THE INFLUENCE OF THE DORSAL PATHWAY ON ENHANCED VISUAL PROCESSING

CAROLYN J. PERRY

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Abstract

Overall our visual experience is such a seamless one that unless specifically told, we might never know that what we “see” is actually the visual system taking the very simple input provided by cells in the retina and constructing an image based on rules and calculations and algorithms neuroscientists have yet to fully uncover. This is an incredible feat given the plethora of visual stimuli within our environment, that this information is used to inform and plan actions, and if that wasn’t enough, the visual system also has the capacity to selectively enhance certain aspects of visual processing if needs be. The research contained within this dissertation seeks to investigate how the dorsal visual pathway enhances both decision-making processes and visual stimuli presented near the hand.

Our findings suggest that the formation of object representations in the dorsal pathway can include both ventral (colour, contrast) and dorsal (speed) stream features (chapters two and three), which in turn greatly speed decision-making processes within the dorsal pathway. In addition, contrast and speed are integrated automatically but purely ventral stream features, such as colour, require top-down attention to facilitate enhanced processing speeds (chapter three). In chapter four we find that visual processing near the hand is enhanced in a novel way. When the hand is nearby, orientation tuning is sharpened in a manner not consistent with either oculomotor-driven spatial or feature based attention. In addition, response variability is reduced when the hand is nearby, raising the possibility that enhanced processing near the hand maybe be driven by feedback from frontoparietal reaching and grasping regions.

The research within this dissertation includes important new information regarding how the dorsal pathway can speed visual processing, and provides insight as to the next stage in understanding how we use vision for action.

Dedication

For my mom and dad who have always shown so much love and support throughout this long journey. Your steadfastness and faith are my foundation and my example, your understanding and help/advice my source of comfort and perseverance. I have been truly blessed to have you as my parents and as I have progressed in life, I discover more and more how well much of what you have taught me over the years has served me. With so much love!

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Foremost I want to thank my supervisor Dr. Mazyar Fallah. For eight years I have had the privilege of having what I believe to be, one of the best supervisors a student can have! My successes are his successes also as I would not be where I am without his constant teaching and guidance. His support and patience, calmness and enthusiasm have made the difficulties and let's face it, sometimes panic, that occur in all graduate experiences much more manageable!

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List of Abbreviations

Abbreviation	**Term**
AIP	Anterior Intraparietal
aIPS	Anterior Intraparietal sulcus
ANOVA	Analysis of Variance
CACC	Canadian Animal Care Committee
CIP	Caudal Intraparietal Cortex
DR	Direction Repulsion
EEG	Electroencephalography
FEF	Frontal Eye Fields
FF	Fano Factor
FINST	Finger of INSTanatiation
HA	Hand Away
HN	Hand Near
IPL	Inferior Parietal Lobule
IT	Inferior Temporal
LGN	Lateral Geniculate Nucleus
LIP	Lateral Intraparietal
MIP	Medial Intraparietal
MST	Medial Superior Temporal
MSTd	Medial Superior Temporal Medial
MSTl	Medial Superior Temporal Lateral
MT	Middle Temporal
OTI	Orientation Tuning Index

PEF	Parietal Eye Field
PIT	Posterior Inferior Temporal Cortex
PMv	Ventral Premotor Cortex
PMvr	Rostral portion of Ventral Premotor Cortex
PMd	Dorsal Premotor Cortex
PO	Parietal Occipital Region
POJ	Parietal Occipital Junction
RDK	Random Dot Kinetograms
RF	Receptive Field
SEM	Standard Error of the Mean
SPL	Superior Parietal Lobule
TMS	Transcranial Magnetic Stimulation
V1	Visual Area One (Primary Visual Cortex)
V2	Visual Area Two
V3	Visual Area Three
V3A	Visual Area Three Accessory
V4	Visual Area Four
V6	Visual Area Six
V6A	Visual Area 6 Accessory
YUACC	York University’s Animal Care Committee

Chapter 1. Introduction and Literature Review

1.1 General Introduction

Early on in my PhD, my six-year-old niece and I were playing out in the back yard. She was trying to learn how to throw and catch a Frisbee, and almost instinctively my instruction to her was to "keep your eyes on the Frisbee, Marissa." Having already started my dissertation research this instruction made me pause for a moment. In so many activities, selectively processing an object we want to act upon improves our chances of successfully completing the task. This is especially true when we want to interact with objects that are moving. For example, it may be helpful for visual processing of the moving Frisbee to speed up so that she has time to make decisions on how to orient her arm and hand accurately for a successful catch. Or, while Marissa is moving her arm and hand to catch the Frisbee, it would also be helpful to improve visual processing of the Frisbee's orientation in order to accurately position her hand. While these two suggestions may seem intuitive, they are quite complex from a neural perspective, and how visual processing may be enhanced in these ways within the brain, form the basis of the research contained in this dissertation.

In order to understand the complexity of the mechanisms that underlie the enhancements of visual processing mentioned above, it is important to recognize that there are certain concepts that are fairly well established in neuroscience, and the research and theories contained within this dissertation somewhat challenge these concepts. For example, it would not be too controversial to suggest that features are integrated and objects are formed within the ventral pathway, with the ultimate goal of allowing the observer to recognize what the object is. However, suggesting that features from both the ventral and dorsal pathways can be integrated to form object representations in the dorsal stream that in turn speed visual processing by as much as a full second in some cases, would garner a bit more skepticism. The research presented in chapter two provides evidence that object representations in the dorsal pathway can greatly speed visual processing. Chapter three expands on the information in chapter two by outlining the constraints that bottom-up and top-down attention have on the integration of colour, speed, *and* contrast, with direction, and the formation of object representations in the dorsal pathway.

Another fairly well established neuroscience concept involves the tight link between enhanced visual processing, the allocation of spatial attention, and the oculomotor system. For example, it has been shown that contrast sensitivity is enhanced at the end point of a planned saccade (Moore, Armstrong, & Fallah, 2003; Moore & Fallah, 2001, 2004) which indicates that the plan to move the eyes allocates spatial attention. To suggest that a similar mechanism, driven by a different effector, may underlie improved visual processing near the hand will likely spawn years of inquiry. Chapter four however, initiates this process by showing that orientation tuning in an early visual area (V2) is improved when the hand is nearby.

Finally, in chapter five I summarize our findings and suggest possible mechanisms that may underlie these enhancements of visual processing. First outlined is a possible neural mechanism for speeded processing times, and also a suggested location for dorsal pathway object representations. Also outlined is a neural mechanism we suggest may underlie improved visual processing near the hand. In each case, suggestions for future experiments, that would test different aspects of the presented hypothesized mechanisms, are also included in chapter five.

To preface this work, in the following chapter one sections I first briefly summarize visual processing in both the ventral and dorsal pathways. Next I outline research that suggests the existence of object representations within the dorsal pathway and the effect they have on neuronal activity and motor output, as well as the influence that object representations have on improving processing speed. I then outline research showing enhanced visual processing near the hand and provide a framework for the neural mechanism that is hypothesized to underlie these enhancements.

1.2 Anatomical and Functional Organization of the Ventral and Dorsal Pathways

The anatomical and functional organizations of the brain have been two key questions for researchers for more than a hundred years now. Since the days of Ramón y Cajal and his pioneering role in neuroscience in the 1800's (Nemri, 2010), continued advancements in research techniques and technology have resulted in a great expansion of our knowledge of the nervous system in general, and of the visual system specifically. Two of the core theories to have come out of this research is the anatomical and functional separation of visual input from the retina, and that visual input is organized hierarchically, although, even these theories are not without their critics and disclaimers (de Haan & Cowey, 2011; Hegdé & Felleman, 2007; Merigan & Maunsell, 1993). Generally speaking, however, the organization of visual input follows two pathways of increasing processing complexity from the retina; subcortical M and P pathways, and corresponding cortical pathways that extend into the parietal (dorsal pathway) and temporal (ventral pathway) lobes (Felleman & van Essen, 1991; Maunsell & Newsome, 1987; Merigan & Maunsell, 1993). Figures 1.1 and 1.2 (from Felleman & Van Essen, 1991) provide a window into the complexity that exists in these two pathways which, at the time, included a mere 32 separate visual areas. The descriptions of these pathways that follow however, will be a much simplified version with only relevant functional descriptions provided.

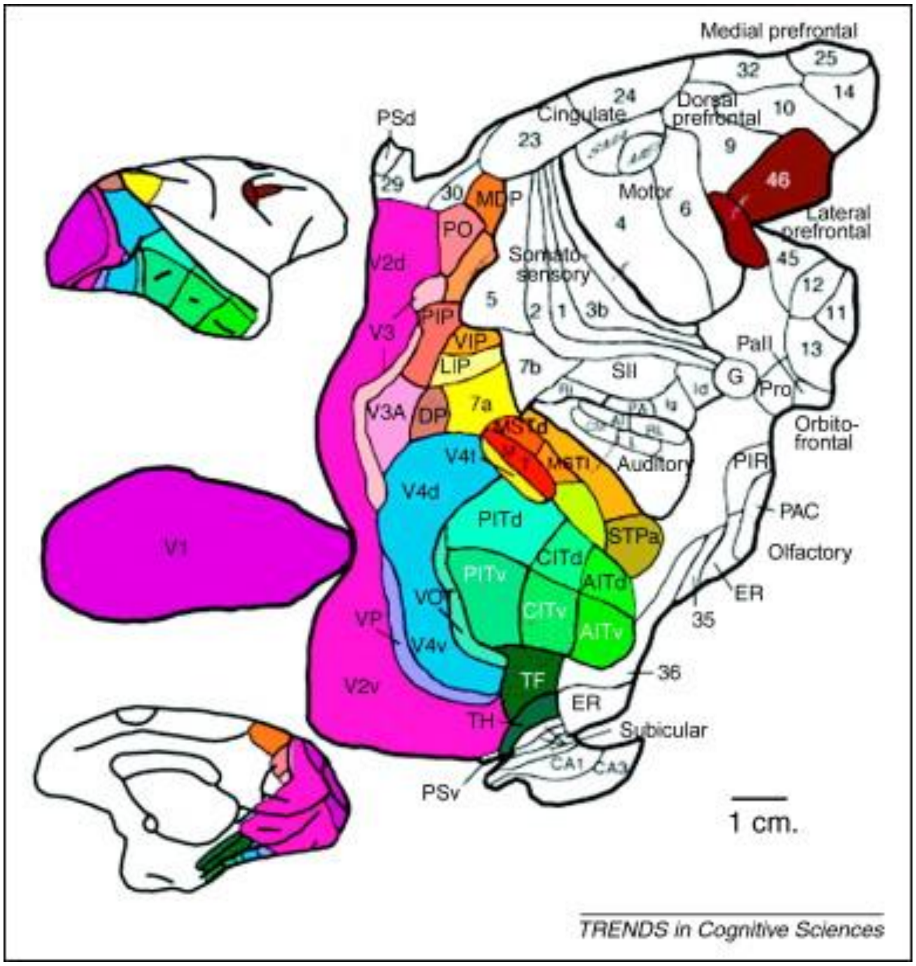

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Figure 1.1: Cortical areas implicated in visual processing. (Taken from Felleman & Van Essen, 1991). Areas deemed as visual are based on either the presence of visually responsive cells, or that the area has major inputs from known visual areas. Occipital lobe areas are shaded in purple, blue, and reddish hues. Parietal lobe regions in yellow, orange, or light brown. Temporal lobe areas in shades of green.

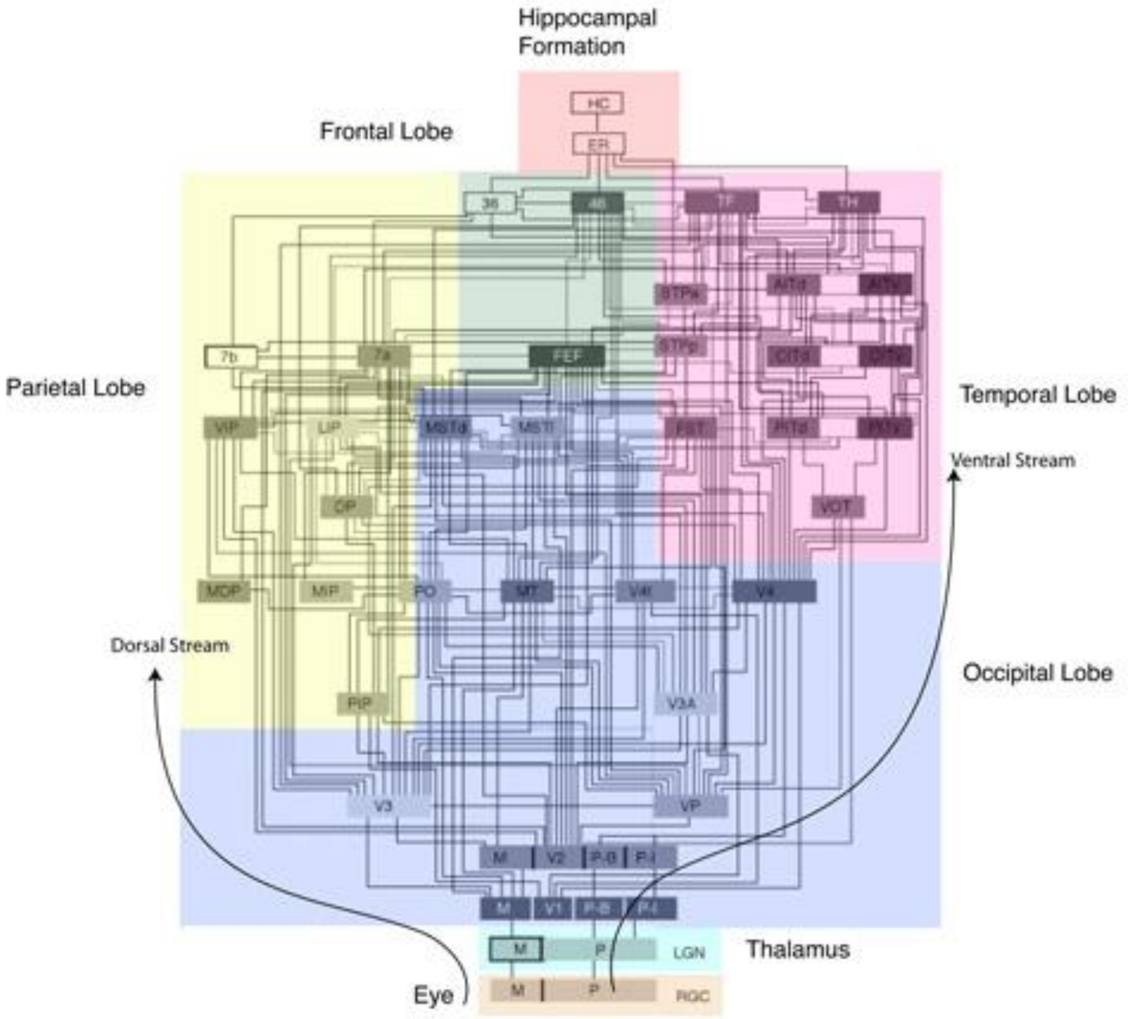

Figure 1.2: Connections and hierarchy of cortical visual areas. (Adapted from Felleman & Van Essen, 1991 by http://vis.berkeley.edu/courses/cs294-10-fa07/wiki/index.php/A1-ArielRokem). Occipital lobe areas are shown in blue, temporal in pink, parietal in yellow, frontal in green.

1.2.1 Ventral Pathway

From the retina, P cells project to the four most dorsal parvocellular layers of the LGN (Shapely & Perry, 1986) and synapse here with parvocellular neurons that terminate in layer 4Cβ of V1 (Merigan & Maunsell, 1993). In V1 parvocellular input is split between blob and interblob regions contained in layers 2 and 3 (Livingstone & Hubel, 1988; Maunsell & Newsome, 1987). Blob cells are either selective for the colour or brightness of a stimulus (Livingstone & Hubel, 1988) while interblob neurons are selective for the orientation of multiple types of stimuli (Hubel & Wiesel, 1968; Hubel, Wiesel, & Stryker, 1978). This subdivision of parvocellular input is thought to underlie the separated processing of form and colour (DeYoe & Van Essen, 1988; Livingstone & Hubel, 1988; Maunsell & Newsome, 1987) in earlier visual processing areas such as V1 and V2. In V2, the division of colour and form information continues as V1 blob and interblob outputs project to the thin and interstripes of V2 respectively (DeYoe & Van Essen, 1988; Livingstone & Hubel, 1988; Maunsell & Newsome, 1987). Notably, cells that encode border ownership (Zhou, Friedman, & von der Heydt, 2000) suggest that object representations in the ventral pathway undergo their first stage of assigning an oriented edge to a particular object as early as V2. In V4 centre-surround interactions allow for the processing of the perceived colour of a stimulus (Schein & Desimone, 1990; Zeki, 1980, 1983a,b). Therefore, V4 represents the first stage at which perceived colour can be incorporated into an object representation. Building on orientation processing in V1 and V2, cells in V4 encode more complicated borders such as angles and curvatures (Pasupathy & Connor, 1999). Object processing in V4 advances from the initial border ownership (Orban, 2008), seen in V2, to responses that encode the relative position of a curvature to the centre of a shape (Pasupathy & Connor, 2001). Later stages of the colour and form pathway include areas in the inferior temporal (IT) cortex. Selectivity in the IT cortex progresses from simpler features posteriorly (PIT or TEO: Kobatake & Tanaka, 1994; Tanaka, Saito, Fukada, & Moriya, 1991) to complex shapes and objects anteriorly (AIT or TE), including combinations of colour or texture with shape (Desimone, Albright, Gross, & Bruce, 1984; Gross, Rocha-Miranda, & Bender, 1972; Tanaka et al., 1991), and body parts (Gross, 2008). This progression of hierarchical processing of form and colour in the ventral pathway results in internal object representations and ultimately, object recognition (Cowey & Weiskrantz, 1967; Dean, 1976; Gross et al., 1972; Gross, Cowey, & Manning, 1971). Not surprisingly then, this pattern of neural responses and selectivities is functionally associated with processing 'What' a stimulus is (Livingstone & Hubel, 1988; Mishkin, Ungerleider, & Macko, 1983), or (based on losses in patients with ventral pathway damage) 'vision for perception' (Goodale & Milner, 1992).

1.2.2 Dorsal Pathway

While associating the ventral pathway with the function of processing 'What' a visual stimulus is remains relatively uncontroversial (Kravitz, Saleem, Baker, & Mishkin, 2011), succinctly and concisely assigning function to the dorsal pathway has been more difficult. Originally classified as the 'Where' pathway (Ungerleider & Mishkin, 1982), based on the pattern of spared and lost functions in patient D.F., the dorsal route later became functionally known as the 'How' or 'vision for action' pathway (Goodale & Milner, 1992). More recently, it has been suggested that even this categorization may be an over-simplification (Kravitz et al., 2011 – see Figure 1.3) with the dorsal pathway giving rise to at least three separate processing streams. The following anatomical and functional description of the dorsal pathway however, will focus on motion processing (from the retina through the Medial Superior Temporal (MST) area and into the parietal cortex), and also on what Mishkin and colleagues refer to as the parieto-premotor pathway (Kravitz et al., 2011) which itself contains relatively separate regions that control either reaching or grasping (Rizzolatti & Matelli, 2003).

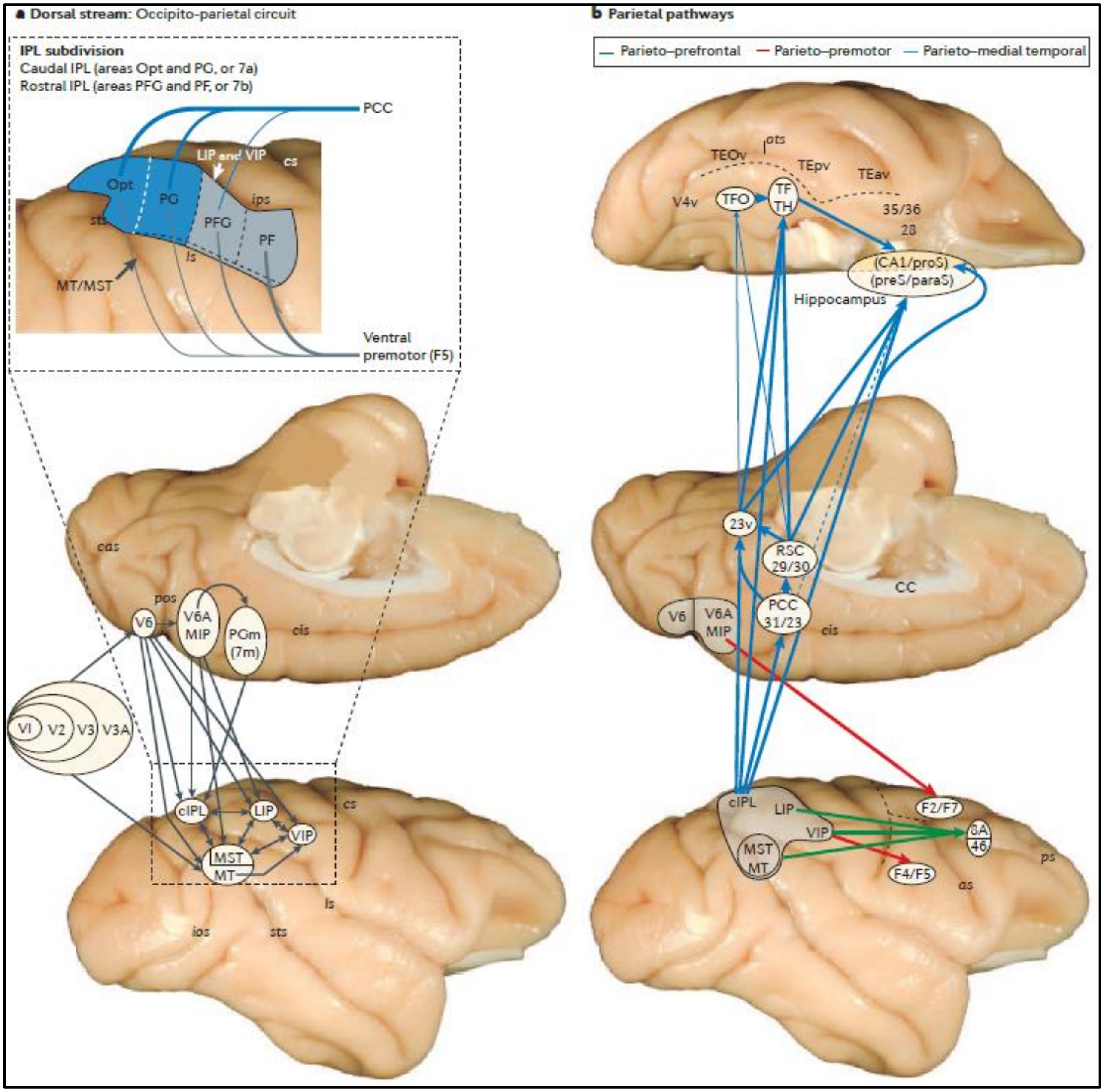

Figure 1.3: Suggested pathways that arise from the dorsal occipito-parietal circuit. (Taken from Kravitz et al., 2011). The parieto-prefrontal, parieto-premotor, and parieto-medial temporal pathways are thought to support spatial working memory, visually guided action, and spatial navigation respectively.

