injury during MRI is less than 1 in 100,000. This risk does not arise from the MRI itself, but from a failure to disclose or detect MRI incompatible objects in or around the body of the subject or the scanner room. Metal objects can be attracted to the scanner with great force. If a metal object hit anyone in the way, it could cause serious injury. It is for this reason that we are cautious in our procedures and ask that you change into metal free clothing and remove jewelry and items from your pockets. Metal can also be located inside your body if you have had a surgery or implant. It is therefore very important that you answer all the questions honestly and fully on the Magnetic Resonance Screening Questionnaire. Some metal objects may move or heat up. Almost all the deaths and injuries related to MRI scans have occurred because the MRI operator did not know that surgically implanted metal hardware (such as a cardiac pacemaker) if was present inside the subject during the MRI scan. You must tell us if you have had surgery, as metal may be left in your body after certain types of surgery.



Please consider if you have any of the following:

- Previous Surgery involving metal, such as: clips, rods, screws, pins, wires.
- Heart pacemaker
- Implanted electrodes, pumps or electrical devices
- Cochlear (inner ear) implants
- Intraocular lens (eye) implants
- Any metallic foreign body, shrapnel or bullet (Have you have ever been a grinder, metal worker, welder, wounded during military service, etc.?)
- Intrauterine contraceptive device (IUD) or contraceptive diaphragm
- Dental work held in place by magnets
- Non-removable dental braces and retainers
- Metal dental work, unless it is composed predominantly of precious or semiprecious alloy or amalgam (Please discuss with the researcher)
- Tattooed eyeliner
- Some tattoos (if you have tattoos, please discuss with the researcher)
- Non-removable metal jewelry (body piercing)

While the scans being used have not been associated with harm to a fetus, there is not personal benefit for you to participate in this research study. Therefore it would be unethical to expose a fetus to a potential risk. If you are, or think you may be pregnant you may not participate in this research study. On the day of your study the researcher will offer you an opportunity to use a restroom prior to entering the MRI. A pregnancy test will be available in the washroom for your use should you wish to confirm your pregnancy status. Should you discover a positive test you should not continue in the study. Participation in the study is voluntary and you are free to withdraw at any time without penalty.

MRI is completely painless, but some people have felt minor, transient discomforts during MRI scans (e.g. dizziness, lightheadedness or a feeling of continued motion after being moved into the magnetic field) which usually subside within a few minutes. In rare cases, the dizziness progressed to the point of nausea, but subsided quickly outside the magnetic field. Some people may have a feeling of claustrophobia while they are in the scanner. Please let us know immediately if you experience claustrophobia or any other discomforts, and we will stop the study. Participation in the study is voluntary and you are free to withdraw at any time without penalty.

No long-term adverse effects of MRI have been reported. We would contact you if any new risks are discovered. Please contact us or ask your physician to contact us if you experience any effects that you feel may be a result of your participation in the study. This is a research study so you will not personally benefit by participating in this study.

This is not a diagnostic scan and the investigator is not clinically trained. We cannot provide you with any medical information regarding your scan. The images obtained use methods that are for research purposes and do not provide enough contrast to provide clinical information. With that said, there is a small possibility that imaging could reveal a variation in anatomy. If there is a variation that is visible to investigator, a copy of a localizing image with no identifying information will be reviewed by a TBRHSC



radiologist. If their review indicates that a follow-up is recommended, a copy of the report will be forwarded to the primary health care professional you have indicated on this form. If you do not have a primary health care professional, you may indicate that you would like a physician to contact you regarding the report.

CAN PARTICIPATION IN THIS STUDY END EARLY?

You have the right to withdraw from the research study at any time and for any reason. The investigators reserve the right to end your participation for any reason. If the study is ended before completion, any information you have already provided will be retained. You may request for acquired data to also be withdrawn.

Signing the consent form does not waive your legal rights.

WHAT ARE THE COSTS OF PARTICIPATING IN THIS STUDY?

There is no cost to participate in this study. We will give you \$25 to cover any expenses you incur to participate in this study.

IS THE STUDY CONFIDENTIAL?

Only people directly involved with the research procedure are allowed in the area while a study is being conducted.

Information gathered in this research may be published or presented in public forums; however your name will not be used or revealed. Records that contain your identity will be treated as confidential in accordance with the Personal Health Information Act. All data obtained during your scan will be stored with an alpha-numerical code instead of your name. Only your file, which is kept securely in the Principal Investigator's office, will have information which relates your name to the code. Identifying information will be kept for 7 years. Anonymous data may be kept indefinitely.

It is possible that our records will be audited by the Research Ethics Board. We have formatted our forms to seal personal information to facilitate inspection of our forms without revealing personal information.