In contrast to the P cell mediated ventral pathway, M cells project from the retina to the two ventral magnocellular layers of the LGN (Livingstone & Hubel, 1988; Shapely & Perry, 1986). From here magnocellular information enters layer 4Cα of V1 and projects to V2 from layer 4B (Livingstone & Hubel, 1988). Cells at this level of the hierarchy are selective for the direction of motion (Movshon & Newsome, 1996; Orban, Kennedy, & Bullier, 1986), respond to motion of oriented gratings, bars, or edges (Adelson & Bergen, 1985; Hubel & Wiesel, 1968; Hubel et al., 1978) and show spatiotemporal tuning indicative of early speed selectivity (Orban et al., 1986; Priebe, Lisberger, & Movshon, 2006). Importantly, cells in V1 only process the local motion of a stimulus, likely due to small receptive field sizes, and not the overall, global motion of a complex visual stimulus (Movshon & Newsome, 1996). They also have little or no selectivity for colour (Livingstone & Hubel, 1985; Movshon & Newsome, 1996). A good portion of the input to the Middle Temporal (MT) visual area comes from layer 4B in V1 (Born & Bradley, 2005; Felleman & Van Essen, 1991; Maunsell & Newsome, 1987) however, some motion information passes to the thick stripes in V2, and V3 prior to reaching MT (Hubel & Livingstone, 1987; Levitt, Kiper, & Movshon, 1994; Livingstone & Hubel, 1988). Along with selectivity for motion direction, speed, and spatial frequency (Albright, 1984; Brooks, Morris, & Thompson, 2011; Lagae, Raiguel, & Orban, 1993; Maunsell & Van Essen, 1983; Perrone & Thiele, 2001; Priebe, Cassanello, & Lisberger, 2003), area MT neurons can process both the local and global motion (Pack & Born, 2001) of multiple types of moving stimuli such as random dot patterns/kinetograms (RDK’s: Britten, Shadlen, Newsome, & Movshon, 1992; Snowden, Treue, & Andersen, 1992) and gratings (Adelson & Movshon, 1982; Rodman & Albright, 1989). As with cells in V1 that are sensitive to motion features, area MT neurons also show no sensitivity to colour (Dobkins & Albright, 1994; Gegenfurtner et al., 1994; Maunsell &

Van Essen, 1983; Shipp & Zeki, 1985; Zeki et al., 1991). Motion processing continues in MST which utilizes 2D motion information from MT to compute complex 3D motion such as rotations and expansions/contractions (Graziano, Andersen, & Snowden, 1994; Saito et al., 1986), optic flow (Duffy & Wurtz, 1991a,b), and self-motion (Duffy & Wurtz, 1995; Gu, Watkins, Angelaki, & DeAngelis, 2006). In addition, lateral MST (MSTl) is thought to be involved in the maintenance of smooth pursuit eye movements as it computes object velocity information (Ilg, 2008; Tanaka, Sugita, Moriya, & Saito, 1993). From MT/MST, motion information is projected to a number of parietal areas, including the lateral intraparietal (LIP) and anterior intraparietal (AIP) areas (Kravitz et al., 2011; Rizzolatti & Matelli, 2003). As an output of MT, LIP has been shown to accumulate motion information that leads to perceptual decision-making (Huk & Shadlen, 2005; Palmer, Huk, & Shadlen, 2005; Shadlen & Newsome, 1996).

Along with the preponderance of motion processing in the dorsal pathway, a second major function arises from dorsal pathway projections into parietal areas. For example, projections from MT/MST to AIP, along with connections to the ventral premotor cortex (PMv) in the frontal lobe, are thought to form a dorsolateral circuit specialized for grasping (Fagg & Arbib, 1998; Filimon, 2010; Gallese, Murata, Kaseda, Niki, & Sakata, 1994; Luppino, Calzavara, Rozzi, & Matelli, 2001; Sakata, Taira, Murata, & Mine, 1995; Taira, Mine, Georgopoulos, Murata, & Sakata, 1990). Although not historically included in the dorsal pathway, recent research has shown that a visual area in the parietal-occipital (PO) region, V6, projects to V6A which in turn forms a dorsomedial circuit, along with the medial intraparietal (MIP) area and the dorsal premotor (PMd) cortex, that is specialized for reaching (Caminiti, Ferraina, & Johnson, 1996; Passarelli et al., 2011; Rizzolatti & Matelli, 2003). What is intriguing about the grasping circuit especially is that activity in AIP has been found to be modulated by the orientation and configuration (Taira et al., 1990), and shape and size (Murata, Gallese, Luppino, Kaseda, & Sakata, 2000) of a to-be-grasped object. It has also been implicated in the appropriate preshaping of the hand during grasping activities (Gallese et al., 1994). These functions would logically appear necessary for the guidance of visuomotor grasping, however, object processing is not a function typically associated with the dorsal pathway.

1.3 Object Processing in the Dorsal Pathway

Based on the anatomical and functional segregation between the pathways it may seem counterintuitive to study object representations in the dorsal pathway as this is generally a function assigned to the ventral stream of processing. Consequently, much of the literature surrounding how an object is formed and where in the processing hierarchy feature integration and object representations occur is generally limited to investigations of the ventral pathway. In spite of this body of work, how the brain integrates features (that are processed in anatomically and functionally separate regions and pathways) into an object is still one of the fundamental unanswered questions in neuroscience. Investigating object representations within the dorsal pathway allows the unique opportunity to understand how information from different visual pathways is combined and utilized. The function and possible location of these dorsal pathway object representations, the constraints under which both ventral and dorsal stream features are incorporated into them, and their impact on visual processing has been a key interest of our lab and some of our findings are presented in chapters two and three of this dissertation.

1.3.1 Evidence for Dorsal Pathway Object Representations

Given that visuomotor regions within the parietal cortex show selectivities for object features (Murato et al., 2000; Taira et al., 1990), and patients with ventral stream damage retain their ability to scale and orient their hand when grasping objects (Goodale et al., 1994; Goodale, Milner, Jakobson, & Carey, 1991; Milner, Ganel, & Goodale, 2012), there appears to be some form of object representation used by the dorsal pathway. Both neurophysiological and neuroimaging studies support the idea that there is some level of object processing within the dorsal pathway. As already mentioned, it has been shown that parietal regions associated with grasping (AIP) show cells that are selective for the type of object presented and the object's axis of orientation (Murata et al., 2000; Taira et al., 1990), and for the shape and size of objects (Murata et al., 2000). In addition to AIP, other parietal areas also show selectivities for object related properties more often associated with ventral stream processing. For example, area LIP has been associated with selectivity of simple, 2D geometric shapes (Sereno & Maunsell, 1998), is sensitive to the shape and depth structure of small 2D objects (Durand et al., 2007), and associated with shape encoding that is distinct from that seen in the anterior IT cortex (Lehky & Sereno, 2007). As well, the caudal aspect of the lateral intraparietal sulcus (CIP), which lies between areas LIP and V3A, has been shown to utilize both disparity and perspective cues in order to perceive the orientation of a surface in depth (Tsutsui, Jiang, Yara, Sakata, & Taira, 2001). A similar pattern of results has been shown to occur in human populations also (Konen & Kastner, 2008; Peuskens et al., 2004). Activity in human dorsal pathway regions has been associated with processing basic object information such as shape, size, and viewpoint, and also the processing of 3D shape. Interestingly, one neurophysiology study suggested that objects may be represented as early as area MT in the dorsal pathway and be formed by features processed in the different pathways. Simple objects, such as a surface defined by a colour (ventral pathway) and direction of motion (dorsal pathway) were shown to capture attention and increase neuronal firing rates over an unattended surface in area MT (Wannig, Rodríguez, & Freiwald, 2007). Of note in this study was the use of superimposed random dot patterns that eliminate the possibility that the modulation of MT firing rates could have been driven by spatial-based attention mechanisms.

A series of human psychophysical studies show this quite eloquently (Reynolds, Alborzian, & Stoner, 2003; Rodríguez, Valdés-Sosa, & Friedwald, 2002; Valdés-Sosa, Cobo, & Pinilla, 1998, 2000). Using superimposed random dot patterns that moved in different directions and were different colours, Valdés-Sosa and colleagues (1998, 2000) found a similar object-based effect to that of Duncan (1984) who tested object-based attention in the ventral pathway. They found that two discriminations of one surface were more accurate than two discriminations made on different surfaces. This was true when the dots in each surface were different colours (Reynolds et al., 2003; Valdés-Sosa et al., 1998, 2000) or if the surfaces were made up of different shapes (circles vs. squares, Rodríguez et al., 2002). This effect was seen whether the surface to attend to was cued endogenously (through the colour of the fixation point) or exogenously through the first brief surface translation (i.e. attention remained on the surface that had translated first - Reynolds et al., 2003). Also of note is the finding that direction discriminations of one surface are more accurate than direction discriminations of both surfaces, an effect that is exacerbated with a decrease in presentation time (Valdés-Sosa et al., 1998). It could be argued that instead of object-based attentional mechanisms underlying this pattern of results, a feature-based mechanism tied to the different colours of the surfaces might result in less accurate judgements of the uncued surface (Mitchell, Stoner, Fallah, & Reynolds, 2003). The authors argued that if this was the case, the impairment seen when discriminations are made of two surfaces instead of one should be eliminated if the surfaces are the same colour. They instead found that, when the surfaces were the same colour, discriminations of two surfaces were still impaired suggesting that feature-based mechanisms could not account for the impairment. Finally, having established that superimposed dots, which are different colours or shapes, and move in different directions, form object representations as early as area MT, Tchernikov and Fallah (2010) wanted to test whether the presence of surface colour differences would automatically modulate motion processing output such as smooth pursuit eye movements. They found that not only did colour modulate smooth pursuit velocity, differences in the colour of superimposed surfaces drove surface selection in a predictable manner. To summarize then, the integration of features processed by different visual pathways appear to form object representations as early as area MT that in turn modulate neuronal firing rates through object-based selection mechanisms and alter the output of dorsal stream dependent processing.

1.3.2 Processing of Superimposed Random Dot Kinetograms in Area MT

Building upon these studies we wanted to know if a feature processed exclusively by the ventral pathway (colour) could alter a perceptual dorsal pathway output, direction discrimination (Perry & Fallah, 2012). To do so we again utilized a paradigm of two superimposed, moving, random dot kinetograms (RDK's). There are a number of benefits to using these stimuli. As mentioned previously, the superimposition of two surfaces controls for the effects of spatial attention and surfaces that are a combination of a colour and direction of motion are not selected through feature-based mechanisms. We can therefore draw conclusions about feature integration, object processing, and object representations in the dorsal pathway. In addition, the use of superimposed RDK's very specifically targets area MT. Due to an increase in receptive field size, neurons at the level of MT show an ability to process both the local (component) and global (plaid/pattern) motion of either RDK (Britten et al., 1992; Snowden et al., 1992) or grating (Adelson & Movshon, 1982; Rodman & Albright, 1989) stimuli and therefore are thought to solve the aperture problem associated with smaller receptive fields by pooling, or integrating, motions (Born & Bradley, 2005 – see Figure 1.4). However, MT is also thought to be able to parse motion directions (Stoner & Albright, 1992, 1996), for example, when two moving surfaces are superimposed. In this case instead of integrating the motion directions, MT can break down the image into its component parts to indicate the direction of motion for both surfaces.

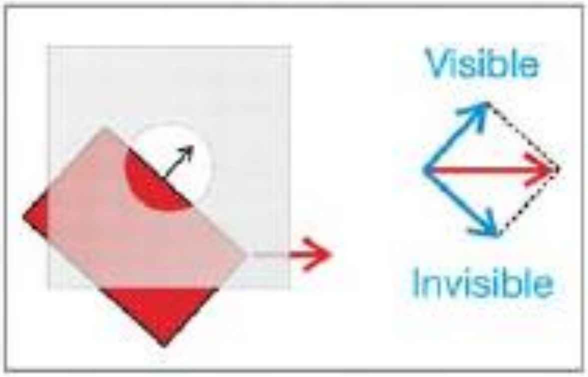

Figure 1.4: The aperture problem. Taken from Born & Bradley, 2005. Neurons with a small receptive field would inaccurately indicate that the motion of this object was up and to the right. With the increase in receptive field size in area MT, both component motions (arrows in blue on the right) that would be computed by two small receptive fields, would be integrated in order to give the real direction of rightward motion.

1.3.3 How Object Colour Affects Dorsal Pathway Processing

In spite of these characteristics that allow MT to both integrate and parse motion information when necessary, the superimposition of either gratings or RDK's actually produces a motion illusion known at direction repulsion (Braddick, Wishart, & Curran, 2002; Curran & Benton, 2003; Hiris & Blake, 1996; Kim & Wilson, 1996; Marshak & Sekuler, 1979; Mather & Moulden, 1980). When two identical surfaces (except for their motion directions) are superimposed, the directions of motion of the surfaces are misperceived as being further away from each other than they really are. Previous literature has shown that the illusion can result in directions being repulsed away from the real directions of motion by between 4 and 20^{o} (Braddick et al., 2002; Marshak & Sekuler, 1979).

This particular illusion allowed our lab to investigate the integration of features from different visual pathways on the perceptual output of direction processing in area MT (Perry & Fallah, 2012). We compared direction repulsion (DR) between two conditions; one in which both of the superimposed surfaces were white (unicolour condition) and the surfaces were only differentiated by their direction, and the other in which one surface was red and the second surface was green (colour-segmented condition). In this condition the surfaces would be more distinct from each other as they would be differentiated by both their direction of motion and their colour. If colour (a ventral stream feature) is integrated into a dorsal stream object representation prior to direction processing in MT, we would expect that direction repulsion would be reduced in the colour-segmented condition over that seen when both surfaces were white and only differentiated by their direction. However, this was not the case; direction repulsion in the unicolour condition was not significantly worse than in the colour-segmented condition (Figure 1.5 – from Perry & Fallah, 2012).

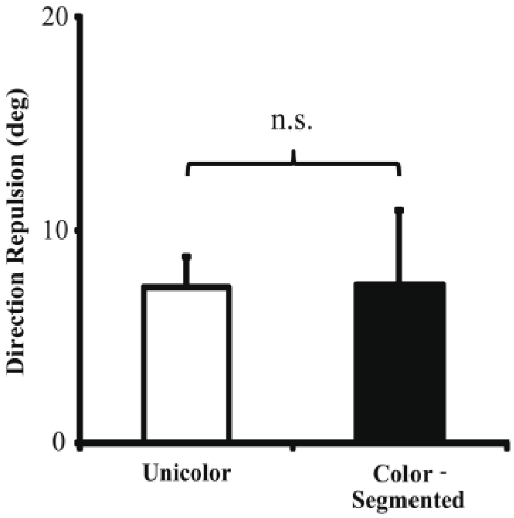

Figure 1.5: Effect of color on direction repulsion. Taken from Perry & Fallah, 2012. There was no significant reduction in DR when the surfaces were segmented by color (color-segmented condition: DR = 7.32 ± 1.45°) compared to when both surfaces were white (unicolor condition: DR = 7.45 ± 3.50°).

This was a bit surprising to us as previous work had found that when signal dots were segmented from noise dots by colour, direction sensitivity improved (Croner & Albright, 1997, 1999). However, the colour of the noise dots in this case, was always known ahead of time and therefore colour could have acted as a filter that removed the influence of the noise dots on the processing of the colour dots that were moving coherently. And in fact, this was the case when the responses of neurons in area MT were recorded (Croner & Albright, 1999). In our study, the dots contained in both surfaces moved with 100% coherence and on each trial the participant had to report the direction of both the red surface and of the green surface and could not just simply ignore the colour of one set of dots. That being said, intuitively there was something that made the colour-segmented task seem easier. We therefore decided to also calculate how often participants were able to correctly determine both directions of motion. Interestingly, total error rates in the unicolour condition were significantly worse than in the colour-segmented condition.

This improvement in the total error rate was driven by how often participants were able to only correctly determine one of the directions of motion, meaning that when both surfaces were white, participants more often did not correctly determine the second direction of motion. We hypothesized that this might be the case due to a stimulus presentation time of 1000ms in both conditions. We wondered if when the surfaces were both white, participants did not always have enough time to correctly process both directions of motion. To investigate this, we used the same stimuli but presented them in a staircase design that allowed us to vary the time that the stimuli were on-screen (stimulus duration). This is turn allowed us to determine the amount of time needed to process both directions of motion. Consistent with our hypothesis there was a significant advantage, in the amount of time needed to process both directions of motion, when the surfaces were segmented by colour (Figure 1.6 – Perry & Fallah, 2012). These results indicated an interesting dichotomy. Colour did not affect the perceptual report of direction (DR was not altered) but did greatly reduce the time needed to process the directions of motion.

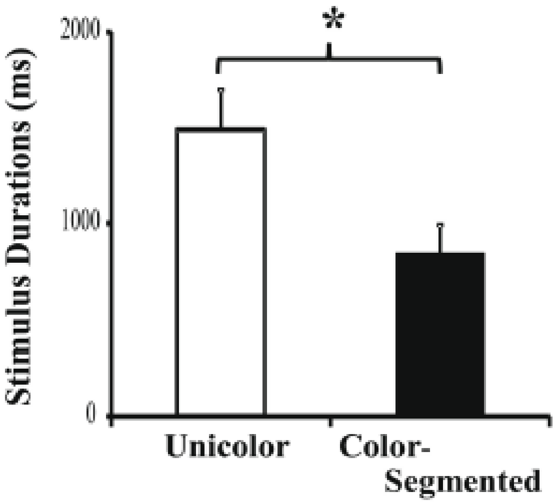

Figure 1.6: Effect of color on stimulus duration and processing time. Taken from Perry & Fallah, 2012. There was a significant reduction in the time needed to process both directions of motion in the color-segmented condition (842 ± 150ms) compared to the unicolor condition (1488 ± 209ms).

This suggested to us that colour was not a part of an object representation prior to the computation of direction in MT but was integrated into a dorsal stream object representation at some point after this as colour did affect processes downstream of area MT which lead to a decrease in processing time. In this case, the presence of an object representation in the dorsal stream that included colour allowed for the selection of one moving object over the other, based not just on motion computations (as in the unicolour condition) but on the increased distinction between the objects created by the differing surface colour. This object based selection in turn enhances visual processing of the object by reducing the time needed to complete the direction processing and decision-making associated with both surfaces.

1.4 Enhanced Visual Processing Near the Hand

A growing body of evidence has shown that visual processing can also be enhanced when a reach places the hand near to-be-processed visual stimuli. These effects include improved target discrimination (Deubel, Schneider, & Paprotta, 1998), reaching and grasping precision (Brown, Kroliczak, Demonet, & Goodale, 2008), and orientation processing (Bekkering & Neggers, 2002; Craighero, Fadiga, Rizzolatti, & Umiltà, 1999; Gutteling Kenemans, & Neggers, 2011, Gutteling, Park, Kenemans, & Neggers, 2013; Hannus, Cornelissen, Lindemann, & Bekkering, 2005), in addition to speeded target detection and figure-ground assignment (Reed, Betz, Garza, & Roberts, 2010; Reed, Grubb, & Steele, 2006; Jackson, Miall, & Balsley, 2010). The results from these studies also reflect the relative importance of the space immediately surrounding the body (peripersonal space). Objects within this space are easily acted upon and, as with a computer desk, objects within this space are also likely used frequently and in non-standard ways (ie. moving a cursor on a vertical screen by moving a mouse across a horizontal surface) while often requiring a dissociation between the location of the eyes with respect to the hand and arm. The research contained in chapter four investigates the neural underpinnings of improved visual processing near the hand and provides a possible mechanism that suggests action-relevant object features may be enhanced near the hand due to links between the reaching and grasping motor networks and earlier visual processing areas.

This possible link between action and improved visual processing is hypothesized to be attentional selection (the preferential processing of a subset of incoming visual information). Attention has been shown to improve visual processing (Corbetta, Miezin, Dobmeyer, & Shulman, 1991; Posner, 1980). It is also well known that the oculomotor system can deploy visual attention and improve visual processing through feedback mechanisms (Corbetta et al., 1998; Deubel & Schneider, 1996; Moore & Armstrong, 2003; Moore & Fallah, 2001, 2004; Sheliga, Riggio, & Rizzolatti, 1994; Shepherd, Findlay, & Hockey, 1986). Work in both normal (Abrams, Davoli, Du, Knapp, & Paull, 2008; Reed et al., 2010; Reed et al., 2006) and patient (Brown et al., 2008; di Pellegrino & Frasinetti, 2000; Schendel & Robertson, 2004) populations has suggested that visual processing near the hand may also be modulated through attentional mechanisms. As with the oculomotor system, in which the plan to move the eyes deploys spatial attention and improves visual processing at the end point of the planned eye movement, it may be that a similar mechanism exists within the motor system that governs reaching and grasping. However, more recently an alternative explanation for near-hand effects has been suggested that involves enhanced magnocellular (dorsal pathway) processing (Gozli, West, & Pratt, 2012). This alternative will be discussed further in chapter five, in relation to the proposed neural mechanism presented in chapter four.

1.4.1 Attention and the Oculomotor System

In spite of its complexity and processing capacity, the brain is limited in how much sensory information it can process at a given time. This limitation drives the need for a mechanism through which relevant stimuli can be selected for in depth processing. This mechanism is known as selective attention and allows for the analysis of certain subsets of stimuli at the expense of other stimuli within the environment. It can be thought of as a means of allocating processing resources to stimuli that are currently relevant to behaviour. Visual selective attention can be directed to locations in space (spatial attention), to features of an object (feature-based attention), or to objects themselves (object-based attention). The simplest way to select certain visual stimuli for further analysis is to look directly at them (overt attention). Selection however, can also occur covertly (without a corresponding eye movement – Sperling & Melchner, 1978).

The relationship between the oculomotor and visual selective attention systems was proposed as the premotor theory of attention (Rizzolatti, Riggio, Dascola, & Umiltá, 1987). The premotor theory suggests that it is feedback from the oculomotor system that deploys spatial attention (Moore & Fallah, 2001, 2004) and enhances neuronal responses at the attended location (Moore & Fallah, 2004). This enhancement results in improved behavioural performance. Planned eye movements improve response times, correct detection rates and discrimination, and temporary inactivation of the frontal eye fields (FEF) using TMS shows a decrease in discrimination performance (Deubel & Schneider, 1996; Dore-Mazars, Pouget, & Beauvillain, 2004; Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995; Neggers et al, 2007; Sheliga et al., 1994; Shepherd et al, 1986). Human neuroimaging studies provide additional support by showing that the same network of brain regions that are involved in saccade planning are also activated by visual spatial attention (Corbetta et al., 1998; Corbetta, et al., 1991; Coull & Nobre, 1998; Hopfinger, Buonocore, & Mangun, 2000; Perry & Zeki, 2000).

1.4.2 Visual Processing Near the Hand

In most situations looking at, or planning to look at, a reach target is possible and preferable. There are circumstances however, that do not lend themselves well to having an attentional system that is driven solely by the oculomotor system. For example: reaching for objects when the eyes are fixated elsewhere (Henriques, Klier, Smith, Lowry, & Crawford, 1998), scanning for future potential targets while currently grasping an object (Terao, Andersson, Flanagan, & Johansson, 2002), and engaging in activities such as driving a car that require ‘non-standard’ transformations (Hawkins, Sayegh, Yan, Crawford, & Sergio, 2013). In such situations it is necessary to dissociate incoming visual information associated with where we are looking from incoming visual information associated with where we are (or are going to be) reaching. Given the need to, on occasion, divide attention between visual and motor tasks, it may be possible that other effector systems, such as the reaching/grasping system, also drive attention-related enhancement of visual processing.

In fact, accumulating evidence in both patient and normal populations suggest a link between the hands as an effector and attentionally driven improvements in visual processing (Abrams et al., 2008; Brown et al., 2008; di Pellegrino & Frassinetti, 2000; Reed et al., 2006; Schendel & Robertson, 2004). Blindsight refers to the remaining, non-conscious, visual ability after damage to primary visual cortex (V1). In this population visual stimuli detection is possible but not perceived by the individual. However, when a patient places their hand within the blind field visual processing is improved. Stimulus detection increases (Schendel & Robertson, 2004) and more accurate size perception occurs (Brown et al., 2008). In extinction, patients have difficulty attending to, and thus perceiving, a visual stimulus in the contralesional hemifield when a second stimulus is presented in the same (ipsilesional) hemifield. In this case, visual stimuli presented near the hand within the affected hemifield results in improved target identification (di Pellegrino & Frassinetti, 2000).