DO THE INVESTIGATORS HAVE ANY CONFLICTS OF INTEREST?

The goal of this study is to better understand which parts of the brain are used for grouping parts of our environment together before we are even aware that it is happening, so that we can make sense of the world around us. We do not have conflicts of interest to disclose or anticipate that the results of this study will directly lead to commercialization.

Please contact us if you would like any more information about the study. Please let us know if you would like copies of any published scientific reports about the research project.

ADDITIONAL INFORMATION SHEET: Magnetic Resonance Imaging

What is magnetic resonance imaging (MRI)?



Magnetic resonance imaging (MRI) is an imaging method based on a large magnetic field. By entering the hole or “bore” of the MRI, you are entering a magnetic field much larger than that experienced by the earth’s magnetic field. In hospitals or research centres, the most common strength of magnetic field is 1.5 or 3 Tesla (T). The research dedicated MRI scanner housed on the first floor of the Thunder Bay Regional Health Sciences Centre is a 3 T system.

MRI uses the water in your body as a source of signal. By applying a radiofrequency (RF) pulse, we are able to disturb the “spins” away from aligning with the magnetic field.

When we remove the RF pulse, the spins realign themselves with the field but how quickly this occurs depends on the type of imaging being performed and the type of tissue that the spins are in. This is how we are able to obtain contrast between bone, fat, muscle, fluid and tissues such as the brain and spinal cord.

Some of the images we acquire show us pictures of how these tissues look. During these scans you will be told to relax and do nothing.

What is Functional magnetic resonance imaging (fMRI)?

Functional magnetic resonance imaging (fMRI) is a method of detecting areas of activity in the brain and spinal cord. When an area of the brain or spinal cord becomes “active” it needs more oxygen. To compensate for this, there is a much greater increase in blood flow and therefore oxygen to the area. Oxygenated and deoxygenated blood have different magnetic susceptibilities therefore, there is a localized change in signal that can be detected in an area of neuronal activity.

During a fMRI scan there will be periods where we will ask you to do nothing or “rest”. During other times you will be asked to participate in a line judgment task. By comparing the signal during the times that you are “resting” and those when you are doing the task, we can identify what areas of the brain are active.



STUDY PRESCREENING FORM (CONTINUED)

MR Safety

Do you have the following:

	Yes	No
Stents, wire mesh, or metal implants	<input type="checkbox"/>	<input type="checkbox"/>
Cardiac pacemaker	<input type="checkbox"/>	<input type="checkbox"/>
Aneurysm clips in head	<input type="checkbox"/>	<input type="checkbox"/>
Neuro/bio stimulator device	<input type="checkbox"/>	<input type="checkbox"/>
Implanted insulin pump	<input type="checkbox"/>	<input type="checkbox"/>
Hearing aid	<input type="checkbox"/>	<input type="checkbox"/>
Cochlear/ear implant	<input type="checkbox"/>	<input type="checkbox"/>
Shrapnel	<input type="checkbox"/>	<input type="checkbox"/>
Piercings	<input type="checkbox"/>	<input type="checkbox"/>
Dental implants (non-removable dentures, bridges, crowns)	<input type="checkbox"/>	<input type="checkbox"/>
Artificial limb or joint	<input type="checkbox"/>	<input type="checkbox"/>
Metal rods, screws, plates, nails	<input type="checkbox"/>	<input type="checkbox"/>
IUD	<input type="checkbox"/>	<input type="checkbox"/>
Tattoos	<input type="checkbox"/>	<input type="checkbox"/>
Have you ever been a metal worker (welder)?	<input type="checkbox"/>	<input type="checkbox"/>
Are you or could you be pregnant?	<input type="checkbox"/>	<input type="checkbox"/>
Have you previously had surgery? If yes what and when?	<input type="checkbox"/>	<input type="checkbox"/>

To the best of your knowledge is any metal left behind?



CONSENT FORM FOR MRI STUDY

For the participant:

By signing this consent form I confirm that:

- The research study has been fully explained to me and all of my questions have been answered to my satisfaction. If I have any more questions, I may call Dr. Jane Lawrence Dewar at the Thunder Bay Regional Research Institute at (807)684-7289.
- I understand the requirements of participating in this research study.
- I have been informed of the risks and benefits, if any, of participating in this research study.
- I have been informed of any alternative to participating in this research study.
- I have been informed of the rights of research participants.
- I have read each page of this form.
- I authorize access to my research study data as explained in this form and understand that information regarding my personal identity will be kept confidential.
- I have agreed to participate in this research study.
- I have received a copy of and I have read the Research Summary and accompanying information sheets.
- I realize that by signing this document I am not waiving any legal rights.
- Should a variation in the images be observed I wish the investigator to (select one):
 - Do nothing
 - Forward the image for review by a TBRHSC radiologist. If a follow-up is required, a report may be communicated with:
 - My primary health care provider:

Name: _____ Clinic: _____

OR

- I do not have a primary health care provider please have Neurologist Dr. Ayman Hassan contact me at the phone number I have provided below.
- You may request a general summary of the results from this study when it is completed. If so, please provide an email or mailing address on the next page.
 - I would like to receive a general summary (select one) YES NO

Thunder Bay Regional Research Institute



190 Dwyer Road
Winnipeg, Manitoba
Canada R3T 2N2
Telephone: (204) 474-9338
Fax: (204) 474-7599

I hereby agree to participate in the research protocol, “**Brain Areas Involved In Visual Grouping**” and I understand that I can end my participation at any time and for any reason. My consent has been given freely.

Seal line (all information below this line is confidential and will be sealed)

Participant information:

Name (Print):

Signature:

Date:

Phone number (required if you have indicated possible contact from the neurologist):

Email or Mailing Address (required if you have indicated you wish to receive a study summary):

For the Investigator:

By signing this form, I confirm that:

- This study and its purpose has been explained to the participant named above.
- All questions asked by the participant have been answered.
- I will give a copy of this signed and dated document to the participant.

Investigator information:

Name (Print):

Signature:

Date:

APPENDIX 3: CONSENT FORM FOR STUDY 3



Department of Psychology

190 Dysart Road
Winnipeg, Manitoba
Canada R3T 2N2
Telephone (204) 474-9338
Fax (204) 474-7599

Perception During Reaching: Effects on Grasping and Lift Force

PRINCIPAL INVESTIGATORS: Tiffany Carther-Krone, PhD Student, Psychology
University of Manitoba
(204) 480-1248

Dr. Jonathan Marotta, Professor, Psychology
University of Manitoba
(204) 474-7057

SOURCE OF SUPPORT: NSERC Discovery Grant

This consent form, a copy of which will be left with you for your records and reference, is only part of the process of informed consent. It should give you the basic idea of what the research is about and what your participation will involve. If you would like more detail about something mentioned here, or information not included here, you should feel free to ask. Please take the time to read this carefully and to understand any accompanying information.

PURPOSE: We are interested in how perceptual information presented at various time points during the course of a reaching movement affects the way we grasp and lift objects in our environment.

DESCRIPTION: This study will take place in the *Perception and Action Lab* in the Duff Roblin Building on the Fort Garry Campus. During the study, you will be asked to either reach out to grasp and lift a three-dimensional block placed on a computer screen or to manually estimate the length of the block. Goggles will be used to monitor how much time you have to view the block, an OPTOTRAK 3-D motion recording system will be used to record your finger and hand movements. Prior to this task, you will be asked to fill out a brief demographics questionnaire that inquires about your age, gender, handedness, whether you wear glasses, and your stereo acuity. The whole procedure will take about an hour to complete. You will earn 2 experimental credits for your participation in this study.

RISKS AND BENEFITS: There are no risks (physical, psychological and/or emotional) inherent in the tasks you will perform but some of the tests may be repetitive. Even though this may be frustrating to you, there will always be an investigator with you to assist you and support you.

COSTS AND PAYMENTS: There are no fees or charges to participate in this study. You will not receive payment.

CONFIDENTIALITY: Your information will be kept confidential. You will be referred to by a code number. All files containing identifying information will be stored in a locked cabinet separate from data with your code number. Your files will only be accessible by the investigators and will be destroyed 5 years after the completion of the study. All papers containing personal information will be shredded. All electronic files will be deleted. Any cds or dvds containing data will be physically destroyed.

VOLUNTARY CONSENT: Your signature on this form indicates that you have understood to your satisfaction the information regarding participation in the research project and agree to participate as a subject. In no way does this waive your legal rights nor release the researchers, sponsors, or involved institutions from their legal and professional responsibilities. You are free to withdraw from the study at any time, and /or refrain from answering any questions you prefer to omit, without prejudice or consequence. This means that should you choose to withdraw at any point from the study, you will still receive 2 participation credits. Your continued participation should be as informed as your initial consent, so you should feel free to ask for clarification or new information throughout your participation.

The University of Manitoba may look at your research records to see that the research is being done in a safe and proper way.

This research has been approved by the Psychology/Sociology Research Ethics Board of the University of Manitoba. If you have any concerns or complaints about this project you may contact any of the above-named persons or the Human Ethics Coordinator (HEC) at 474-7122. A copy of this consent form has been given to you to keep for your records and reference.

Signature of the Participant

Date

Signature of Investigator

Date

If you would like to receive general summary of the results from this study when it is completed, please complete your mailing (or email) address below:

Mailing Address: _____