Visual processing is also altered near the hand when normal populations are tested using attentional paradigms. In a classic spatial attention task (Posner, 1980), participants fixate centrally and are then presented with a flashed cue (to draw attention) and subsequently a target to which they respond as quickly as possible. The cue and the target are presented in one of two locations on either side of the fixation point and can appear in the same location or in different locations. Under normal conditions, reaction times are faster when the cue and the target appear in the same location and slower when the cue appears on the opposite side to the target. When a hand is placed near one of the target locations however, reaction times are faster when the target appears near the hand regardless of whether the cue was on the same or opposite side (Reed et al., 2006). This suggests that when the hand is present spatial attention is deployed to the region near the hand and offsets the allocation of attention to the cue when it appears on the side opposite to the target. Using three additional visual attention tasks (visual search, inhibition of return, attentional blink), Abrams and colleagues (2008) showed why the hand may facilitate reactions times even when a cue on the opposite side should under normal conditions draw attention away and increase reactions times to the target. The results of these experiments showed that participants were slow to disengage their attention when the objects under inspection were close to the hands. They suggest that this would facilitate more detailed processing of objects that may be action targets. In the preceding cases, a sustained reach plan was utilized in the hand conditions. The hand was placed near the visual display and this posture was maintained throughout the block of trials. Because of this, it could be argued that no movement occurred and a link between the reaching/grasping networks and attentionally driven improvements in visual processing is unlikely. In these cases, the execution of a reach plan would result in a dynamic movment that placed the hand in the location used for testing. In order to keep the hand in this position however, a static reach position would need to be maintained through a continued activation of some, if not all of the muscles, used in the dynamic reach plan. In essence, the end goal of the reach plan must be maintained. This continued activation may be the input needed to inform attentionally driven improvements in visual processing near the hand.

There is evidence showing that when a reach placing the hand near to-be-processed visual stimuli is either planned (with no resulting movement) or executed (involving a dynamic movement), there is attentional deployment and improved visual processing in these cases also (Bekkering & Neggers, 2002; Craighero et al., 1999; Deubel et al., 1998; Fagioli, Ferlazzo, & Hommel, 2007; Hannus et al., 2005; Symes, Tucker, Ellis, Vainio, & Ottoboni, 2008). Using a deviant detection task, Fagioli and colleagues (2007) showed that the detection of both location and size deviants was facilitated when a hand movement was viewed prior to the presentation of the visual stimuli. When a pointing movement was viewed, detection of location deviants was facilitated and when a grasping movement was viewed, detection of size deviants was facilitated. In addition, Symes and colleagues (2008) found that size processing could also be altered with planned hand movements. Using a change blindness paradigm consisting of an array of both small and large objects, they showed that when participants prepared a whole-hand power grasp, detection of changes in large objects was facilitated. However, when preparing a forefinger-and-thumb precision grip, detection of changes in small objects was facilitated. Furthermore, employing a 2-alternative forced choice task, it has been shown that discrimination between two similar letter objects is improved when a pointing movement is made to the location in which the visual stimulus appears (Deubel et al., 1998).

In addition to changes in processing of location, size and shape with intended and executed hand movements, a number of studies have shown that processing of orientation is also altered with planned movements of the hand (Bekkering & Neggers, 2002; Craighero et al. 1999; Gutteling et al., 2011; Hannus et al., 2005). Grasping movements made towards congruent targets (those that matched the orientation of the cue) were faster than those to incongruent or neutral (cue was a circular object rather than a bar) targets. Furthermore, it appears that the plan to move the hand is enough to facilitate orientation processing; the previous results were replicated even when the foot was used as the response effector (Craighero et al., 1999). This suggests a link between the planned hand movement and altered visual processing in the absence of an execution of the hand movement and without the hand being close to the visual target. Of note are two studies that suggest that action-relevant object features (orientation) that are to be grasped, show enhanced processing. Bekkering and Neggers (2002) found that orientation selection was improved when participants were to grasp the visual target (oriented bars) as opposed to when they were to point to the target. Color selection however, was not improved in the grasp condition. In more recent work it was again shown that orientation sensitivity was improved, but not luminance sensitivity, when a grasp versus a pointing action was executed (Gutteling et al., 2011), suggesting that it may be action-relevant features that are affected by planned or executed hand movements and not just any object feature.

1.4.3 Motor Control Networks

Evidence from human neuroimaging studies suggest a prioritization of near-hand space in fronto-parietal regions involved in reaching and grasping (Brozzoli, Gentile, Petkova, & Ehrsson, 2011;

Gallivan, Cavina-Pratesi, & Culham, 2009; Makin, Holmes, & Zohary, 2007). Priortization, in these terms, simply means that if multiple stimuli compete for attentional resources across a scene, stimuli near the hand receive preference for further processing. In other terms, the processing of stimuli near the hand is prioritized over the processing of stimuli appearing away from the hand. This can be seen in the work by Reed and colleagues (2006), where attention remained tied to the hand even when the cue had been presented away from the hand, potentially drawing attention away from the hand. A link between arm movements and attentional processes has also been suggested recently (Galletti et al., 2010) through neuronal recordings in area V6A, an area known to be involved in reaching movements. The proposal here then, is that much like feedback from the oculomotor system deploys spatial attention and improves visual processing, feedback from the reaching and/or grasping networks will deploy attention to near-hand space and improve visual processing of stimuli within this region. To understand feedback mechanisms, it is first helpful to know a little about the fronto-parietal neural networks that are involved in reaching and grasping.

Reaching Network

In the non-human primate, there are consistently three main regions shown to be involved in reaching movements. They are V6A (PO) and the medial intraparietal (MIP) areas, also collectively known as the parietal reach region (PRR - Andersen & Buneo, 2002; Cohen & Andersen, 2002), and the dorsal premotor cortex (PMd) in the frontal lobe (Caminiti, Johnson, Galli, Ferraina, & Burnod, 1991; Crammond & Kalaska, 1996; Johnson, Ferraina, Bianchi, & Caminiti, 1996). V6A neurons show modulation during arm movements (Galletti, Fattori, Kutz, & Battaglini, 1997), and during reaching movements to visual or remembered targets (Fattori, Gamberini, Kutz, & Galletti, 2001). They have also been found to be modulated by the location of the target, the direction of arm movement, the position of the arm/hand in space and the orientation of the object to be grasped (Fattori, Kutz, Breveglieri, Marzocchi, & Galletti, 2005). Although commonly thought to be a reach-related area, recent work also suggests a role for V6A in grasping-related activity in both human and non-human primate populations (Fattori et al., 2009, 2010; Fattori, Breveglieri, Raos, Bosco, & Galletti, 2012; Gallivan, McLean, Valyear, Pettypiece, & Culham, 2011; Monaco et al., 2011). Direct anatomical connections between V6A and early visual processing areas (Passerelli et al., 2011; Fattori, Breveglieri, Bosco, Gamberini, & Galletti, 2015) would facilitate feedback connections that could drive enhanced visual processing in the proposed mechanism.

Damage to area MIP causes misreaching errors (Rushworth, Nixon, Passingham, 1997) and under normal conditions neurons in this area are selective for hand direction (Eskander & Assad, 1999). In addition, neurons in MIP are selective for stimulus direction (Eskander & Assad, 1999). Information from these areas passes forward to PMd where responses are modulated by the direction and amplitude of arm movements (Caminiti et al., 1991; Johnson et al., 1996). However, activity tends to be confined to the period prior to movement onset (Crammond & Kalaska, 1996) suggesting a role for PMd in the selection and planning of movements. PMd responses indicate coding of movement direction or trajectory as opposed to the final position of the limb in space (Caminiti et al., 1991) which is consistent with reaching-related activity.

Grasping Network

As with reaching, it has been suggested that there is a circuit specialized for grasping (Fagg & Arbib, 1998; Filimon, 2010; Matelli & Luppino, 2001), and that this circuit is mainly dependent upon connections between the anterior intraparietal (AIP) region and the ventral premotor cortex

(PMv), specifically the rostral portion (PMvr – Luppino, Murata, Govoni, & Matelli, 1999). AIP neurons have been found to be modulated by the orientation and configuration (Taira et al., 1990), and shape and size (Murata et al., 2000) of the object to be grasped. AIP activity has also been implicated in the appropriate preshaping of the hand (Gallese et al., 1994). These studies combined show the intimate relationship between AIP activity and the shaping of the hand in response to object specifications. Despite any known *direct* anatomical connections with early visual processing areas it is possible that feedback mechanisms could be mediated through area V6A (Fattori et al., 2015) which does have direct connections with both AIP and early visual processing regions.

Recordings in PMvr (Rizzolatti et al., 1988) show that neuronal activity is related to grip type: different groups of neurons were active during precision grips, during finger prehension (grasping), or during whole hand prehension. Purely motor neurons within PMvr (F5) also show this selectivity for grip type regardless of the object to be grasped; if different objects are grasped but with the same grip type, neuronal activity is similar in each case (Murata et al., 1997). In contrast, activity of visuomotor neurons (neurons that respond during grasping but also upon object presentation) within PMv is so selective for object shape/grip type, that modeling the activity of as few as 16 neurons predicts the grip type with 95% accuracy (Carpaneto et al., 2011). Furthermore, inactivation of visuomotor neurons in PMv impairs hand posture preshaping (Fogassi et al., 2001).

Oculomotor Network

The oculomotor system for saccade generation also involves a frontoparietal network consisting of the lateral intraparietal (LIP) and frontal eye field (FEF) regions. As detailed previously, it has been found that this system deploys spatial attention and that moving, or planning to move, the eyes improves visual processing at the location of the intended eye movement. We suggest that a similar mechanism may exist for visual processing near the hand. Planning or execution of a reach/grasp would deploy attention to space near the hand and visual processing would be improved through feedback from the reaching and grasping networks.

1.4.4 Neuronal Response Patterns

Given that we are suggesting that the presence of the hand may alter neuronal responses in visual processing areas through attentional mechanisms, there is a need to understand how attention has previously been shown to alter neuronal responses. When attention is directed to a spatial location, neuronal responses undergo gain modulation (McAdams & Maunsell, 1999; Treue & Martinez-Trujillo, 1999). A neuron selective for orientation for example, will respond maximally when shown its preferred orientation and minimally for orientations orthogonal to the preferred. Responses for a full range of orientations tend to produce a bell-shape known as a tuning curve. With attention, this curve undergoes gain modulation, in which responses to all orientations will increase through a multiplicative factor. This means that if responses to the preferred orientation increase by 15%, responses to all orientations will increase by the same 15%.

Tuning curves may also appear to sharpen through a mechanism known as feature-similarity gain (Martinez-Trujillo & Treue, 2004). In this model of feature based attention, neuronal response to the preferred stimulus is enhanced when attended while responses are suppressed when the non-preferred stimulus is attended. This suggests that the strength of neuronal modulation is based on the similarity between the attended stimulus and the neuron’s preferred stimulus. In area MT, this differential modulation results in an improvement of direction selectivity in that neurons preferring the attended direction will show enhanced neuronal response rates while neurons tuned to the opposite direction will be suppressed (Martinez-Trujillo & Treue, 2004).

Evidence also indicates that a form of gain modulation occurs with object-based attention (Fallah, Stoner, & Reynolds, 2007). This mechanism known as biased competition (Chelazzi, Duncan, Miller, & Desimone, 1998; Desimone & Duncan, 1995; Luck, Chelazzi, Hillyard, & Desimone, 1997), supposes that visual objects compete for neuronal resources and that attention acts to bias resources to one stimulus over others in a cluttered environment. This bias results in enhanced neuronal response to the attended object (Chelazzi, Miller, Duncan, & Desimone, 1993; Chelazzi et al., 1998).

In chapter four, we specifically chose to investigate an *early* visual processing area (V2). Cells in V2 are well known for being orientation selective (Burkhalter & van Essen, 1986; Hubel & Livingstone, 1987; Levitt et al., 1994; Van Essen & Zeki, 1978), an action-relevant object feature, but do not respond to more complex stimuli (objects) as does the inferior temporal (IT) cortex (Kobatake & Tanaka, 1994; Komatsu & Ideura, 1993). For that reason, we expected that attentionally driven enhancement of neuronal responses in V2 would follow either the spatially or feature-based response patterns described above.

1.5 Research Objectives

There were a number of objectives that drove the following research. The first general objective was to understand more about feature integration and object representations within the dorsal pathway and their effect on visual processing. More specifically we wanted to know if dorsal stream features were integrated into dorsal pathway object representations and what effect this had on visual processing (chapter two), and understand what attentional constraints there may be on feature integration in the dorsal pathway (chapter three). The second general objective was to investigate improved visual processing near the hand. Specifically, we wanted to understand how the presence of the hand affected neuronal firing rates in area V2, if they followed a pattern consistent with either spatial or feature-based attention, and if the presence of the hand affected neuronal firing rate variability, which has been suggested to be a marker of feedback within the oculomotor system (chapter four).

Chapter 2. Manuscript 1: Feature Integration Within and Across Visual Streams Occurs at Different Visual Processing Stages.

This manuscript is published in the ***Journal of Vision***. The co-authors of this publication are Abdullah Tahiri, and Dr. Mazyar Fallah. Carolyn J Perry and Dr. Mazyar Fallah conceived, designed, and implemented the experiment. Carolyn J Perry and Abdullah Tahiri collected the data. Carolyn J Perry and Abdullah Tahiri analyzed the data. Carolyn J Perry and Dr. Mazyar Fallah reviewed the data. Carolyn J Perry prepared the manuscript. Carolyn J Perry and Dr. Mazyar Fallah revised and edited the manuscript.

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2.1 Summary

Direction repulsion is a perceptual illusion in which the directions of two superimposed surfaces are repulsed away from the real directions of motion. The repulsion is reduced when the surfaces differ in dorsal stream features such as speed. We have previously shown that segmenting the surfaces by color, a ventral stream feature, did not affect repulsion but instead reduced the time needed to process both surfaces. The current study investigated whether segmenting two superimposed surfaces by a feature co-processed with direction in the dorsal stream (ie. speed) would also reduce processing time. We found that increasing the speed of one or both surfaces reduced direction repulsion. Since color segmentation does not affect direction repulsion, these results suggest that motion processing integrates speed and direction prior to forming an object representation that includes ventral stream features such as color. Like our previous results for differences in color, differences in speed also decreased processing time. Therefore, the reduction in processing time derives from a later processing stage where both ventral and dorsal features bound into the object representations can reduce the time needed for decision making when those features differentiate the superimposed surfaces from each other.

2.2 Introduction

An object in the visual system is a representation of bound features from within and across the two visual streams (ventral and dorsal). However, it is not known at which stage of visual processing these features are bound together. Neurons within the middle temporal area (MT) possess the ability to process both local (component) and global (pattern/plaid) motion (Britten et al., 1992; Recanzone, Wurtz, & Schwartz, 1997) and are able to determine global motion direction apart from other randomly moving stimuli. This suggests that the inputs to MT are integrated in order to determine the global motion of several moving objects. Binding these features together makes area MT suitable for determining the motion directions of multiple objects within the same spatial location (Adelson & Movshon, 1982; Stoner & Albright, 1992, 1996) and in turn allows for the segmentation of a visual scene into objects and surfaces (Snowden, Treue, Erickson, & Andersen, 1991).

In spite of these characteristics that allow MT to process superimposed global motion, this type of motion has been shown to produce a perceptual illusion known as direction repulsion (Braddick et al., 2002; Curran & Benton, 2003; Hiris & Blake, 1996; Marshak & Sekuler, 1979; Mather & Moulden, 1980). In this case, the directions of motion of two superimposed surfaces are misjudged perceptually. Observers perceive the directions of motion as being further away from each other, e.g. repulsed from 4º to 20º away from each surfaces' real direction (Braddick et al., 2002; Marshak & Sekuler, 1979). In the classic direction repulsion paradigm, the surfaces are identical except for the direction in which they are moving. This means that first the local motion of the dots in each surface must be calculated before they can be segmented into two surfaces and then the overall direction of each surface can be processed and a decision threshold reached. However, the addition of a second surface feature, making the surfaces more distinct from one another, should provide additional information that could be used to reduce the competition between the surfaces' directions and attenuate the repulsion. And in fact, this is what occurs when the surfaces are different speeds (Curran & Benton, 2003; Marshak & Sekuler, 1979), or in the case of superimposed gratings, when the surfaces are different spatial frequencies (Kim & Wilson, 1996). Stereoscopic viewing, producing a real depth difference between the two surfaces, does not reduce direction repulsion however (Hiris & Blake, 1996). This is thought to be because superimposed surfaces are already perceived as being at different apparent depths (Hiris & Blake, 1996) and therefore stereoscopic depth cannot be used as an additional feature to aid in segmenting the surfaces.

Speed and direction, along with spatial frequency and depth, are all constituents of motion processing that occurs within the dorsal stream. Previously (Perry & Fallah, 2012), we tested whether the integration of a ventral stream feature, such as color, could also alter direction perception. Color is a motion-irrelevant feature, and neurons in area MT are not known to be color sensitive (Maunsell & Van Essen, 1983). In order for color to alter direction perception then, color information from the ventral stream would have to be integrated (or bound) to the surface before or at the time of motion processing in MT. We found that segmenting two superimposed surfaces by color did not alter direction repulsion but surprisingly, did significantly decrease processing time. This shows that color is not bound to motion before global direction processing in area MT occurs. However, color does affect processing time suggesting that color may affect decision-making in areas downstream of area MT (Huk & Shadlen, 2005; Hussar & Pasternak, 2013; Shadlen & Newsome, 1996, 2001; Zaksas & Pasternak, 2006). Therefore, color and motion are bound after global motion processing in area MT.

Based on those findings, we hypothesized that all segmentation cues bound to an object should speed up decision making about features of that object. Ventral stream features such as color showed just such an effect (Perry & Fallah, 2012). In the current study, we investigated whether speed segmentation cues would also reduce processing time. This is important to determine as motion processing in area MT is based on the conjunction of speed and direction, and thus the features are potentially linked before being integrated into the object’s representation. We expect that due to the conjunction, differences in speed will affect direction repulsion. However, that by itself should not reduce processing time. If we find that differences in surface speeds also produce reductions in processing time, then it suggests that speed information is also treated as a feature independent of direction at a later stage of decision making, similar to the effects of color differences. Alternatively, no changes in processing time would occur if velocity, aka the conjunction of speed and direction, is the feature bound into the object representation used by the decision-making circuitry.

2.3 Methods

2.3.1 Participants

Twelve naive participants (ages 18-23, 5 female) completed the 3/6:unicolor paradigm and an additional set of 12 participants (ages 18-39, 10 female) completed the 6/6:unicolor paradigm. All participants provided informed consent, had normal or corrected-to-normal visual acuity and none tested positive for color blindness using Ishihara color plates. Ethics approval was provided by the York University Human Participants Review Committee.

2.3.2 Procedure

Experiments were performed in a darkened, quiet room. Participants sat 57cm from a computer monitor (21” Viewsonic, 1028 x 1024 resolution, 60 Hz) with their head positioned and stabilized on a headrest (Headspot, UHCOtech). Participants wore a head-mounted infrared eye tracker (Eyelink II, SR Research Ltd., 500 Hz) monitoring the left eye. Superimposed random dot kinetograms (RDKs) were created using Matlab (The Mathworks Corp.) and experimental control was maintained using Presentation (Neurobehavioral Systems) software.

Each trial commenced with the participant fixating a white cross (Figure 2.1) centered on a black screen. 200ms later a circular aperture appeared in the lower right quadrant containing two superimposed surfaces containing 100% coherent RDKs (white: 122 cd/m^2, dot size = 0.04º, aperture size = 5º, dot density = 1.54 dots/degree^2). The experimental paradigm is the same as used previously (Perry & Fallah, 2012) except that instead of varying surface color we varied surface speed in the current study. In the 6/6:unicolor condition both surfaces moved at 6º/s. In the 3/6:unicolor condition one surface of dots moved at 3º/s and the other at 6º/s.

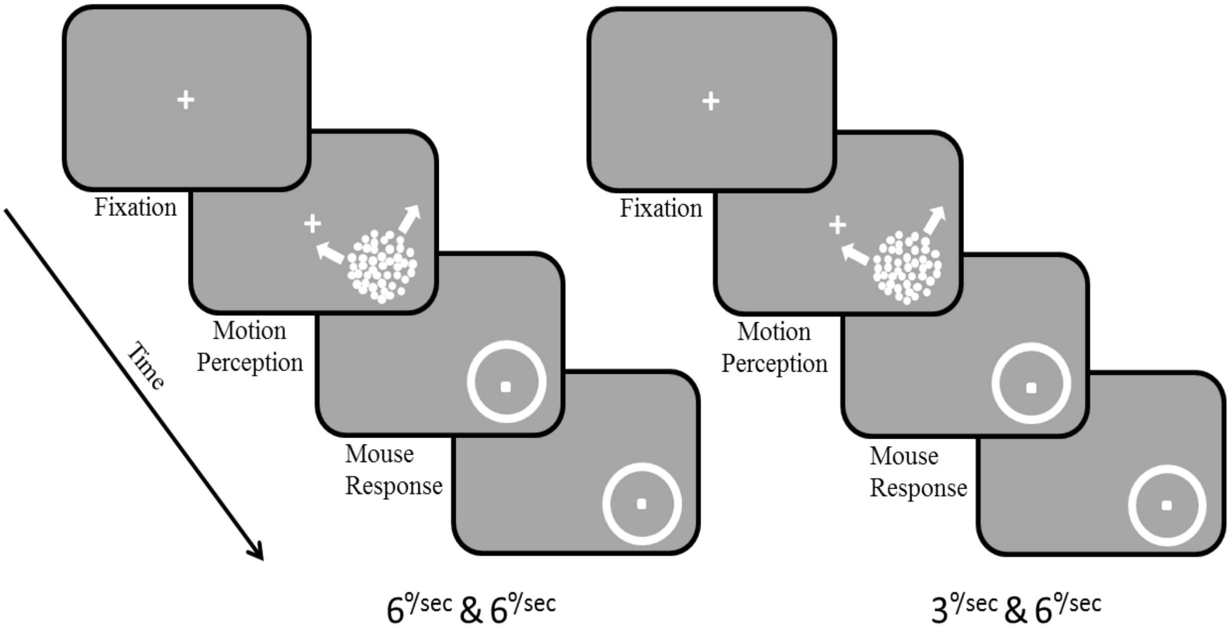

Figure 2.1: Experimental paradigm. In each condition, a trial is initiated with the appearance of a fixation point in the middle of the screen. When fixation has been maintained for 200ms, the superimposed RDK's are then presented in the lower right quadrant of the screen. Once the stimulus has disappeared, a circular outline is presented at the same location as the stimulus. Participants were to make two clicks on the same circle indicating the directions in which the two surfaces were moving. In the 6/6:unicolor condition, the surfaces both move at 6º/sec and in the 3/6:unicolor condition one surface moves at 3º/sec and the other at 6º/sec.

The surfaces moved in 12 directions relative to both the vertical and horizontal axes (±2º, 6º and 10º from either up or down and left or right). All directions appeared with equal frequency creating differences between the two directions that ranged from 70º and 100º. If fixation was broken before or during stimulus presentation, the trial was aborted and randomly replaced. After the stimulus disappeared, a circular outline (the response circle) replaced the aperture. The participant was required to make two mouse clicks on the response circle indicating the directions in which the two surfaces were moving.

Stimulus duration was varied using a staircase design (Perry & Fallah, 2012). A block consisted of 8 trials at a given stimulus duration (initial duration: 2000ms). If performance (the ability to get both directions correct) in a given block was ≥ 87.5% (7/8) the stimulus duration in the next block was decreased. When performance fell below this threshold, indicating the stimulus duration was not long enough to correctly determine both directions, stimulus duration in the subsequent block was increased. The staircase had two stages. In the first, stimulus duration increased or decreased by 500ms step sizes. Upon reaching a double reversal, stage two commenced in which the step size was 100ms. The staircase ended when a second double reversal occurred. This allowed us to estimate the time needed to correctly process both directions of motion to within ±50 ms.

2.3.3 Data Analysis

Correct responses were defined to allow for repulsion as in the previous study (Perry & Fallah, 2012): responses that fell within a range that extended from halfway between the two directions to 45º away from each real direction. A correct trial was defined as being any trial in which the participant determined both directions of motion within the ranges described above. Direction repulsion was calculated as the perceived direction minus the real direction of motion, so that positive values were indicative of direction repulsion. Means were calculated for both direction repulsion and processing time and independent t-tests were used to assess any statistical differences between the conditions. When comparing the data to the 3/3:unicolor condition from the previous study, one-way ANOVAs with Tukey post-hoc tests to control for multiple comparisons were utilized. The data was analyzed using Matlab and SPSS (SPSS Inc.).

2.4 Results

Previous work has found that increasing the strength of surface segmentation, using features processed within the dorsal stream, improved perception of direction (Kim & Wilson, 1996; Marshak & Sekuler, 1979). However, we previously determined that increasing the strength of surface segmentation using a ventral stream feature did not affect direction perception but instead reduced processing time (Perry & Fallah, 2012). In this study we wanted to determine if increasing the strength of surface segmentation using a dorsal stream feature would similarly reduce processing time in addition to improving direction perception. From the results, we can then determine when different features are bound together.

2.4.1 Direction Repulsion

To determine how a difference in speed: 3/6:unicolor, affects direction repulsion compared to equal speeds: 6/6:unicolor, and 3/3:unicolor from the previous study (Perry & Fallah, 2012), we performed a one-way ANOVA and post-hoc Tukey HSD tests. We found a significant effect of surface speeds on direction repulsion (Figure 2.2A, F(2,33) = 4.51, $p = 0.019$). Increasing the speed of both surfaces, in the 6/6:unicolor condition (DR: 10.10º ± 0.74 *SEM*), significantly reduced direction repulsion when compared to the 3/3:unicolor condition (DR: 13.93 ± 1.38 *SEM*, $p = 0.027$), consistent with increased speed of motion reducing direction repulsion

(Braddick et al, 2002). If there were no additional effect of speed segmentation on the attenuation of direction repulsion, then the repulsion in the 3/6 condition should fall between the repulsion in the 3/3 and 6/6 conditions, as the sum of the repulsion produced by one 3º/sec surface (13.93º/2 = 6.97º) and one 6º/sec surface (10.10º/2 = 5.05º) estimates a 12.02º repulsion. However, the repulsion in the 3/6 condition (10.47º) was significantly less from that seen in the 3/3: unicolor (previous study) condition (DR: 13.93º ± 1.38 *SEM*, $p < 0.05$) and was nearly identical to that in the 6/6 condition (10.10º, Fig 2A, $p = 0.961$). Therefore, speed segmentation likely provided additional attenuation of direction repulsion above that produced by an increase in the speed of one surface. Next we addressed the question of interest: does speed segmentation affect processing time?

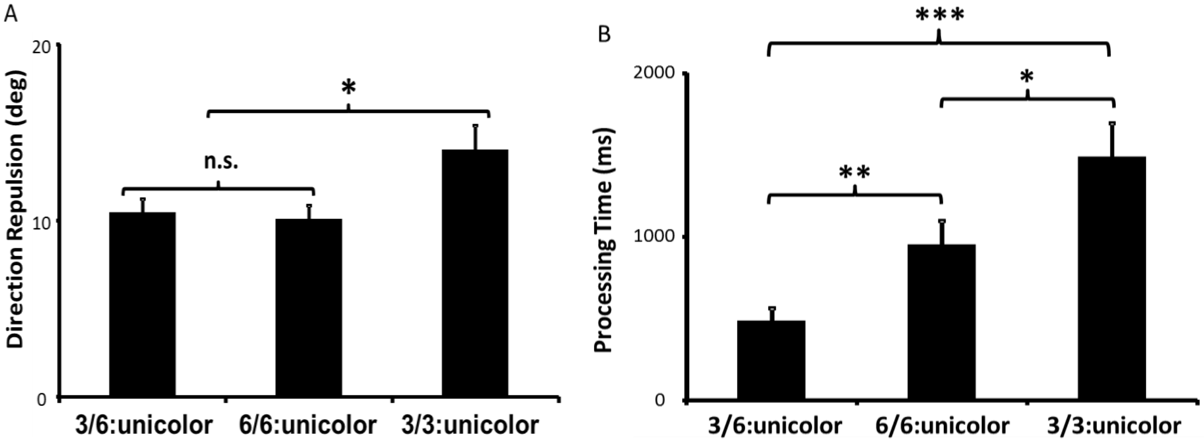

Figure 2.2: Direction repulsion and processing time. These graphs combine results from the current study and Perry & Fallah, 2012. **2A.** Direction Repulsion in the 3/6:unicolor (10.47º ± 0.74 *SEM*) and 6/6:unicolor (10.10º ± 0.74 *SEM*) conditions was not significantly different. Repulsion in these two conditions was significantly less than in the 3/3:unicolor (13.93º ± 1.38 *SEM*) condition. **2B.** Processing Time in the 3/6:unicolor (483ms ± 80.09 *SEM*) condition was significantly less than in the 6/6:unicolor (950ms ± 132.57 *SEM*) and the 3/3:unicolor (1488ms ± 208.5 *SEM*) conditions. Errors bars represent *SEM*.

2.4.2 Processing Time

When we compared the time needed to process both surfaces correctly (processing time, Figure 2.2B) in the 6/6:unicolor and 3/6:unicolor conditions, we found that speed segmentation afforded a significant (t(22) = 3.013, $p = 0.006$) advantage. The average time needed in the 6/6:unicolor condition, 950ms (± 132.57 *SEM*), was reduced by nearly 500ms (467ms) when the surfaces were different speeds (3/6:unicolor = 483ms ± 80.10 *SEM*). When compared to the results from our previous study, we found a significant effect of surface speed on processing time (F(2,33) = 11.23, $p < 0.001$). Segmenting the surfaces by increasing the speed of one surface (3/6:unicolor condition) significantly reduced processing time by ~1000ms when compared to the slower speed 3/3:unicolor condition (1488ms, ± 208.54 *SEM*, $p < 0.001$). However, increasing the speed of both surfaces (6/6:unicolor condition) reduced that benefit by half from ~1000ms to ~500ms, ($p = 0.042$). Therefore task-irrelevant speed segmentation cues reduce the processing time needed for direction judgments.

2.5 Discussion

2.5.1 Direction Repulsion

Using the same experimental paradigm as used previously (Perry & Fallah, 2012) we were able to determine how the speed of the surfaces affect direction repulsion under a number of conditions: two matching speeds (3/3:unicolor, 6/6:unicolor), and a speed segmentation condition where the speeds differed (3/6:unicolor). Consistent with previous literature, we found in the current study that differences in surface speed attenuated direction repulsion (Curran & Benton, 2003; Marshak & Sekuler, 1979). Also consistent with prior research (Braddick et al., 2002; Curran & Benton, 2003), we found that increasing the speed of both surfaces

(6/6:unicolor) similarly reduced direction repulsion, likely due to increases in speed strengthening the representation of motion information (Maunsell & Van Essen, 1983; Palmer et al., 2005). With the addition of speed differences or increase in the speed of both surfaces, attenuation of direction repulsion reached its limit: ~10 deg for two direction judgments (Braddick et al, 2002) or ~4deg for a single direction judgment (Curran & Benton, 2003). In comparison, differences in surface color do *not* attenuate direction repulsion (Perry & Fallah, 2012). Therefore, direction repulsion is modulated by features processed within the dorsal stream, such as speed and spatial frequency, but not by features processed within the ventral stream, such as color. This suggests that direction repulsion occurs prior to color and motion being bound into an object representation. Thus it is likely that direction repulsion is driven by a local circuit in area MT prior to forming an object representation that includes ventral stream information.

2.5.2 Neural Circuitry – Direction Repulsion

Direction repulsion was originally described as arising from mutual inhibition (Marshak & Sekuler, 1979; Mather & Moulden, 1980) where the neurons responding to one direction inhibit the neurons responding to the other direction. The amount of mutual inhibition also varied by the difference in directions, with repulsion decreasing as the difference increased (Marshak & Sekuler, 1979; Mather & Moulden, 1980). We propose a mutual inhibition circuit wherein each direction inhibits the other based on the overlap in tuning between the neurons representing each direction (Figure 2.3). Figure 2.3A depicts a population of area MT neurons with preferred directions of -15º, 0º, and +15º all of which respond to rightward motion (0º). The population tuning curve to the right of the polar plot depicts how the responses are integrated to determine the direction of motion (peak population response). When a second surface is added moving downwards (270º), the responses to that direction proportionally inhibit the first direction's responses based on the amount of overlap in the tuning curves. The population tuning curve is reduced but more importantly, the peak direction is shifted away, i.e. it is repulsed (Figure 2.3B). This model is supported by the following aspects. First, as the angular difference between the directions increases, the overlap in tuning decreases which reduces the repulsion as was previously found (Marshak & Sekuler, 1979; Mather & Moulden, 1980). Secondly, direction tuning, like orientation tuning, is wider at oblique angles and sharper on the cardinal axes (Coletta, Segu & Tiana, 1993; Gros, Blake & Hiris, 1998; Hiris & Blake, 1996). When one direction is on a cardinal axis, the range of angles that produce repulsion is more limited (Marshak & Sekuler, 1979; Mather & Moulden, 1980) compared to when both directions are oblique (Braddick et al., 2002; Perry & Fallah, 2012).

We further propose that the mutual inhibition circuit is based not only on the overlap of direction tuning between neurons, but more so on the overlap of multi-dimensional tuning across conjunctions of motion features such as speed, spatial frequency and direction selectivity (Albright, 1984; Lagae et al., 1993; Maunsell & Van Essen, 1983; Perrone & Thiele, 2001). When other motion features are identical between the two surfaces, the multidimensional tuning is reduced to directionality alone (Figure 2.3C). But adding a second distinguishing motion feature such as speed would reduce the overlap between the multidimensional tuning curves and thus reduce mutual inhibition and direction repulsion (Figure 2.3D). As speed and spatial frequency are features that form conjunctions with direction tuning in the dorsal stream, this model supports the reduction in direction repulsion seen with differences in speed (current study; Marshak & Sekuler, 1979) or spatial frequency (Kim & Wilson, 1996). Finally, this model also describes the effects that attending to one surface has on direction repulsion. Attention to speed or luminance changes in one superimposed surface reduced direction repulsion but dividing attention across both surfaces did not (Chen, Meng, Matthews & Qian, 2005). The authors suggest that the results when attending to one surface can be explained based on feature-similarity gain (Treue & Maunsell, 1999, Martinez-Trujillo & Treue, 2004) in which attention enhances the representation of the attended feature and simultaneously reduces the influence of the unattended feature. Since the features in question are dorsal stream features co-processed by directionally selective cells in area MT, the effect of attending to one surface while suppressing the other would be to reduce the gain of the suppressed surface and thus reduce the overlap for mutual inhibition (Figure 2.3E). This would produce the attenuation in direction repulsion that was seen (Chen et al., 2005). Finally, as color differences did not reduce direction repulsion, color is not a feature dimension used by the mutual inhibition circuitry. The multidimensional tuning for mutual inhibition works on dorsal stream, not ventral stream, features (Figure 2.3F).

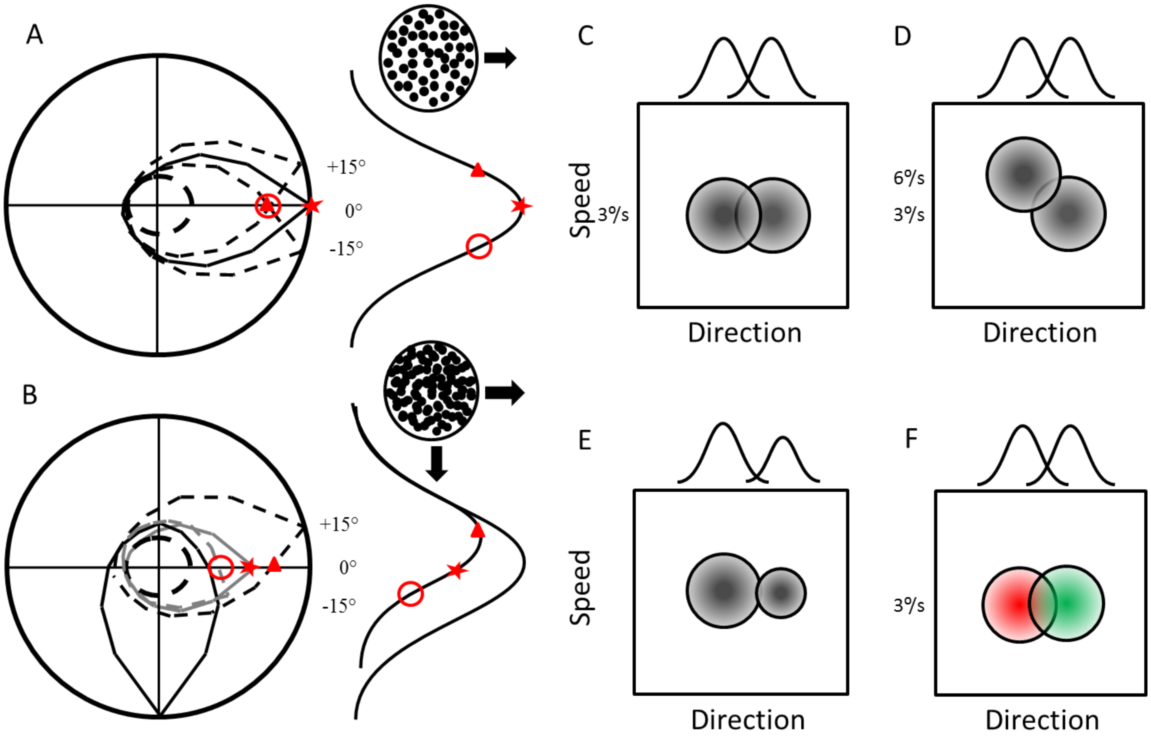

Figure 2.3: Uni- and multidimensional mutual inhibition. 2.3A. Depicts individual neurons and population tuning curves for rightward motion. **2.3B.** The addition of a second surface suppresses the neuronal responses and shifts the population tuning away from the real direction due to inhibition whose strength is based on the overlap between the tuning curves. **2.3C-F.** Multidimensional tuning curves for speed and direction. Above each polar plot is a depiction of the direction tuning overlap for comparison. The greater the size of the overlapping region, the greater the mutual inhibition. **2.3C.** When all motion features are identical except for direction, multidimensional tuning is reduced to direction alone, or is uni-dimensional. **2.3D.** Segmenting the surfaces by an additional motion feature (such as speed) changes the population of neurons engaged in mutual inhibition, thus diminishing the area of overlap and reducing direction repulsion. Note that the overlap in the direction dimension (curves above) is no different than when the speeds are the same (3C). **2.3E.** Attention to one of the surfaces suppresses the influence of the second surface. This reduction in gain of one surface shrinks the population response underlying that surface, which in turn reduces the overlap between the two causing a reduction in direction repulsion. **2.3F.** The addition of a ventral stream (color) feature difference, unlike speed, did not influence direction repulsion, and thus was not a feature dimension in the mutual inhibition circuit.

2.5.3 Processing Time

Having previously found that color segmentation did not affect direction discrimination but did increase the speed of processing, we investigated whether speed segmentation also reduces the processing time needed to make direction discriminations. There is a time cost associated with the integration of features over the processing of single features (Bartels & Zeki, 2006; Bodelón, Fallah, & Reynolds, 2007). Also, adding additional features increases the perceptual load which generally slows processing (Lavie, 1995) Thus, further segmenting the surfaces by adding irrelevant features, such as speed or color differences, requires binding and should take longer than processing direction alone. However, we have found that there is a substantial advantage to be had by integrating features when the end result is to increase segmentation between superimposed surfaces. Using differences in surface speed (current study) and color (Perry & Fallah, 2012) we have shown that the time needed to process the direction of two superimposed surfaces can be reduced by over 500ms. Therefore, the integration of features within the dorsal stream (speed and direction), where features are often co-processed by neurons (Gross, Bender, & Rocha-Miranda, 1969; Holcombe & Cavanagh, 2001; Maunsell & Van Essen, 1983), and binding of features between the ventral and dorsal streams (color and direction) both produce a significant advantage in how quickly the information is processed.

While increasing the speed of one surface to 6°/sec produces speed segmentation (vs 3°/sec), increasing both surfaces' speeds to 6°/sec does not. If in the speed segmentation (3/6:unicolor) condition, the reduction in processing time is solely due to increasing the speed of the one surface, then increasing the speed of both surfaces should reduce processing time further, or if processing time is already at its lower limit, produce the same processing time advantage. Instead, we found that increasing both surfaces' speeds to 6°/sec reduced the processing advantage. Differences in speed provide a greater advantage to direction judgments than just moving at faster speeds. Note that there was still a (smaller) advantage for the matched faster speeds (6/6:unicolor) over the matched slower speeds (3/3:unicolor). An equivalent increase in speed raised the response rates of area MT neurons (Maunsell & Van Essen, 1983) presumably increasing the strength of the motion representation. As others have shown reduced reaction times from increasing stimulus strength by luminance (Pins & Bonnet, 1996) or motion coherence (Palmer et al., 2005), increasing motion strength by increasing surface speed should also reduce reaction times. Our results show how reduced processing time would underlie these faster reaction times.

2.5.4 Neural Circuitry – Processing Time

We propose that the large decrease in processing time that occurs with increases in surface segmentation by additional features is most likely due to speeding up decision making (see Perry & Fallah, 2012). Motion direction is processed in area MT (Albright, 1984; Mikami, Newsome, & Wurtz, 1986; Newsome & Paré, 1988; Salzman, Murasugi, Britten, & Newsome, 1992) and passed forward to frontal and parietal areas which can accumulate the direction information in order to reach a decision threshold (Huk & Shadlen, 2005; Hussar & Pasternak, 2013; Shadlen & Newsome, 1996, 2001; Zaksas & Pasternak, 2006). When two surfaces are identical except for direction of motion, each surface’s direction information interferes with the processing of the other surface’s direction, creating a “noisy walk” towards the decision threshold (accumulator model – Palmer et al., 2005). By introducing differences in color (Perry & Fallah, 2012) or speed (current study), the objects become more distinct from each other, providing additional features through which the direction information can be separated. Filtering out the input from the other surface would reduce the noise in the walk to threshold, increasing the slope of information accumulation. Thus the decision threshold would be reached sooner resulting in decreased processing time.

2.5.5 Conclusion

Irrelevant speed segmentation cues reduce the processing time required to make direction judgments. Color segmentation cues also reduce the processing time required to make direction judgments (Perry & Fallah, 2012). However, only speed affects direction processing as measured by changes in magnitude of direction repulsion, an illusion linked to a local mutual inhibition circuit within area MT. Therefore, motion processing integrates speed and direction prior to global motion processing. The output of global motion processing feeds forward to decision-making areas, where color segmentation cues, as well as speed, reduce processing time. Therefore, by this stage the object representation includes ventral (color) and dorsal (speed and direction) information. Thus, the integration of features within and across the streams occurs at different stages of processing along the visual hierarchy.

Chapter 3. Manuscript 2: The Influence of Top-down Attentional Control and Bottom-up Processing on Feature Integration in the Dorsal Stream.

This manuscript has been submitted to the journal ***Attention, Perception, & Pyschophysics***. The co-authors of this publication are Prakash Amarasooriya, Henna Asrar, Alica Rogojin, and Dr. Mazyar Fallah. Carolyn J Perry and Dr. Mazyar Fallah conceived, designed, and implemented the experiment. Prakash Amarasooriya, Henna Asrar, and Alica Rogojin collected the data. Carolyn J Perry and Prakash Amarasooriya analyzed the data. Carolyn J Perry and Dr. Mazyar Fallah reviewed the data. Carolyn J Perry and Prakash Amarasooriya prepared the manuscript. Carolyn J Perry and Dr. Mazyar Fallah revised and edited the manuscript.

Citation: Perry, C. J., Amarasooriya, P., Asrar, H., Rogojin, A., & Fallah, M. (submitted). The influence of top-down attentional control and bottom-up processing on feature integration in the dorsal stream. *Attention, Perception, & Psychophysics.*

3.1 Summary

Using a perceptual illusion known as direction repulsion, we investigated the influence that bottom-up, stimulus driven mechanisms and top-down attentional task demands have on the feature integration of superimposed objects in the dorsal stream. It has been suggested that spatial overlap is enough to integrate features into the same object file. However, when two superimposed surfaces are differentiated by color, we found that color and motion integration only occurred when participants were required to actively bind the two through top-down attentional mechanisms. This allowed for selection of the surfaces by color, significantly reducing *motion* processing time but surprisingly without a corresponding improvement in direction perception. Bottom-up processing was sufficient for contrast and speed to be automatically integrated into dorsal stream object representations, significantly reducing processing time. While neither bottom-up processing of, nor top-down attention to, contrast affected direction perception, bottom-up differences in speed decreased direction repulsion magnitudes, resulting in more veridical perception. Since cross-stream feature integration did not affect motion circuitry that produces the direction illusion, we hypothesize that these object-based selection mechanisms operate at the later evidence-accumulation stage reducing the other surface's impact on the "noisy walk" to the direction decision threshold. Therefore, feature integration in the dorsal stream produces intermediate object representations at its later stages that can be used to improve processing time through object-based selection mechanisms. These results suggest that bottom-up processing automatically integrates dorsal stream features into dorsal stream object representations, but top-down attention is necessary to integrate a purely ventral stream feature, such as color, into the dorsal stream.

3.2 Introduction

How attention is captured and allocated has been the subject of much research for decades now. One of the fundamental distinctions involves goal-directed (top-down) and stimulus-driven (bottom-up) attentional control. In the first, attentional selection is driven by the behavioral goals of the observer (either their own or constraints placed on them by task instructions). In the latter, attentional selection is driven by the neuronal response to an attribute or feature of a stimulus and occurs independently of any goals the observer may have (Yantis, 2000; Yantis & Hillstrom, 1994). It is thought that this type of selection occurs as a result of certain fundamental computations within the brain that occur automatically and regardless of observer goals (Rensink & Enns, 1998). For this reason, Yantis (2000) argues that studying one in isolation of the other, or asking whether one type of attention is at work over the other, may be an outdated way of studying bottom-up and top-down attention. This study seeks to understand the influence of bottom-up and top-down attention on feature integration within the dorsal stream.

When two moving surfaces are superimposed, the perceived direction of each surface is repulsed away from each real direction of motion. This gives rise to a perceptual illusion known as direction repulsion in both superimposed random dot kinetograms (RDK's – Hiris & Blake, 1996; Marshak & Sekuler, 1979; Mather & Moulden, 1980) and superimposed gratings (Kim & Wilson, 1996; Wilson & Kim, 1994). Direction repulsion has been frequently used to investigate motion processing within the dorsal pathway. For example, the addition of dorsal stream features such as differences in surface speed or spatial frequency that make the superimposed surfaces more distinct from each other also reduce the magnitude of direction repulsion (Curran & Benton, 2002; Kim & Wilson, 1996; Marshak & Sekuler, 1979; Perry, Tahiri, & Fallah, 2014). Other studies have investigated the motion processing stage at which the illusion occurs (Benton

& Curran, 2003; Grunewald, 2004; Wiese & Wenderoth, 2007, 2010) and mutual inhibition as the neural mechanism underlying the illusion (Chen, Maloney, & Clifford, 2014; Dakin & Mareschal, 2000; Farrell-Whelan, Wenderoth, & Brooks, 2012; Hiris & Blake, 1996; Marshak & Sekuler, 1979; Mather & Moulden, 1980; Rauber & Treue, 1999; Treue, Hol, & Rauber, 2000). This paradigm has not been limited to investigations of motion processing; it has also been used to investigate object-based attention (Chen, Meng, Matthews, & Qian, 2005; Ernst, Boynton, & Jazayeri, 2013; Felisberti & Zanker, 2005; Schoenfeld, Hopf, Merkel, Heinze, & Hillyard, 2014) as superimposed surfaces allow for the investigation of object properties irrespective of spatial location (Blaser, Pylyshyn, & Holcombe, 2000; Fallah, Stoner, & Reynolds, 2007; Mitchell, Stoner, Fallah, & Reynolds, 2003; Reynolds, Alborzian, & Stoner, 2003; Rodríguez, Valdés-Sosa, & Friewald, 2002; Stoner, Mitchell, Fallah, & Reynolds, 2005; Valdés-Sosa et al., 1998; Wannig, Rodriquez, & Freiwald, 2007). We have used superimposed surfaces and the direction repulsion illusion to investigate feature integration (Treisman & Gelade, 1980) and object representations in the dorsal stream (Perry & Fallah, 2012, 2014; Perry et al., 2014).

Direction repulsion is thought to arise through mutual inhibition circuits within area MT (Benton & Curran, 2003; Kim & Wilson, 1996; Marshak & Sekuler, 1979; Mather & Moulden, 1980; Perry et al., 2014, Perry & Fallah, 2014; Rauber & Treue, 1999; Treue, Hol, & Rauber, 2000; Wilson & Kim, 1994). Mutual inhibition simply suggests that the responses of neurons processing one direction of motion are inhibited by the responses of the neurons processing the second direction of motion. This leads to each direction judgement being repulsed away from the other, producing direction repulsion. The competition between the two pools of directional neurons is dependent upon the similarity in directions: smaller differences in direction result in greater repulsion than larger differences (Marshak & Sekuler, 1979; Mather & Moulden, 1980).

It has already been shown that bottom-up processing of dorsal stream features, such as speed and spatial frequency that are integrated into global motion processing in area MT, result in decreased direction repulsion. For example, when two superimposed surfaces move at different speeds, direction repulsion is attenuated (Curran & Benton, 2003; Marshak & Sekuler, 1979; Perry et al., 2014). Similarly, when superimposed moving gratings are segmented by spatial frequency, direction repulsion is also reduced (Kim & Wilson, 1996). In these cases, a second surface feature, that makes the surfaces more distinct from each other, functions to reduce the competition between the directions of each surface and consequently improves the perceived direction. Neurons within area MT show selectivity for the combination of these features (Albright, 1984; Lagae, Raiguel, & Orban, 1993; Maunsell & Van Essen, 1983; Perrone & Thiele, 2001). Therefore, this improvement is likely due to the competition between the surfaces' direction of motion not being based on direction alone, but instead on the multi-dimensional tuning exhibited by these area MT neurons (Perry & Fallah, 2014; Perry et al., 2014). In other words, neurons that prefer the direction and speed of one of the superimposed surfaces do not respond as strongly to the other surface that is moving at both a different speed and direction. This reduces the competitive inhibition and thus direction repulsion magnitude is attenuated. While area MT also includes neurons that encode depth plane information, stereoscopic depth segmentation does not decrease direction repulsion (Hiris & Blake, 1996), suggesting that depth information is only processed after direction, spatial frequency, and speed information. This is consistent with the fact that without stereoscopic depth cues, two superimposed surfaces are automatically segmented into separate depth planes based on direction alone (Grunewald, 2000), thus direction has to be processed prior assigning depth planes.

Color, however, is a motion-irrelevant feature for which MT neurons are not selective (Dobkins & Albright, 1994; Gegenfurtner et al., 1994; Maunsell & Van Essen, 1983; Shipp & Zeki, 1985; Zeki et al., 1991). For color (a ventral stream feature) to affect perceived direction (direction repulsion magnitude), it would have to be integrated into the object representation at or before direction computations in area MT. We have found previously (Perry & Fallah, 2012) that surface segmentation by color did not reduce direction repulsion (i.e. did not make direction responses more veridical) but instead improved participants' performance by reducing the time needed to process each surface. We suggest that this improvement in processing time is a result of selection mechanisms affecting decision making circuitry downstream of area MT (Huk & Shadlen, 2005; Hussar & Pasternak, 2013; Shadlen & Newsome, 1996; Zaksas & Pasternak, 2006). When the two surfaces are identical except for direction, the competition between the directions of each surface creates a "noisy walk" to a decision threshold (accumulator model – Palmer et al., 2005). We have determined that correctly processing both surface directions takes more than ~1500ms (Perry & Fallah, 2012; Perry et al., 2014, the current study). When the surfaces are different colors however, this additional differentiating feature can be used to selectively filter out the noise from the other surface, which in turn speeds decision-making. To do so requires that the second feature (color) be integrated with the primary feature to be discriminated (direction) to form an intermediate object representation or object file (Kahneman, Treisman, & Gibbs, 1992).

The prior studies of feature integration and motion processing have used top-down attention to color (Perry & Fallah, 2012) and bottom-up attention to speed (Curran & Benton, 2003; Marshak & Sekuler, 1979; Perry et al., 2014). Since goal-directed (top-down) and stimulus-driven (bottom-up) attention rely on separate mechanisms (Connor, Egeth, & Yantis, 2004; Pinto, van der Leij, Sligte, Lamme, & Scholte, 2013; Yantis, 2000), it is not reasonable to assume that they work the same for feature integration and decision-making in the dorsal stream. This is especially true as multiple forms of attention are involved. While spatial location is controlled through the use of superimposed surfaces, direction discrimination could be performed by feature-based attention, object-based attention, or their combination, even though the task could be performed on that feature (direction) alone. As Yantis (2000) argued, “early visual segmentation processes that parse a scene into perceptual object representations enable object-based selection, but they also enforce selection of entire objects, and not just isolated features”. Therefore, in this study, we wanted to systematically investigate the effects of top-down versus bottom-up attention on feature integration and object-based selection within the dorsal stream and their effects on perception and processing time. Consistent with Yantis’ hypothesis, we found that perceptual decision-making circuitry in the dorsal stream necessarily works on objects, and not the feature in question, as soon as stimulus-driven selection mechanisms are activated. This produced a behavioral advantage where processing time was reduced when two features were bound even though binding requires additional time (Bodelón, Fallah, & Reynolds, 2007) and increases perceptual load (Bartels & Zeki, 2006; Lavie, 1995). Features that are processed within the dorsal stream such as speed and contrast are automatically integrated into these intermediate object representations through stimulus-driven mechanisms. In the case of contrast, the initial representation based on dorsal stream contrast processing can be updated with more informative ventral stream information. However, color, which is not processed in the dorsal stream, requires top-down attention to actively link it into a dorsal stream object representation. We also found that these intermediate object representations occur after area MT in the dorsal stream, as feature integration did not affect the percept arising from global motion processing in area MT. In summary, these results show that stimulus-driven and goal-directed attentional mechanisms have different roles in integrating features into dorsal stream object representations and in affecting the speed of decision-making processes.

3.3 Experiment 1: Differences in Object Color

In this experiment we wanted to determine if top-down attention to both the color and direction of an object *is required* to improve motion processing in the dorsal stream or if motion processing can be improved simply through bottom-up color segmentation of superimposed surfaces.

3.3.1 Methods

Ten different participants completed each of the following three experimental conditions: 1) Unicolor Control (ages 18-21, 5 females, 5 males, Figure 3.1A), 2) Bottom-up Color (ages 18-24, 7 females, 3 males, Figure 3.1B), and 3) Top-down Color (ages 17-31, 7 females, 3 males, Figure 3.1C). Visual acuity was normal or corrected-to-normal in all participants and none tested positive for color blindness using Ishihara plates. Informed consent was obtained from all participants and the research was approved by York University’s Human Participation Research Committee.

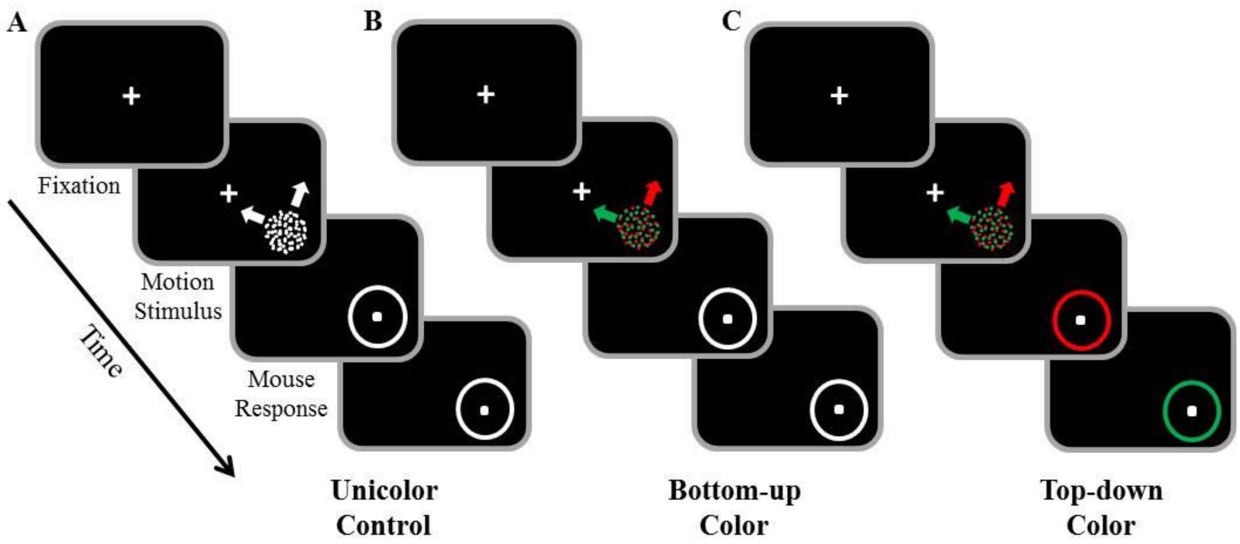

Figure 3.1: Experimental paradigm for experiment 1. In each condition participants were first asked to fixate on the "+" in the center of the screen. 200ms later, two superimposed moving dot fields appeared in the bottom right quadrant. After a variable amount of time, the stimulus disappeared and was replaced with a response circle. Participants were to make one click on each circle provided in the directions they perceived the surfaces to be moving. In the Unicolor Control condition (A), both surfaces were white and participants simply had to give two direction judgements. In the Bottom-up Color condition (B), one of the surfaces was red and the other green, but participants were still only asked to give two direction judgements. In the Top-down Color condition (C), the two superimposed surfaces were different colors but participants had to give the direction of the surface matching the response circle color, requiring them to have actively linked color and direction during the presentation phase.

Experimental Procedure

In each condition, trials were initiated with the appearance of a white fixation cross centrally positioned on a black background (see Figure 3.1A). After fixation was maintained for 200ms, a circular aperture (radius = 5º, eccentricity = 10dva) appeared in the lower right quadrant in which the motion stimulus appeared. If fixation was broken before or during the presentation of the stimulus, the trial was aborted and randomly replaced. The stimulus consisted of two superimposed random dot kinetograms (RDKs) moving with 100% coherence. The RDKs moved in two different directions which were selected from an array of 12 directions that were relative to both the horizontal and vertical axes (± 2º, 6º and 10º from either up or down and left or right). All directions appeared with equal frequency creating angles between the two directions that ranged from 70º to 110º. Once the stimulus had disappeared, a circular outline (the response circle) replaced the aperture. The participants were required to make a mouse click for each perceived direction on the response circle indicating the directions in which the two surfaces were moving. In the Unicolor Control and Bottom-up Color conditions, participants were tasked with simply reporting the directions of motion without the added task demands of linking a direction of motion to the appropriately colored surface. In the top-down condition, participants were required to indicate the direction of motion of each colored surface (red or green) on the corresponding colored response circles (Figure 3.1B), whose order was randomly interleaved across trials. This task demand requires top-down attention to both the color and direction of the surface, and thus the binding of color to motion.

Duration of the motion stimulus was varied by utilizing a staircase design used previously (Perry & Fallah, 2012; Perry et al., 2014), as a means of isolating the time each participant needed to complete visual processing of both surfaces. Each block of eight trials presented the stimulus at a given duration. If performance (the ability to correctly determine both directions of motion) in a given block was 87.5% (7/8) or more, stimulus duration in the following block was decreased. Performance that did not meet this threshold indicated that the participant could not correctly determine both directions of motion in the allotted time, and consequently, stimulus duration in the subsequent block was increased. For greater efficiency, the staircase had two stages. Stimulus duration increased or decreased by a step-size of 500ms in stage one. After reaching a double reversal, the step-size was reduced to 200ms in stage two. The experiment was completed when a second double reversal ended stage two. This paradigm allowed us to estimate the time needed to process both directions of motion correctly to within ± 100ms.

Stimuli and Apparatus

The number of dots (121), their size (0.04º), density (1.54 dots/degree^2), and velocity (3º/sec) did not vary between conditions. In the Unicolor Control condition, both of the surfaces were white (126.01cd/m^2). In the color conditions (Bottom-up Color and Top-down Color), one of the stimulus surfaces was red and the other green (CIE - red: x=0.64, y=0.33; green: x=0.29, y=0.60; isoluminant, 24.4cd/m^2).

The experiments took place in a darkened and quiet room with participants 57cm away from the computer monitor (21" ViewSonic, 1280x1024 resolution, 60Hz). Stimuli were created using MATLAB (The Mathworks Corp.) and experimental control was maintained by Presentation (Neurobehavioral Systems). Photometric isoluminance for all stimuli was determined using a Photo Research Inc. photometer (model #: PR-655). Participants' head position was stabilized by a headrest (Headspot, UHCOtech) and right eye position was monitored with a head-mounted, infrared eye tracker (EyeLink II, SR Research Ltd., 500Hz). Participants were instructed to keep their eyes on a centrally located fixation point throughout the stimulus presentation period. If fixation was broken by movements of the eye outside of a 2° fixation window, the trial was aborted and randomly reinserted into the trial list.

Data Analysis

The data was processed using MATLAB and statistical testing performed using SPSS (IBM Corporation). Correct responses were defined as previously (Perry & Fallah, 2012; Perry et al.,

2014) to allow for repulsion effects: mouse clicks that fell within a range from halfway between the two directions to 45º away from each real direction. Correct responses therefore, were defined as those in which participants made each mouse click within the range corresponding to each direction presented (as described above). Direction Repulsion (DR) is a measure of the perceptual illusion produced by the competition between two directions of motion. It was calculated as the difference between the perceived angle and the actual angle created by the two directions of motion *on both-correct trials only*. Positive values reflect direction repulsion. Processing Time for each participant was determined by the double reversal that ended stage two. For example, if the participant fluctuated between a stimulus presentation time of 500ms and 700ms, the time needed to correctly process the direction of both surfaces (Processing Time) was considered to be 600 ±100ms. To test for differences between conditions for DR, a one-way, independent measures ANOVA with Tukey post hoc corrections for pairwise comparisons was performed. Due to violations of homogeneity of variance, differences in Processing Time between the conditions were tested using the non-parametric equivalent of the one-way ANOVA, the Kruskal-Wallis test with adjustments for multiple pairwise comparisons.

3.3.2 Results

Direction Repulsion

We found that there was no effect of either bottom-up or top-down task demands on direction repulsion ($F(2,27) = 1.12$, $p = 0.34$). Direction repulsion (Figure 3.2A), when the surfaces were differentiated by color with either bottom-up (M = 14.75º ± 2.11SEM) or top-down (M = 11.87º ± 1.15SEM) task demands, was not significantly different than when both surfaces were white (M = 15.36º ± 1.87SEM).

Direction repulsion was not significantly different when both surfaces were the same color, when the surfaces were segmented through bottom-up cues alone, or when the surfaces were segmented by bottom-up cues with the addition of top-down task demands. This differs slightly from the results of Croner and Albright (1997, 1999), who found that direction discrimination was improved in both human and animal populations when color was used to separate randomly moving distracter dots from coherently moving target dots. In their paradigm, the distracter dots were always the same color and thus color could be used to filter out the input of the distracter dots to area MT. In the current study, direction repulsion did not differ between the Unicolor Control and either the Top-Down or Bottom-Up Color conditions, suggesting that color filtering of input to area MT did not occur, likely because participants had to process the direction of motion of both surfaces.

The current results indicate that regardless of bottom-up or top-down selection, color is not a feature that is integrated into motion processing circuits prior to direction computations in area MT. If color were integrated prior to this point, we would have expected direction repulsion to be reduced. Color does not reduce the competition between directions of superimposed surfaces and must therefore be integrated at some point beyond these local circuits within MT.

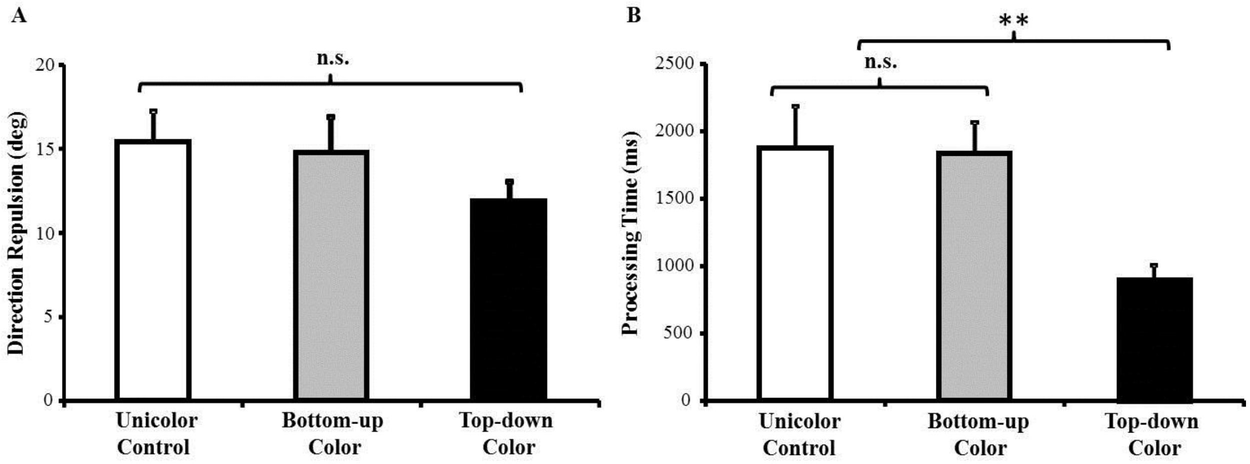

Figure 3.2: The effect of color and attentional task on direction repulsion and processing Time. A. There was no significant difference in Direction Repulsion (DR) across the three conditions ($F(2, 27) = 1.12$, $p = 0.340$. Unicolor Control: M = 15.36° ± 1.87SEM, Bottom-up Color: M = 14.75° ± 2.11SEM, Top-down Color: M = 11.87° ± 1.15SEM. **B.** There was a significant effect on Processing Time however, ($H(2) = 10.04$, $p = 0.007$) which was driven by a significant decrease in Processing Time only in the Top-down Color condition (M = 900ms ± 107SEM) when compared to the Unicolor Control (M = 1870ms ± 312SEM, $W_s = 16.50$, $z = -2.55$, $p = 0.009$). Processing Time in the Bottom-up Color condition (M = 1830ms ± 236SEM) was not different than in the Unicolor Control ($W_s = 47.50$, $z = -0.19$, $p = 0.853$).

Processing Time

We did find however, that there was a significant difference in Processing Time ($H(2) = 10.04$, $p = 0.007$) across conditions. Processing Time (Figure 3.2B) in the Bottom-up Color condition (M = 1830ms ± 236SEM) was not significantly different than in the Unicolor Control (M = 1870ms ± 312SEM) condition ($W_s = 47.50$, $z = -0.19$, $p = 0.853$). However, processing time in the Top-down Color condition (M = 900ms ± 107SEM) was significantly less than in the Unicolor Control condition ($W_s = 16.50$, $z = -2.55$, $p = 0.009$) and the Bottom-up Color condition ($W_s = 12.00$, $z = -2.89$, $p = 0.003$).

These results suggest that when superimposed surfaces are segmented by color without top-down task demands that link surface color to direction discrimination, no improvement in processing time occurs. This means that binding of color to motion did not occur automatically. However, active binding of color and motion in the Top-Down Color condition improves processing time without affecting the direction computations in MT that produce repulsion, a result that is consistent with previous work (Perry & Fallah, 2012). This is interesting, as having to report both the direction and color, instead of just the direction of two surfaces, actually increases task difficulty, requires binding which takes additional time (Bodelón et al., 2007), and increases the perceptual load which generally slows processing (Bartels & Zeki, 2006; Lavie, 1995). In this case, the advantage of having a second feature by which to select between object representations in accumulating direction information was large enough to overcome the costs associated with binding and perceptual load and still reduce the time needed to make a perceptual decision.

3.3.3 Discussion

Treisman has suggested that shared location mediates feature integration (Treisman, 1992, 1998; Treisman & Gormican, 1988); a step that facilitates the creation of object files (van Dam & Hommel, 2010). In fact, it is suggested that spatial overlap of features results in the automatic integration of features into the same object file, even if integration is not necessary or not all of the features are task relevant (van Dam & Hommel, 2010). While some recent imaging work (Ernst et al., 2013; Schoenfeld et al., 2014) supports that hypothesis, the current results suggest that automatic feature integration does not always occur when integrating color into the dorsal stream. In the Bottom-up Color condition, each superimposed surface had two features; direction and color. If features are simply integrated based on shared spatial location, we would have expected color to improve processing time over that seen in the Unicolor Control. It did not however, except when top-down task demands required that color and direction be actively linked. There has been some debate over whether integration of features occurring within the same spatial location occurs under exogenous (bottom-up), endogenous (top-down), or exogenous + endogenous cue conditions (Briand, 1998; Briand & Klein, 1987; Henderickx, Maetens, & Soetens, 2010; Kawahara & Miyatani, 2001). The results of the current study would suggest that under conditions in which multiple features occur at the same location and constitute two different surfaces, integration of color into dorsal stream motion processing does not occur unless top-down attention is used to actively bind color and direction together. Exogenous (bottom-up) surface cues, while helping to segment the dots into two distinct surfaces, do not by themselves, facilitate the use of color downstream of MT to improve processing time.

3.4 Experiment 2: Differences in Object Contrast

Having found that differences in object color are not automatically integrated into dorsal stream motion processing, we wanted to test whether this extended to other ventral stream features to determine if top-down attention is generally needed for cross-stream feature integration. As neurons in the dorsal stream saturate at low contrast (Fallah & Reynolds, 2012; Sclar, Maunsell, & Lennie, 1990; Thiele, Dobkins, & Albright, 2000), we used contrast differences above the saturation point, to which the ventral stream was sensitive In order to test the effect of ventral stream contrast on motion processing in the dorsal stream, we utilized the same experimental design as in Experiment 1 and simply differentiated the superimposed objects by contrast levels, in the ventral stream's dynamic range, instead of by color.

3.4.1 Methods

Twenty new participants completed the following experimental conditions: 1) Bottom-up Contrast (ages 17-22, 8 females, 2 males, Figure 3.3B), and 2) Top-down Contrast (ages 17-25, 8 females, 2 males, Figure 3.3C). Direction Repulsion and Processing Time in these two conditions were compared to the data previously collected in the Unicolor Control condition (Figure 3.3A) from Experiment 1. Visual acuity was normal or corrected-to-normal in all participants and none tested positive for color blindness using Ishihara plates. Informed consent was obtained from all participants and the research was approved by York University's Human Participation Research Committee.

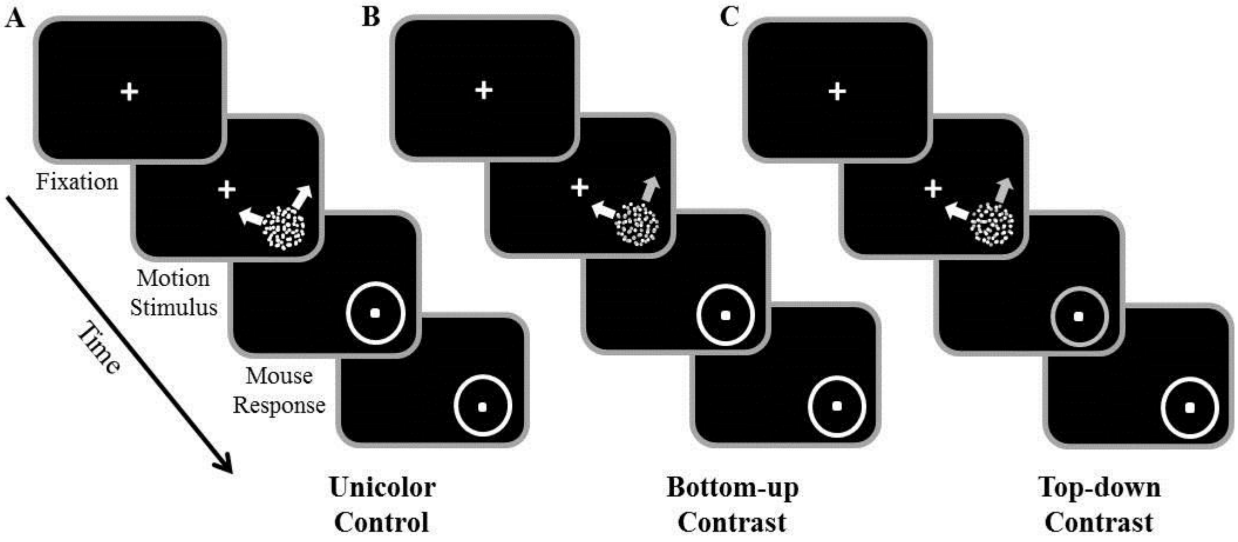

Figure 3.3: Experimental paradigm for experiment 2. The procedure was identical to that utilized in Experiment 1. The only difference was that instead of different surface colors, the superimposed surfaces were different contrasts. One surface was set to an RMS-contrast of 100% while the contrast of the other surface was set to 10% RMS-contrast. These are both contrast levels to which the ventral stream is sensitive, while both are above saturation in the dorsal stream.

The stimuli were the same as used in Experiment 1 except that one of the surfaces was set to an RMS-contrast of 100% (dot contrast: 126.01cd/m^2) and the other to an RMS-contrast level of 10% (dot contrast: 39.24cd/m^2), with a constant background luminance of 0.22cd/m^2 (Figure 3.3). These contrasts are well above the levels that saturate the dorsal stream and therefore tested the effect that ventral stream contrast had on motion processing. In the Top-down Contrast condition, participants were asked to indicate the direction of either the bright or dim surface on response circles that were set to the same luminance contrast as the dots in each surface. All other procedures and data analyses are the same as those used in Experiment 1.

3.4.2 Results

Direction Repulsion

We found that there was no effect of contrast on Direction Repulsion across the experimental conditions ($F(2, 27) = 0.53$, $p = 0.596$). Direction Repulsion (Figure 3.4A) in the Bottom-up Contrast (M = 13.52° ± 2.16SEM) condition and the Top-down Contrast condition (M = 12.78° ± 1.39SEM) were not significantly different from that in the Unicolor Control condition (M = 15.36° ± 1.87SEM). This suggests that ventral stream features (contrast and color) are *not* integrated into dorsal stream object processing prior to direction computations in area MT. Whether contrast is integrated beyond this point would be determined by whether different surface contrasts affect Processing Time.

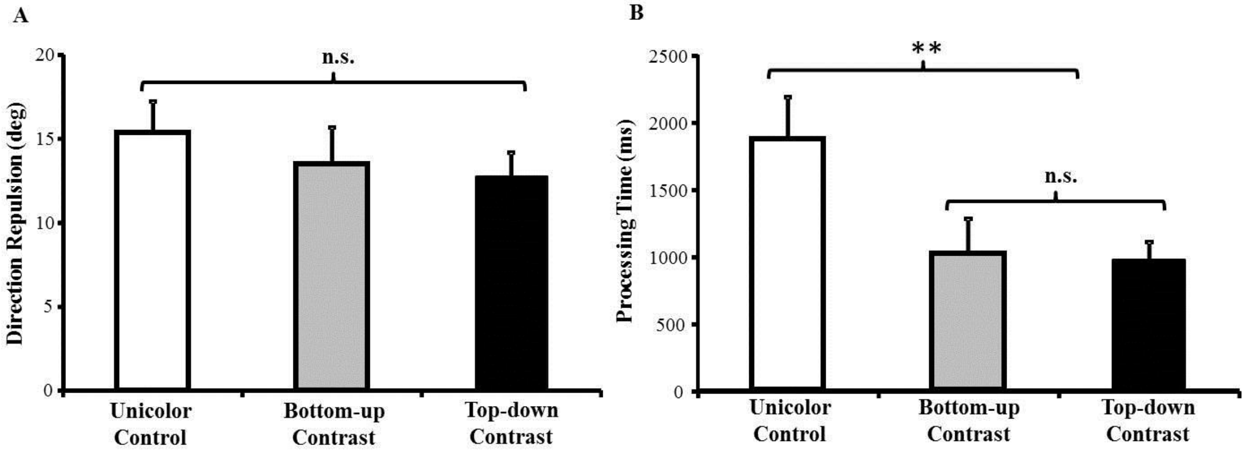

Figure 3.4: The effect of contrast and attentional task on direction repulsion and processing time. A. As with color, there was no significant change in DR across conditions ($F(2, 27) = 0.53$, $p = 0.596$). Unicolor Control: M = 15.36° ± 1.87SEM, Bottom-up Contrast: M = 13.52° ± 2.16SEM, Top-down Contrast: M = 12.78° ± 1.39SEM. **B.** Processing Time was significantly reduced ($H(2) = 8.65$, $p = 0.013$) in both the Bottom-up (M = 1020ms ± 256SEM, $W_s = 15.00$, $z = -2.66$, $p = 0.007$) and Top-down (M = 970ms ± 135SEM, $W_s = 18.50$, $z = -2.39$, $p = 0.015$) Contrast conditions when compared to the Unicolor Control condition (M = 1870ms ± 312.00SEM).

Processing Time

As with color, there was a significant effect of object contrast on Processing Time ($H(2) = 8.65$, $p = 0.013$). The pattern of results differed from that seen with differences in object color however. Processing Time (Figure 3.4B) in *both* the Bottom-up Contrast (M = 1020ms ± 256SEM) and Top-down Contrast conditions (M = 970ms ± 135SEM) were significantly less than in the Unicolor Control (M = 1870ms ± 312SEM) condition ($W_s = 15.00$, $z = -2.66$, $p = 0.007$ and $W_s = 18.50$, $z = -2.39$, $p = 0.015$ respectively). In addition, there was not a significant difference between the Bottom-up and Top-down Contrast conditions ($W_s = 47.00$, $z = -0.23$, $p = 0.853$). Therefore surface contrast is *automatically* integrated into dorsal stream object representations, as bottom-up attention was sufficient and there was no additional advantage gained through top-down attentional mechanisms.

3.4.3 Discussion

The pattern of results is similar to color in that processing time was affected by contrast but direction repulsion was not. Thus ventral stream features are integrated after direction processing in area MT, forming an intermediate object representation that is used beyond this point to speed up decision-making.   However, color, unlike contrast, was only integrated through top-down task demands. As stated earlier, contrast is processed in both streams, though the dorsal stream saturates at low contrast levels. Very low contrast levels in RDKs result in misrepresenting speed as slower than the object is actually moving in perception (Thompson, 1982), smooth pursuit eye movements (Fallah & Reynolds, 2012) and at the neuronal level in area MT (Krekelberg, van Wezel, & Albright, 2006). So contrast is integrated into motion processing prior to area MT, however, we found no effects of contrasts above the dorsal stream saturation point on direction repulsion. Yet ventral stream contrast differences reduced processing time. This dichotomy is resolved if contrast is integrated originally based on dorsal stream contrast input and then the intermediate object representation after area MT is updated with ventral stream contrast information (Fallah & Reynolds, 2012), similar to updating object files in the ventral stream (Mitroff & Alvarez, 2007; Noles, Scholl, & Mitroff, 2005).

3.5 Experiment 3: Differences in Object Speed

Having tested the effects of top-down and bottom-up attention to ventral stream features on dorsal stream motion processing, we wanted to determine the attentional effects when the object feature that differentiates the superimposed surfaces is also processed in the dorsal stream. We have previously shown that bottom-up attention to speed differences reduces both direction repulsion and processing time (Perry et al., 2014). However, what remains unknown is the effect that top-down task demands have on perceived direction, and if they impart the same advantage of speeded processing times, as seen with differences in surface color and contrast, when the superimposed objects are differentiated by speed. Will top-down attention to speed differences produce an additional advantage over bottom-up speed differences, suggesting separate mechanisms that are additive in nature? Or will there be no difference between top-down and bottom-up speed conditions suggesting early stimulus-driven integration of speed that cannot be further enhanced by top-down mechanisms?

3.5.1 Methods

Twenty new participants completed the following experimental conditions (10 each): 1) Bottom-up Speed (ages 17-22, 8 females, 2 males, Figure 3.5B), and 2) Top-down Speed (ages 17-25, 8 females, 2 males, Figure 3.5C). Direction Repulsion and Processing Time in these two conditions were compared to the data previously collected in the Unicolor Control condition (Figure 3.5A) from Experiment 1. Visual acuity was normal or corrected-to-normal in all participants and none tested positive for color blindness using Ishihara plates. Informed consent was obtained from all participants and the research was approved by York University's Human Participation Research Committee.

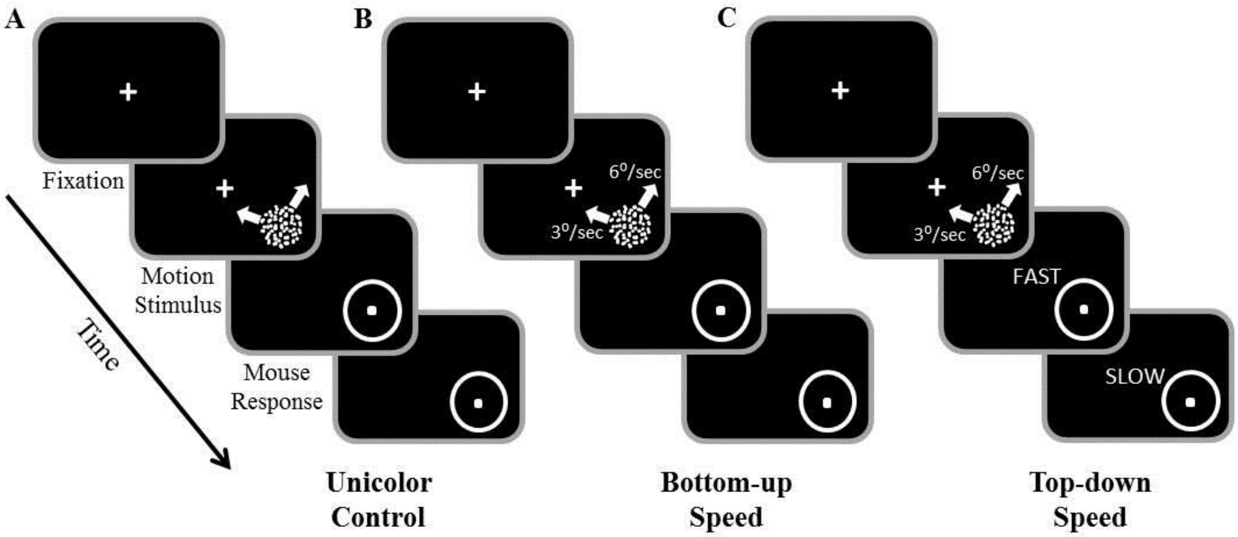

Figure 3.5: Experimental paradigm for experiment 3. Again, the procedure was similar to that used in Experiments 1 and 2. Instead of differences in surface color or contrast however, in this experiment one surface moved at 3°/sec and at 6°/sec in the other surface.

The stimuli were the same as used in Experiment 1 except that one of the surfaces moved at 3°/sec and the dots in the other surface at 6°/sec. In the Top-down Speed condition, participants were asked to give a direction response for the “fast” surface and the “slow” surface randomly ordered trial-by-trial, which required actively linking the speed to the direction of the surface. These top-down task demands require the categorization of speed into fast and slow, separate from the direction discrimination, so that judgements of each feature, rather than the combined velocity, is encoded into the object representation of each surface. All other procedures and data analyses are the same as those used in Experiments 1 and 2.

3.5.2 Results

Direction Repulsion

There was a significant effect of attentional task on Direction Repulsion when the superimposed objects were different speeds ($F(2, 27) = 6.96$, $p = 0.004$, Figure 3.6A). This effect was driven by a significant reduction in Direction Repulsion in the Bottom-up Speed condition (M = 8.42° ± 0.57SEM) compared to the Unicolor Control (M = 15.36° ± 1.87SEM, *p* = 0.003). Surprisingly, the addition of top-down task demands that actively link the speed of the surface to the corresponding direction reduced this advantage. Direction Repulsion in the Top-down Speed condition (M = 11.29° ± 4.14SEM) was not significantly different than in the Unicolor Control (*p* = 0.094), though there was also no significant difference in Direction Repulsion between the Bottom-up and Top-down Speed conditions (*p* = 0.289).

We have previously suggested (Perry et al., 2014) that multidimensional feature selectivity likely underlies this reduction in direction repulsion with stimulus-driven differences in surface speed. Speed is a feature that forms conjunctions with direction in the dorsal stream. In other words, neurons in MT will co-process speed and direction, and in essence respond selectively to different object velocities. In doing so, each velocity vector can then be processed by a separate pool of neurons within MT, and reduce the interference caused when trying to process two superimposed objects. This advantage of multidimensional tuning appears to be diminished when participants are required to actively attend to the speed category of the surface and report it along with the direction. By focusing on categorizing the speeds, the stimulus-driven effects are diminished. This is consistent with other studies which show that stimulus-driven attentional effects can be diminished by top-down task demands (Folk, Remington, & Johnston, 1992; Hillstrom & Yantis, 1994; Jonides & Yantis, 1988; Yantis & Egeth, 1999).

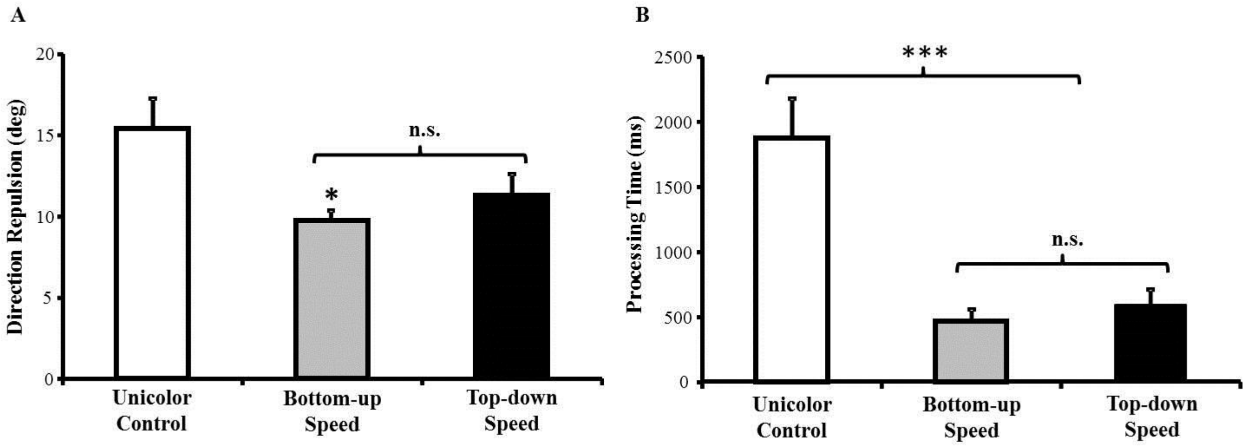

Figure 3.6: The effect of speed and attentional task on direction repulsion and processing Time. A. There was a significant effect of attentional task on Direction Repulsion (DR) when the surfaces were different speeds ($F(2, 27) = 6.96$, $p = 0.004$). DR in the Bottom-up Speed condition (M = 8.42° ± 0.57SEM) was significantly less than in the Unicolor Control condition (M = 15.36° ± 1.87SEM, $p = 0.003$). This advantage was reduced in the Top-down Speed condition (M = 11.29° ± 4.14SEM) when compared to the Unicolor Control condition ($p = 0.289$). **B.** There was also a significant effect of task demands on Processing Time when the surfaces were differentiated by speed ($H(2) = 18.92$, $p < 0.001$). In both the Bottom-up Speed (M = 350ms ± 43SEM) and Top-down Speed (M = 590ms ± 122SEM) conditions, Processing Time was significantly less than in the Unicolor Control condition ($W_s < 0.01$, $z = -3.79$, $p < 0.001$ and $W_s = 6.00$, $z = -3.34$, $p < 0.001$).

Processing Time

Across the three conditions, we found that there was a significant effect of task-demands on Processing Time ($H(2) = 18.92$, $p < 0.001$, Figure 3.6B). Of particular interest, Processing Time was significantly reduced through bottom-up (M = 350ms ± 43SEM) and top-down (M = 590ms ± 122SEM) task demands when compared to the Unicolor Control (1870ms ± 312SEM; $W_s < 0.01$, $z = -3.79$, $p < 0.001$ and $W_s = 6.00$, $z = -3.34$, $p < 0.001$ respectively). There was no significant difference in Processing Time between the Bottom-up and Top-down condition (W_s = 28.50, z = -1.66, p = 0.105).

3.5.3 Discussion

As with contrast, stimulus-driven differences in surface speed are automatically integrated into dorsal stream object representations and in turn improve visual processing speed. Again, similar to contrast, top-down task demands to attend to the speed in addition to the direction of the surfaces did not add to the stimulus-driven advantage. Combined with the previous effects on direction repulsion, these results support two different mechanisms for motion processing along the dorsal stream: direction selectivity in area MT, which works on velocities and improves direction perception, and later decision-making circuits that work on object representations to improve processing time.

Our hypothesis is that when there is only one object feature differentiating the superimposed surfaces, interference between the processing of each surface slows processing time, as is seen in the Unicolor Control condition. If the dorsal stream simply combined speed and direction into a velocity vector and passed this information downstream, the two superimposed surfaces would again only be differentiated by one object feature (velocity) and processing time would slow, similar to when both surfaces are only differentiated by direction (Unicolor Control condition). Instead, speed, independent of direction, is integrated into a dorsal stream object representation downstream of direction computation in area MT. Evidence for this comes from the speed categorization necessitated by the top-down task demands that requires independent speed and direction processing. Processing Time in this case is no different from that seen with bottom-up task demands, which suggests that decision-making circuits work on object representations that treat speed and direction as independent object features. Speed can then be used as a second distinguishing object feature, like color and contrast, that allows for object selection mechanisms resulting in faster processing speeds.

3.6 General Discussion

The superimposition of coherently moving random dot kinetograms (RDKs) controls for the effects of spatial location and produces the perception of two superimposed objects that allows for investigations of object properties and non-spatial attentional mechanisms (Fallah et al., 2007; Khoe, Mitchell, Reynolds, & Hillyard, 2005; Mitchell et al., 2003; Reynolds et al., 2003; Rodriguez, Valdés-Sosa, & Freiwald, 2002; Stoner et al., 2005; Valdés-Sosa et al., 1998; Wannig et al., 2007). Superimposed surfaces also produce a motion illusion known as direction repulsion, an illusion that can be used to distinguish between changes in direction perception (due to alterations in direction computation in MT) and motion decision-making beyond this stage (Perry & Fallah, 2012, 2014; Perry et al., 2014). This distinction allows for investigations into the constraints under which feature integration occurs in the dorsal stream. In the current study, we have shown that bottom-up attention is sufficient to integrate contrast and speed with direction into object files at stages beyond global motion processing in area MT as they reduced the processing time needed for direction discrimination. We suggest that these integrated features form intermediate object representations, or object files, which are used by decision-making circuitry and are affected by object-based selection mechanisms. Kahneman and colleagues (1992) define object files as: “temporary episodic representations of real world objects.” Essentially, an object file can be thought of as a folder into which different features of the same object are placed, at least temporarily. Therefore, an object file can also be thought of as an intermediate object representation as it allows for features to be associated with an object without necessarily leading to object recognition.

The contrast differences that produced stimulus-driven integration were above the saturation point for the dorsal stream but within the dynamic range for the ventral stream. This suggests that the object file's contrast information is automatically updated with ventral stream contrast information prior to decision-making in the dorsal stream. However, color, a ventral stream feature that is not initially processed by the dorsal stream, required top-down attention to bind it to motion which again resulted in faster processing time. This suggests that purely ventral stream features need top-down attentional control to be integrated into the dorsal stream, and once again that integration occurs after motion processing in area MT.

3.6.1 Integrating Speed with Direction

When the objects are moving at different speeds, direction repulsion is significantly reduced even if participants are only tasked with reporting just the direction of the two surfaces. Conversely, when participants are tasked with actively attending to the speed of the surface to categorize it as fast or slow along with reporting the direction of the corresponding surface, the improvement in direction perception is diminished. We propose that reductions in direction repulsion, when objects are different speeds, are driven by multidimensional feature selectivity. MT neurons can be selective for combinations of features (Mikami, Newsome, & Wurtz, 1986), or alternatively, selective across multiple feature dimensions. This simply means that a population of MT neurons could have a preferred direction and speed, essentially making them selective for a given velocity. Having populations of neurons with different preferred velocities would mean that the overlap in the multidimensional tuning curves associated with each surface's motion would be reduced when the speeds varied. Since the amount of overlap in tuning is thought to influence the mutual inhibition that produces direction repulsion, reducing the amount of overlap would consequently reduce direction repulsion. Therefore, since area MT neurons are selective for the conjunction of speed and direction, when the speed is the same between the two surfaces, the mutual inhibition and direction repulsion was greater than when the speed differed and the inhibition decreased. Our results are consistent with this proposed mechanism. Interestingly, having to actively attend to the speed category of each surface (in the top-down attention condition) interfered with this advantage and diminished the improvements in direction perception. This is consistent with prior studies showing that stimulus-driven selection can be reduced based on task demands (Hillstrom & Yantis, 1994; Jonides & Yantis, 1988; Yantis & Egeth, 1999), for example in contingent attentional capture paradigms (Folk et al., 1992).

Differences in object speed also reduce processing time regardless of attentional demands, therefore bottom-up attentional mechanisms are sufficient to select between surfaces moving at different speeds. This suggests that speed is automatically integrated into dorsal stream intermediate object representations after direction computations in area MT. This is interesting as it suggests that the dorsal stream processes global motion (e.g. direction repulsion) based on conjoined feature information (velocity), but accumulates decision-making evidence using object representations where the features are represented independently as speed and direction. This allows decision-making circuitry to use speed as a distinguishing feature for object-based selection. It is the independent integration of speed and direction into the object representation that allows for object-based mechanisms to select the objects based on speed alone and thus reduce competition between the surfaces that results in reduced processing time for direction judgments. In the case of speed, both bottom-up and top-down attention reduced processing time, providing evidence that decision-making circuitry in the dorsal stream works on object representations that object-based selection mechanisms utilize regardless of the source of attentional control. Once stimulus-driven selection has occurred, top-down attention cannot provide additional improvements in processing time.

3.6.2 Integrating Color into the Dorsal Stream

Neither bottom-up nor top-down attentional mechanisms produce integration of ventral stream features prior to direction selection in area MT, as direction repulsion magnitudes were no different when attending to the color of the moving surfaces than the unicolor control. This suggests that, unlike speed, color is only integrated after direction computation circuits in area MT. Furthermore, bottom-up mechanisms are not sufficient to drive changes in processing time when superimposed surfaces are different colors, suggesting that stimulus-driven object-based selection in the dorsal stream is not sensitive to color. Importantly, the addition of top-down task demands (Top-down Color condition) that require the *active* binding of color to motion does reduce processing time. Therefore, top-down object-based selection in the dorsal stream is sensitive to color. This reduction in processing time when required to report the combination of color and direction is counterintuitive as binding requires additional time (Bodelón et al., 2007) and increases perceptual load, which slows processing (Bartels & Zeki, 2006; Lavie, 1995). Thus, the addition of color should theoretically slow down processing speed. Instead, we find that the advantage produced by actively binding color to motion was much greater than the cost arising from the time needed for binding added to the cost of the increased perceptual load.

Overall then, dorsal stream features are automatically integrated together, and stimulus-driven mechanisms are sufficient to activate object-based selection. But ventral stream features require top-down attentional control to both be integrated into the dorsal stream and to activate object-based selection. This pattern proposes that while stimulus-driven mechanisms are, not surprisingly, constrained to the features within that visual stream, top-down attention is required for feature integration to occur across streams. Thus the two attentional control systems have different functional relevance to feature integration.

3.6.3 Integrating Contrast into the Dorsal Stream

We tested contrast differences within the dynamic range of the ventral stream, which we have termed ventral stream contrast. These contrast levels, while differing between the two surfaces, were both well above the saturation point for the dorsal stream. Neurons in area MT respond equally to motion information at both of the tested contrast levels (Krekelberg et al., 2006; Fallah & Reynolds, 2012) and therefore cannot distinguish between them. Ventral stream contrast had no effect on direction repulsion with either bottom-up or top-down attention, consistent with the results for color. Unlike ventral stream color, which required top-down attention to speed up processing, ventral stream contrast reduced processing time through bottom-up and top-down selection mechanisms. Therefore, stimulus-driven selection based on ventral stream contrast was sufficient to produce processing time benefits. This is surprising as the contrast levels tested are only differentiated in the ventral stream and based on the results seen with differences in surface color, we would expect that top-down attention to ventral stream color would be required in order to affect processing time. Instead, the effects of contrast on processing time were similar to the effects of speed on processing time. This suggests that contrast is automatically integrated into dorsal stream intermediate object representations after motion processing. Yet if that integration occurred for the dorsal stream's encoding of contrast, then both surfaces would have saturated and equal contrasts in those object representations, and object-based selection would not be able to distinguish between the two surfaces based on contrast.

Therefore, we propose that since contrast is also processed in the dorsal stream, it is automatically integrated into the object file, similar to speed. The contrast levels used here were saturated in the dorsal stream and thus did not distinguish the objects. As the saturated contrasts were equal, direction repulsion was not affected since area MT would process the surfaces the same as in the Unicolor Control condition. However, the contrast integrated into the object file must be updated automatically at a later stage in the dorsal stream with ventral stream contrast information that is more informative. The updated contrast information now allows for object-based selection mechanisms to distinguish between the two surfaces, which results in the improved speed of processing.

3.6.4 Object-based Selection in Dorsal Stream Decision-making

We proposed (Perry & Fallah, 2012, 2014; Perry et al., 2014) that the integration of additional distinguishing features allows for object-based selection mechanisms to reduce the noisy walk (Huk & Shadlen, 2005) to a decision threshold and in turn reduce processing time. Figure 3.7A (adapted from Perry & Fallah, 2014) depicts a hypothetical accumulator neuron (such as is found in area LIP, Huk & Shadlen, 2005) acquiring motion information to make a rightward decision. Information in support of this decision is depicted by a (+) while negative information derived from the second direction of motion in turn pushes the neuron further away from the decision threshold. Together, this produces a noisy walk to the decision threshold and gives rise to the time required to make a decision. When the surfaces are different colors, contrasts or speeds, as depicted in Figure 3.7B, this second feature can be used to selectively filter out the competing input from the second object, reducing the noise in the walk which in turn speeds decision-making. The current study extends the model by determining that contrast and speed are automatically integrated to form the object representations that stimulus-driven selection operates on. The addition of top-down attentional task demands does not further reduce processing time, suggesting that stimulus-driven attention is sufficient to drive competitive selection between objects that differ in speed or contrast. Therefore, competitive selection in these decision-making circuits can be dynamically allocated by stimulus-driven attentional mechanisms for features processed within the dorsal stream. Conversely, stimulus-driven attention is not sufficient and top-down task demands are necessary to integrate color with motion, which then also allows top-down attention to drive competitive selection in the decision-making circuitry, reducing processing time (Fig 3.7B). Therefore, features not processed within the dorsal stream require top-down attentional control mechanisms to integrate into dorsal stream object representations, and drive competitive selection in these decision-making circuits.

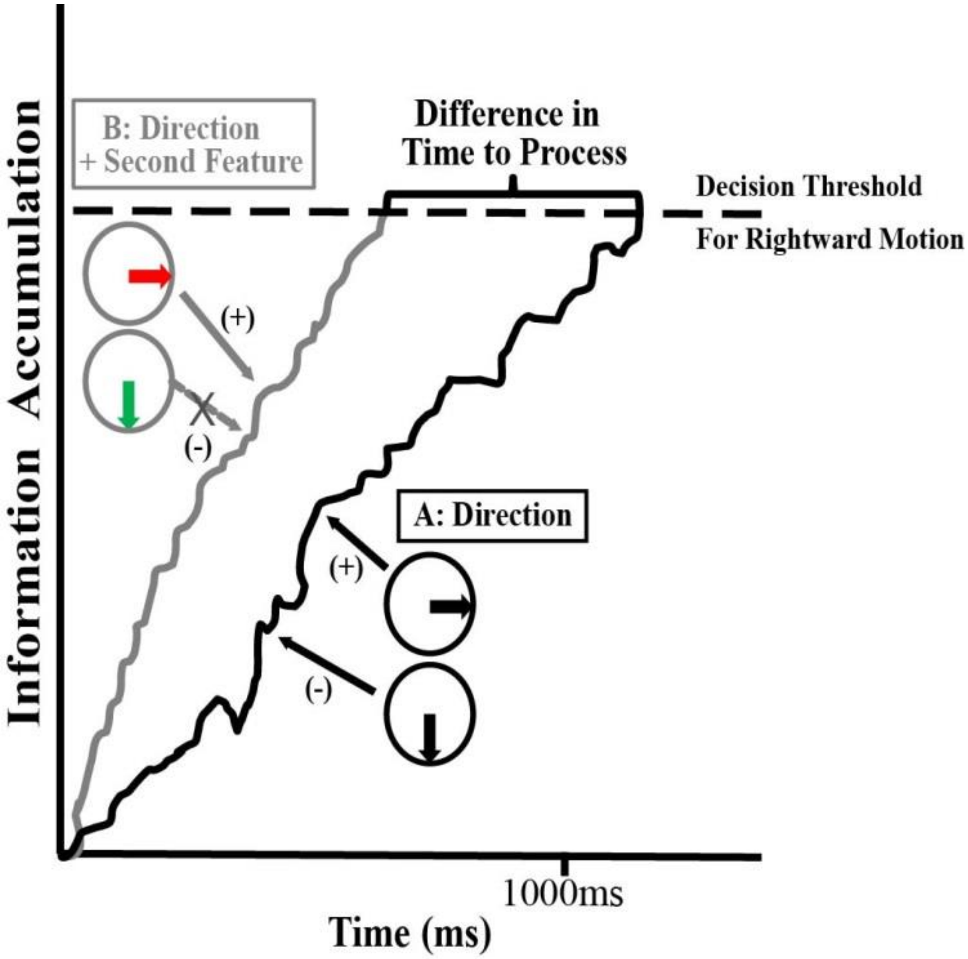

Figure 3.7: Noisy walk to decision threshold (adapted from Perry & Fallah, 2014). Information in favor of rightward motion is accumulated (+) but the presence of the second surface reduces this evidence (-) and pushes the decision away from threshold. **(A)** When there is only one surface feature, direction, to segment the surfaces from each other, the presence of the second surface creates interference in information accumulation and creates a noisy walk to the decision threshold. **(B)** When a second feature also differentiates the surfaces, selection mechanisms can reduce the interference of the second surface and the decision threshold is reached more quickly.

4.6.5 Intermediate Object Representations Along the Dorsal Stream Visual Hierarchy

We propose that dorsal stream decision-making mechanisms work on intermediate object representations that are built up within the dorsal stream and include information integrated from the ventral and dorsal pathways by different attentional control mechanisms.

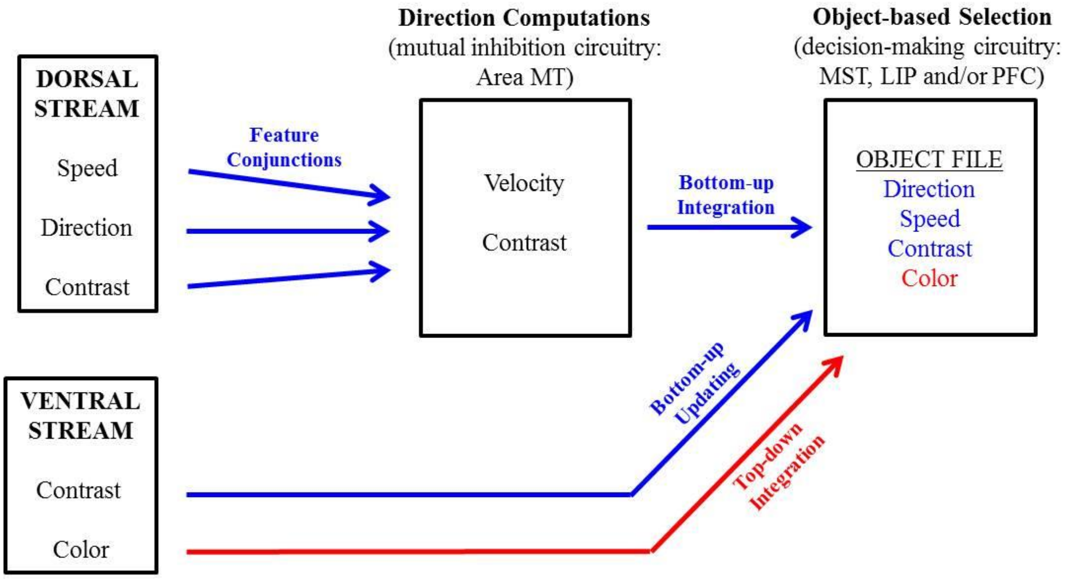

Figure 3.8: Effects of attentional control mechanisms on feature integration. Dorsal stream features such as speed, direction and contrast form feature conjunctions that are encoded as multidimensional feature selectivity within area MT. Speed and direction conjunctions produce velocity vectors that are used to reduce mutual inhibition in area MT and in turn improve direction perception. Speed, direction, and contrast are then integrated through automatic, bottom-up attention, into an object file allowing for object-based selection mechanisms to affect decision-making circuitry downstream of area MT. Ventral stream color information is integrated into the dorsal stream object file through top-down attentional mechanisms, while ventral stream contrast information updates dorsal stream contrast processing automatically beyond direction computation in area MT.

Ventral stream color and contrast information is integrated into dorsal stream object representations at some point after direction computations within area MT as neither reduces direction repulsion (Figure 3.8 bottom). This would suggest that parallel processing of color and contrast with motion occurs up until area MT. However, color and contrast do improve processing speed which would suggest that this ventral stream information is eventually integrated into the dorsal stream. This integration may occur as early as area MST (Tchernikov & Fallah, 2010; Fallah & Reynolds, 2012) but may also occur in later stages such as LIP or PFC. Alternatively, decision making circuits in the dorsal stream may be modulated by object representations that are contained within the ventral pathway. In this case, motion information would be a tag (FINST: Pylyshyn, 1989, 1994) associated with an object representation within the ventral pathway. Object-based selection would then occur in the ventral stream but the results of competitive selection would need to be passed back to the dorsal stream in time to facilitate decision-making processes downstream of area MT. This would still give rise to a late stage object representation in the dorsal stream, but one that would be dependent on ventral stream feature integration, and in essence would be a copy of the ventral stream object file. As the two visual streams have different functional outcomes (perception and action: Goodale & Milner, 1992; what and where: Mishkin, Ungerleider, & Macko, 1983), it is more reasonable to expect that the object representations in each stream would be tailored to the function of that stream.

3.7 Conclusions

The results of these experiments provide new information as to the attentional constraints under which binding of different object features occurs within the dorsal stream. Only speed differences were integrated with direction information early enough to affect perception. Stimulus-driven selection mechanisms were sufficient for these speed differences to reduce direction repulsion, likely due to the multidimensional feature selectivity of area MT neurons. As color, or contrast above the dorsal stream's saturation, had no effect on direction repulsion even with top-down task demands, ventral stream features are not integrated prior to motion processing in area MT. After area MT, perceptual decision-making in the dorsal stream depends on object representations that both bottom-up and top-down attentional mechanisms can bias. When the surfaces differed in speed or contrast, there was no difference in processing time between bottom-up and top-down attention conditions, suggesting that bottom-up attention is sufficient for those features to drive object-based selection of dorsal stream object representations. However, top-down attention is *required* for the integration of color from the ventral stream into dorsal stream object representations and for competitive selection to occur. Taken together, dorsal stream features are automatically integrated into intermediate object representations used by decision-making circuitry after area MT. Ventral stream information is automatically updated in the object representation if that feature is also processed by, and thus already integrated into, the dorsal stream. However, purely ventral stream features require top-down attention to be integrated into dorsal stream object representations. These results show that stimulus-driven and goal-directed attentional mechanisms have different roles in integrating features into the dorsal stream affecting both perception and the speed of decision-making processes.

Chapter 4. Manuscript 3: Hand Placement Near the Visual Stimulus Improves Orientation Selectivity in V2 Neurons.

This manuscript is published in the ***Journal of Neurophysiology***. The co-authors of this publication are Dr. Lauren E Sergio, Dr. J Douglas Crawford, and Dr. Mazyar Fallah. Carolyn J Perry, Dr. Lauren E Sergio, Dr. J Douglas Crawford, and Dr. Mazyar Fallah conceived and designed the experiment. Carolyn J Perry implemented the experiment and collected the data. Carolyn J Perry and Dr. Mazyar Fallah analyzed and reviewed the data. Carolyn J Perry and Dr. Mazyar Fallah prepared the manuscript. Carolyn J Perry, Dr. Lauren E Sergio, Dr. J Douglas Crawford, and Dr. Mazyar Fallah revised and edited the manuscript.

Citation: Perry, C. J., Sergio, L. E., Crawford, J. D., & Fallah, M. (2015). Hand placement near the visual stimulus improves orientation selectivity in V2 neurons. *Journal of Neurophysiology, 113*, 2859-2870.

4.1 Summary

Often, the brain receives more sensory input than it can process simultaneously. Spatial attention helps overcome this limitation by preferentially processing input from a behaviorally-relevant location. Recent neuropsychological and psychophysical studies suggest that attention is deployed to near-hand space much like how the oculomotor system can deploy attention to an upcoming gaze position. Here we provide the first neuronal evidence that the presence of a nearby hand enhances orientation selectivity in early visual processing area V2. When the hand was placed outside the receptive field, responses to the preferred orientation were significantly enhanced without a corresponding significant increase at the orthogonal orientation. Consequently, there was also a significant sharpening of orientation tuning. In addition, the presence of the hand reduced neuronal response variability. These results indicate that attention is automatically deployed to the space around a hand improving orientation selectivity. Importantly, this appears to be optimal for motor control of the hand, as opposed to oculomotor mechanisms which enhance responses without sharpening orientation selectivity. Effector-based mechanisms for visual enhancement thus support not only the spatiotemporal dissociation of gaze and reach, but also the optimization of vision for their separate requirements for guiding movements.

4.2 Introduction

A growing body of human psychophysical evidence shows that visual processing is altered near the hand. In blindsight, simply placing the hand in the blind field near to visual stimuli improves detection and size perception (Brown et al., 2008; Schendel & Robertson, 2004). In extinction, patients fail to attend to a second stimulus presented in the contralesional hemifield but when the hand is placed within the affected field, detection of the second stimulus is improved (di Pellegrino & Frassinetti, 2000). An improvement in detection near the hand, especially in cases involving extinction, would suggest that attention is deployed to near-hand space much like how the oculomotor system deploys spatial attention (Moore et al., 2003). Studies using classic spatial attention paradigms have shown this to be true. In a spatial cueing paradigm, reaction times to targets near the hand were facilitated regardless of cue location (Reed et al., 2006). In another study involving visual search, inhibition of return (IOR) and attentional blink paradigms, the presence of the hand slowed the shifting of attention between visual items (Abrams et al., 2008). These studies suggest that improved visual processing near the hand is linked to attentional prioritization of the space near the hand.

These behavioral studies suggest that attentional prioritization occurs in “near-hand space”, when movements are sustained. However, there is currently no single-unit neurophysiological evidence to support these findings and the neuronal mechanisms underlying this enhancement are as yet unknown. To determine if and how a nearby hand affects early visual processing, we recorded from neurons in macaque area V2, an early visual area shown to be modulated by attention (Luck et al., 1997; Motter, 1993), selective for orientation (Motter, 1993), a feature necessary for accurate reaching (Fattori et al., 2009; Murata et al., 2000; Raos, Umiltá, Gallese, & Fogassi, 2004), and is directly connected with fronto-parietal reaching and grasping networks to guide the hand (Gattas, Sousa, Mishkin, & Ungerleider, 1997; Passarelli et al., 2011). We measured the responses of V2 neurons to oriented rectangles when the animals maintained their grasp on a touchbar, placing their hand near to but *outside* the neuron’s receptive field (Figure 4.1 – Hand Near). As we wanted to be able to dissociate the effects of oculomotor driven spatial attention from those of near-hand attention, we separated the grasp target (touchbar) from the visual stimulus in the receptive field. Eye movements precede arm movements towards a reach target (Ballard, Hayhoe, Li, & Whitehead, 1992; Biguer, Jeannerod, & Prablanc, 1982; Fisk & Goodale 1985; Neggers & Bekkering, 2000, 2001, 2002; Prablanc, Echallier, Komilis, & Jeannerod, 1979) and the oculomotor system deploys spatial attention (Moore & Armstrong, 2003; Moore & Fallah, 2001, 2004; Müller, Philiastides, & Newsome, 2005). Thus if the visual stimulus was also the reach target, oculomotor driven spatial attention would be deployed to the reach target and would at the least confound and at the most completely mask modulation due to the nearby hand. To avoid this we did not make the visual stimulus the reach target but placed the hand nearby to take advantage of the spatial extent of attention afforded by the nearby hand.

Prior studies of spatial attention (McAdams & Maunsell, 1999; Moran & Desimone, 1985; Motter, 1993; Treue & Martinez-Trujillo, 1999) have used “Attend-In” and “Attend-Away” paradigms to compare the neuronal modulation when a spatial location is attended versus when attention is located elsewhere. In Attend-In conditions a cue, presented prior to the visual target, is used to allocate attention to a certain spatial location. In Attend-Away conditions the cue allocates attention to a location away from where the target is presented. Under these circumstances neuronal responses undergo a gain modulation when the spatial location is attended. We modified this paradigm so that the presence of the hand acted in a similar manner as the spatial cue in those studies. We hypothesized that if the hand is the center of an attentional field, as suggested by prior research (Abrams et al., 2008; Brown et al., 2008; di Pellegrino & Frassinetti, 2000; Reed et al., 2006; Schendel & Robertson, 2004), neuronal responses in “Hand-Near” and “Hand-Away” conditions should be similar to the neuronal responses seen in Attend-In and Attend-Away conditions respectively. As the relationship between oculomotor-driven spatial attention and the effect of hand position on early visual responses is unknown, the stimuli measuring V2 neurons' orientation selectivity were task irrelevant. If the task had instead required attending to and making judgments of the stimuli within the receptive fields, the effects of spatial attention would have confounded neuronal responses associated with hand attention. This task design is similar to real-life situations where you're reading a paper and reach, without looking, to pick up your cup of coffee: would orientation processing improve when the hand is near the cup? Across the population, we found that in the Hand-Near condition orientation tuning sharpened. This suggests that the mechanisms of near hand attention are different than gain modulation seen with oculomotor-driven spatial attention. In addition, we found that the presence of a nearby hand reduced the variability of neuronal responses. Together, these results show that orientation selectivity is improved near the hand which could increase the accuracy of subsequent reaches and grasps in the peripersonal workspace.

4.3 Materials and Methods

4.3.1 Electrophysiology

Two adult female rhesus monkeys were each implanted with a head holding device and a recording chamber positioned over left V2 using stereotaxic coordinates. Placement was confirmed by assessing receptive field size and eccentricity, topographic organization and feature selectivity (Gattass et al., 1981; Hubel and Livingstone, 1987; Levitt et al., 1994; Roe & Ts'o, 1995). A microdrive (3-NRMD-A2, Crist Instruments) was used to advance a tungsten electrode (FHC Inc). Neuronal data was acquired and stored using a Multichannel Acquisition Processor (Plexon Inc.). Single neurons were isolated online using Rasputin software (Plexon Inc). Receptive fields were mapped with a manually controlled flashing oriented bar that could be varied in orientation, size, and position. The diameter of the receptive field varied across neurons but ranged between 1.3 and 4.2 degrees of visual angle (“dva”: mean = 1.8, SD = 0.5). Note that the experiment was carried out if a receptive field was plotted; orientation selectivity was not tested at this point. This allowed for including neurons that only developed orientation selectivity in the presence of the hand. Neurons were isolated offline using Offline Sorter (Plexon Inc.) for subsequent analyses. All experimental and surgical procedures complied with animal care guidelines as defined by the CACC (Canadian Animal Care Committee) and York University’s Animal Care Committee (YUACC).

4.3.2 Stimuli and Task

Experimental control was maintained using Cortex software (http://dally.nimh.nih.gov/). Eye gaze was tracked using an infrared eye tracker (ISCAN Model ETL-200, 240Hz). Stimuli were presented on a computer monitor (Viewsonic G225f, 1024x768 resolution, 60Hz) that was placed 36cm from the monkey. This distance allowed the animal to comfortably reach with its right hand to a vertically oriented touch bar immediately adjacent to the front of the monitor (Figure 4.1) which was present throughout the experiment and positioned outside of the visual receptive field. The distance from the right edge of the RF to the touch bar ranged between 5.6cm (8.8dva) and 7.9cm (12.5dva). As the monkeys would grasp the touch bar by wrapping their fingers around it, the distance to the fingers (1.8 dva wide) ranged between 7-10.7 dva (see Figure 4.1). This minimum distance of 7 dva reduced the possibility of the hand encroaching upon the RF and modulating baseline firing rates, even if hand-mapping underestimated the size of the RF center. With this spacing, visual stimulation within the RF was identical across both conditions (Hand-Away and Hand-Near). The experiments were conducted in a darkened room illuminated by the ambient light from the computer monitor. The hand and touch bar were low contrast but visible to the animals.

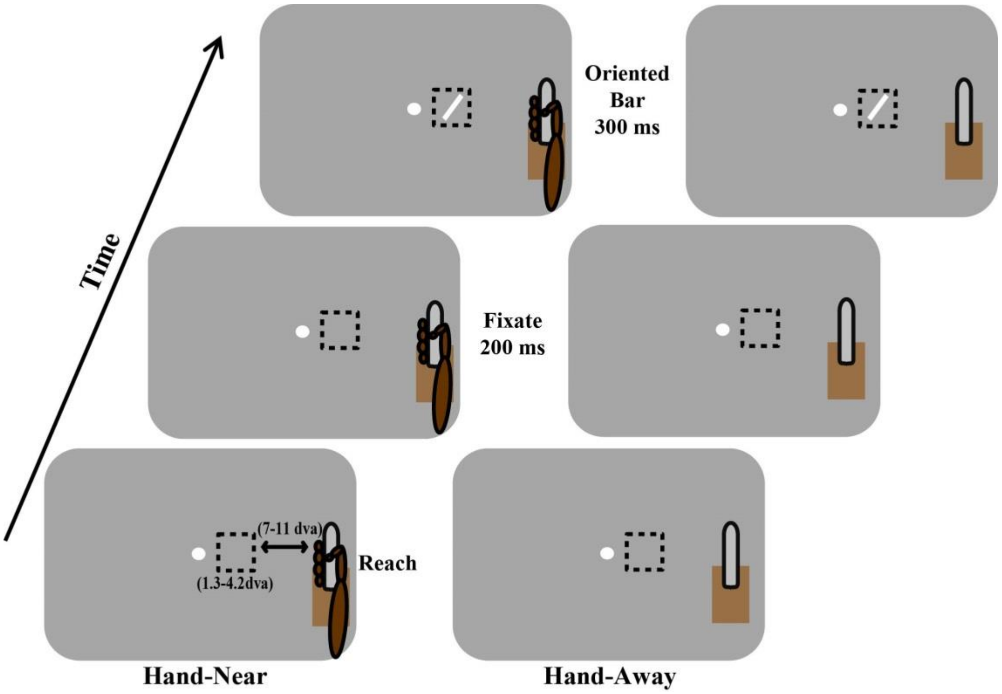

Figure 4.1: Experimental paradigm. In a Hand Near block the animal grasps a vertically orientated touch bar placed outside the RF at which time a fixation point appears. 200ms later an oriented bar is displayed within the RF for 300ms. In a Hand Away block, the touch bar apparatus remains visible but no reach is made by the animal. Reward is given for maintaining fixation and grasp (Hand Near) or simply maintaining fixation (Hand Away). The lower left panel shows the variation in receptive field (RF) diameter (1.3-4.2 dva) and also the distance between the right edge of the RF and the edge of the fingers (7-10.7 dva). This figure represents a depiction and is not drawn to scale or matched for the color and contrast of the experimental apparatus or the animal.

In a Hand-Near block, once the animal had grasped the touch bar each trial began with the appearance of a fixation point (Figure 4.1 left). When the animal maintained fixation within a 2dva window for 200ms, a task-irrelevant oriented rectangle was presented for 300ms in the center of the RF. The rectangle varied in orientation (0, 22.5, 45, 67.5, 90, 112.5, 135, and

157.5°) and size (based on the size of the receptive field). If fixation and grasp of the touch bar was maintained throughout this period, the animal received a reward (Monkey A: juice, Monkey B: fruit). In a Hand-Away block (Figure 4.1 right), the touch bar apparatus remained in place but the animal did not reach and grasp the touch bar. Trials again commenced with the appearance of the fixation point. Each orientation was tested 10-20 times in each hand condition.

We used this paradigm as it replicates the hand position of studies in which a sustained reach placed the hand near visual stimuli and showed improved visual processing and attentional prioritization of near–hand space (Abrams et al., 2008; Brown et al., 2008; Reed et al., 2006). This links the current research to previous neurophysiological work on spatial attention, with “Hand-Near” and “Hand-Away” substituting for “Attend-In” and “Attend-Away” (McAdams & Maunsell, 1999; Moran & Desimone, 1985; Motter, 1993; Treue & Martinez-Trujillo, 1999).

4.3.3 Data Analysis

We computed baseline rates from -175-0 ms prior to the onset of the oriented rectangle and stimulus response rates from 0-300 ms after stimulus onset. From these we computed the following measures:

Orientation Tuning Index

In order to quantify possible changes in tuning between Hand Near and Hand Away conditions, we computed an orientation tuning index (OTI): R_{pref}/R_{orth} in each condition, where R is the response rate of the neuron for preferred or orthogonal orientation. The preferred orientation was the orientation that produced a maximal response and the orthogonal orientation was 90 deg to the preferred orientation. In contrast to curve-fitting, this index, based on response rates, avoids the use of interpolated data when determining changes in tuning.

Response Modulation

We quantified the effect of hand position by computing a number of modulation indices. First we computed the percentage change of firing rate based on whether a reach had occurred or not: ((HN-HA)/HA)*100, where HN represents the average response in the Hand Near condition and HA represents the average response rate in the Hand Away condition. We similarly computed the percentage change in the response rate to the preferred direction only: $((HN_{Pref}-HA_{Pref})/HA_{Pref})*100$. Finally, we computed the modulation of the tuning indices to determine whether changes in tuning occurred between the Hand Near and Hand Away conditions: $((OTI_{HN} – OTI_{HA})/OTI_{HA})*100$. Significant shifts were tested using the Wilcoxon signed-rank test.

Curve Fitting

We fit the orientation tuning data for unimodally oriented neurons with a von Mises function, a circular form of the Gaussian function, used for orientation selectivity (Kohn & Movshon, 2004). The function takes the form:

$$\mathrm{vM}(\theta) = \mathrm{a}e^{\kappa\cos(\theta-p)} + \mathrm{m}$$

where a is the multiplicative scaling factor, κ (kappa) is the concentration or bandwidth of tuning, p is the preferred direction, and m is the baseline rate. Fits were performed in Matlab with the *nlinfit* function (based upon LSE). For each neuron, fits were computed for Hand-Near and Hand-Away conditions separately. Two neurons in the main population and two neurons in the baseline shifted population were removed from further analysis due to poor fits. For these neurons, *nlinfit* did not converge to a solution (ill-conditioned Jacobians) and they were rejected from further analysis (similar to Kohn & Movshon, 2004). Significant shifts in the fit parameters were tested using the Wilcoxon signed-rank test.

Fano Factors

To quantify response variability we computed fano factors (FF = spike count variance/mean spike count; Chang, Armstrong, & Moore, 2012; Cohen & Maunsell, 2009; McAdams and Maunsell, 1999; Mitchell et al., 2007) in the HN_{pref} and HA_{pref} conditions. To eliminate the possibility that changes in the FF were influenced by neuronal firing rates, we mean-matched response rates in the HNpref and HApref conditions and then compared the FFs in each using a Wilcoxon signed-rank test.

4.4 Results

4.4.1 Inclusion and Exclusion Criteria

Neurons were only included for further analysis if they had a significant visual response over baseline (t-test). As we wanted to test the effect of the hand on orientation tuning, we then limited our analysis to neurons exhibiting significant orientation tuning (one-way ANOVA, e.g. Jansen-Amorim, Lima, Fiorani, & Gattass, 2011; Motter, 1993) in either the Hand-Near or Hand-Away condition. The only difference between the conditions was the presence or absence of the hand on the touch bar. To eliminate the possibility that the hand or arm visually encroached on the classic receptive field, neurons were excluded if they showed a significant modulation in the baseline firing rate between Hand-Near and Hand-Away conditions (t-test). Eliminating cells from analysis that had a significant shift in their baseline firing rate also removed the possibility that responses were altered due to other variables such as arousal. Of 93 neurons from which data was obtained, 41 were removed as they were not orientation tuned in either the Hand-Near or Hand-Away conditions (26) or did not have a significant visual response above baseline to the oriented bars (15 neurons). 52 neurons were orientation selective. Although studies have shown that spatial attention can increase baseline responses in area V2 (Luck et al, 1997), 14 cells (baseline-shifted neurons) were analyzed separately as they had a significant baseline modulation between the Hand-Near and Hand-Away conditions, which could also reflect the animal's arm impinging on the receptive field center. The remaining 38 neurons became the main population for analysis. Note that of the 52 orientation selective neurons, 15 were only orientation selective in the Hand-Near condition. These cells would have been missed if we only tested neurons that exhibited orientation selectivity during the mapping of the receptive field.

4.4.2 Gaze Position

To ensure that gaze position did not shift dependent on hand placement, we calculated the difference between the average horizontal eye position shift between the baseline period and the presentation of the stimulus for each included neuron's experimental session and computed any potential shifts between the Hand-Near and Hand-Away conditions. There was no significant shift ($F(1,27) = 0.34$, $p = 0.568$) of the eye position towards the hand (Hand-Near – Hand-Away = -0.002 dva ± 0.001SEM). This indicates that the presence or absence of the hand did not influence gaze position. There was however, a significant shift of gaze towards the receptive field during stimulus presentation ($F(1,27) = 7.73$, $p = 0.010$). This suggests that the onset of the stimulus was salient enough to slightly (0.046 dva) draw the eyes towards the receptive field regardless of the hand position. This indicates that the hand was not the target of a saccade and an oculomotor-driven shift in attention.

4.4.3 Neuronal Analysis

Figure 4.2 shows the tuning curves of 2 example neurons. Neuron A depicts a neuron whose responses increased slightly at the preferred orientation but sharpened during the Hand-Near condition (Figure 4.2a) due to a reduction in response to the orientations on the flank of the tuning curve. Neuron B instead showed an increase in response to the preferred orientation with no corresponding change in response at the orthogonal orientation (Figure 4.2b). While spatial attention classically results in a proportional increase to responses across the tuning curve, neither Neuron A or B show this pattern of response.

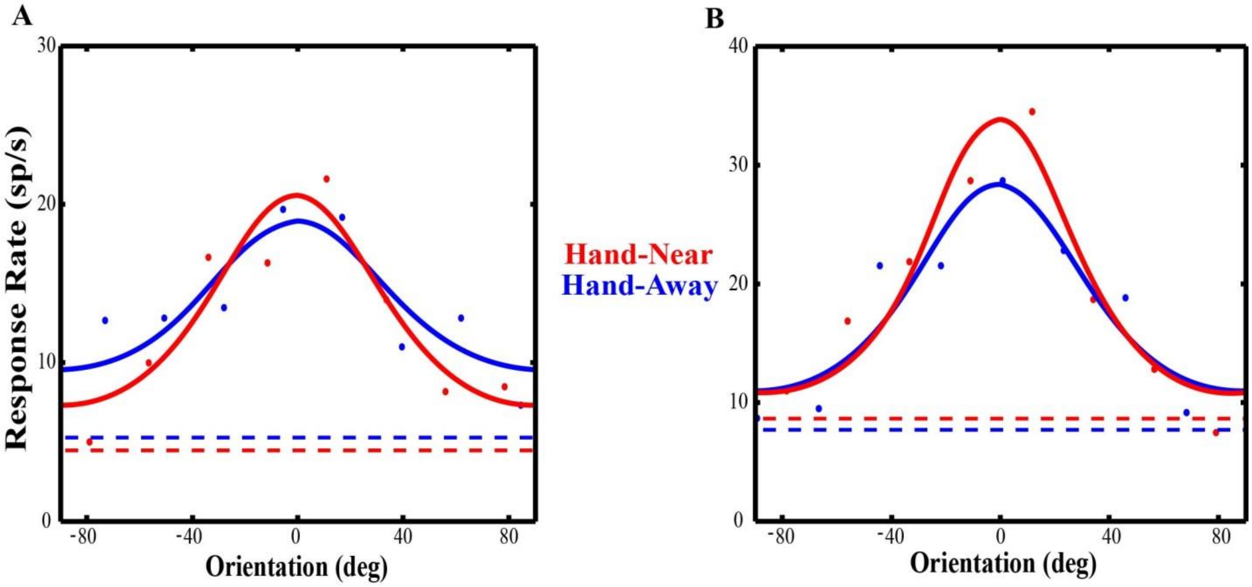

Figure 4.2: Example cells. The data from two cells fitted with von Mises functions. a) This neuron shows responses that are increased at the preferred orientation and reduced at the orthogonal orientation resulting in a sharpening of tuning. b) While showing a larger increase response at the preferred orientation, this neuron instead had no modulation at the orthogonal orientation.

4.4.4 Effect of Hand Position on Preferred and Orthogonal Responses

Figure 4.3a plots the distribution of neuronal responses to the preferred orientation in the Hand-Near vs the Hand-Away condition. Points that lie above the line of unity indicate cells in which the response rate to the preferred orientation in the Hand-Near condition was greater than in the Hand-Away condition. More of the neurons lie above the line of unity than below (red and black dots). Across the population (n = 38), the response to the preferred orientation significantly increased (*Z* = 2.12, *p* = 0.034) by 10.76% (± 4.69 SEM) in the Hand-Near vs Hand-Away condition (Figure 4.3b). In contrast, the population showed no significant increase in the response rate at the orthogonal orientation with the Hand-Near (*Z* = 1.50, *p* = 0.133, Mean: -3.69% ± 6.69 SEM). It is important to note that previous studies of classic spatial attention have shown little to no effect on neuronal responses to irrelevant stimuli when attention is directed outside of the receptive field (e.g. Moran & Desimone, 1985). Finding enhanced responses when grasping a touch bar outside of the receptive field is not only surprising but also provides neurophysiological evidence that attention is deployed to near-hand space. Based on the distance between the touch bar and the stimulus in the receptive field, near-hand-related visual enhancement appears to operate with a larger spatial focus than oculomotor-driven spatial attention. In addition, hand position preferentially enhances responses at the preferred orientation and not at the orthogonal orientation.

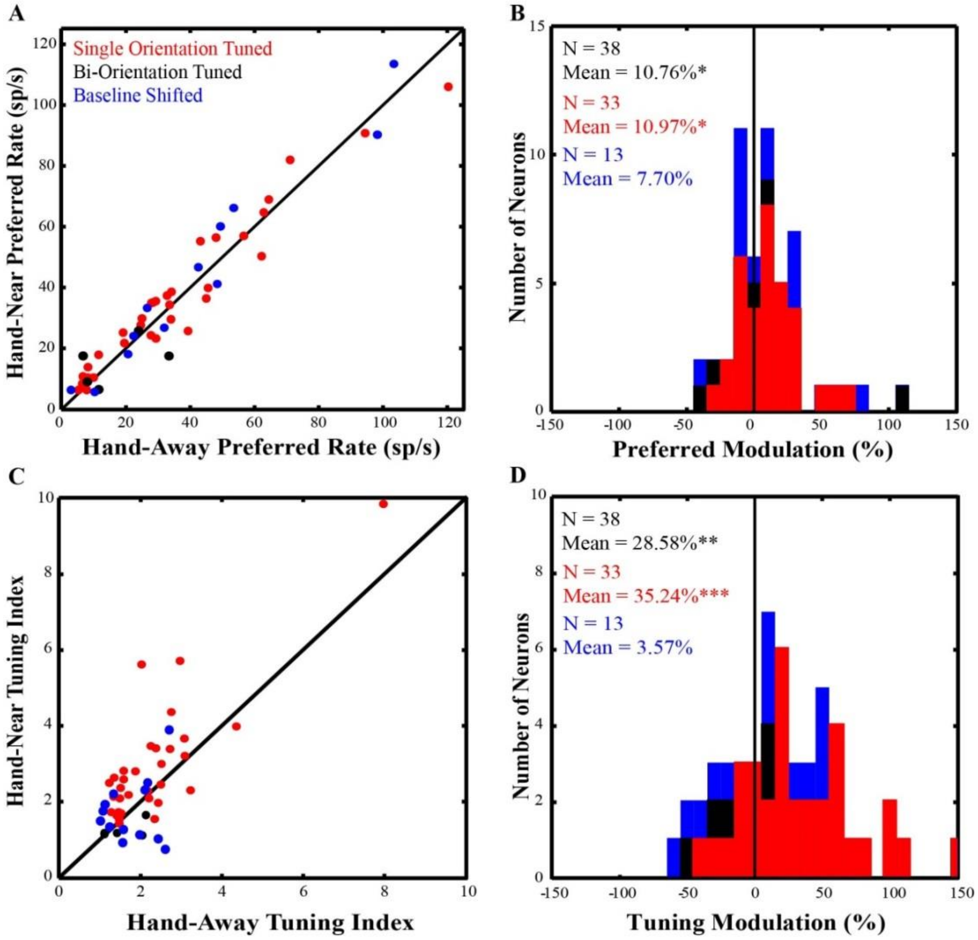

Figure 4.3: Modulation of preferred rate and tuning. (a) The response of each neuron to the preferred orientation in the Hand Away (x-axis) condition is plotted against the response of each neuron in the Hand Near (y-axis) condition. The diagonal line on the plot represents the line of unity; the majority of points fall above this line indicating an increased response to the preferred orientation when the hand was nearby. (b) We quantified this change in response by computing a modulation index and found that the presence of the hand significantly increased neuronal response to the preferred orientation (seen as a shift of the population to the right of zero). (c) The tuning index of each neuron in the Hand Away condition (x-axis) is plotted against the tuning index in the Hand Near condition (y-axis). Again more units fall above the line of unity. (d) We used the same modulation index to quantify tuning modulation and found that the presence of the hand significantly sharpened tuning. Data in red represents all neurons in the dataset that were tuned for a single orientation. Data in black represents neurons that were tuned for two orientations, and data in blue are neurons that were excluded from the main analysis as they showed a significant baseline shift between the Hand-Near and Hand-Away conditions.

4.4.5 Effect of the Hand on Orientation Tuning

Multiplicative gain modulation, proportional increases across stimulus selectivity (McAdams & Maunsell, 1999), is a mechanism commonly used to describe how spatial attention affects the responses of visual neurons. That is, multiplicative gain modulation increases responses across the tuning curve without changing the shape of the tuning curve. If, similar to spatial attention, the presence of the hand enhances early visual processing through gain modulation, there should be no change in the orientation tuning index (OTI = R_{Pref}/R_{Orth}). Plotting the tuning index in the Hand-Near vs the Hand-Away condition (Figure 4.3c, red and black dots) shows that the majority of the neurons fall above the line of unity. Tuning is significantly sharpened by 28.58% (± 7.71 SEM, $Z = 3.30$, $p = 0.001$ – Figure 4.3d) across the population (n = 38). Thus unlike classic spatial attention which does not affect tuning, hand-related attention sharpened orientation selectivity by almost 30%.

4.4.6 Effect Without Bi-orientation Tuned Cells

Previous work (Anzai, Peng, & Van Essen, 2007) has found that up to 20% of V2 neurons show enhanced responses at two orthogonal orientations (ie. are bi-orientation tuned). These types of cells have been shown to be used to determine contours and occlusion (Rubin, 2001). Figure 4.4 shows the responses of an example bi-orientation tuned neuron. While the polar plot (panel A) doubles up the orientation information, it clearly shows the crossed axes of the two preferred orientations. Panel B shows the same data plotted as an 180deg tuning curve.

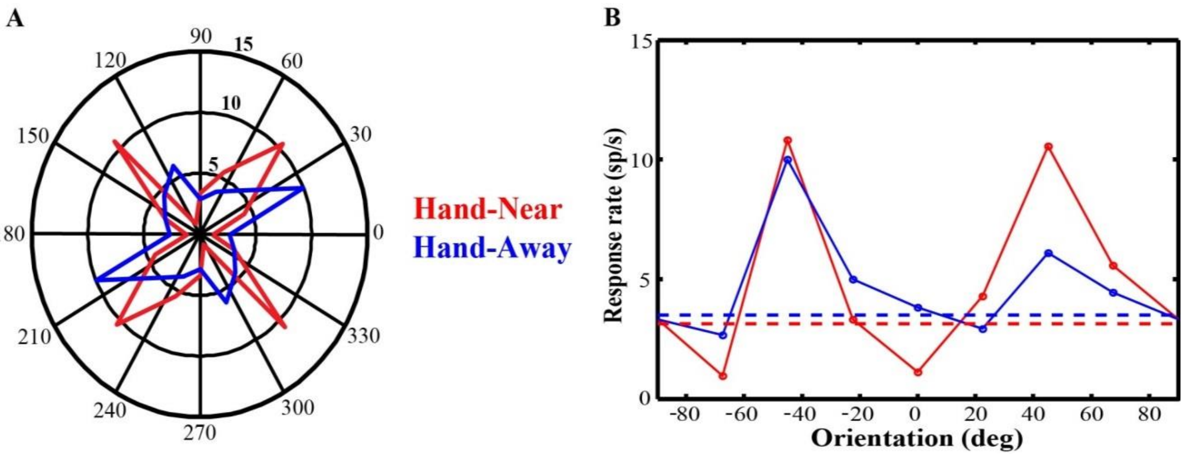

Figure 4.4: Example bi-orientation tuned cell. Polar (panel A) and 180º (panel B) plots for the same example neuron. The firing rate in the polar plot is depicted as the distance away from the center, and the responses to each orientation are mirrored 180 degrees to depict a circular tuning plot. In the Hand-Near condition there is an increased response along the minor axis (orthogonal orientation) with no change in the major axis (preferred orientation), compared to the Hand-Away condition). Also, with the hand present, responses to orientations between the two axes are suppressed below baseline (Panel B).

When the hand is present (Hand-Near), the major axis of orientation (e.g. the longer one in the Hand-Away condition) is little changed. However the response to the minor axis increases. The responses to the orientations in between these two axes are suppressed and drop below baseline. Changes in tuning, then, are hard to determine in bi-orientation cells as any increase in response in the lesser of the two preferred orientations would reduce the tuning index because the OTI reflects tuning to a single orientation. As tuning indices do not accurately reflect bi-orientation cells, we re-examined our population and found 5 bi-orientation cells (~13%). We then removed them from our cell population and performed the analyses again. Due to the small sample size (n=5) we did not analyze the bi-orientation tuned cells on their own, however they are depicted separately (black dots and bars in Figure 4.3, and Figure 4.6).

With the bi-orientation cells removed, the single orientation population (n=33) still produced an increase in response when the hand was present (Figure 4.3b, red bars). Responses at the preferred orientation were significantly (Z = 2.53, p = 0.011) increased by 10.97% (± 3.86 SEM) in the Hand-Near vs Hand-Away condition (Figure 4.5b). Responses to the orthogonal orientation were now significantly decreased in the presence of the hand (-9.41% ± 5.76 SEM, Z = 2.17, p = 0.030). The presence of the hand not only improves responses to the preferred orientation, but also decreases responses to the orthogonal orientation. This was masked by the bi-orientation cells in the whole population because the bi-orientation cells also preferred the orthogonal orientation. Consistent with these results, the tuning index showed a greater decrease with the hand present when the bi-orientation cells are removed (Figure 4.3d, red bars). Tuning was sharpened by 35.24% (± 8.03 SEM, Z = 3.76, p < 0.001) in Hand-Near vs Hand-Away; an increase from that seen across the full population (28.58%).

4.4.7 Effect of Hand Position on Baseline Shifted Cells

Although studies have shown that spatial attention can increase baseline responses in area V2 (Luck et al., 1997), 14 neurons that had a significant baseline shift between the Hand-Near and the Hand-Away condition were not included in the main analysis. This was done to ensure that the effect of hand position was not being driven by the arm encroaching on the visual receptive field. We now analyzed the baseline-shifted neurons to determine whether their responses were similar to the rest of the population. None of the cells were bi-orientation tuned. It should be noted however, that one cell within this population was removed as an extreme outlier (Preferred Modulation = 387%, Orthogonal Modulation = 742%). In the presence of the hand, the remaining baseline shifted cells (n=13) were not significantly modulated by hand position in their responses to the preferred (Mean: 7.70% ± 7.71 SEM, p = 0.267) or the orthogonal orientations (Mean: 20.16% ± 14.87 SEM, p =0.414). Nor was there a significant modulation of the tuning index (Mean: 3.57% ± 11.11 SEM, p = 0.787). Figure 4.3 shows the distribution of the baseline shifted cells in blue with the rest of the population (red) and bi-orientation cells (black). The baseline shifted cells are also depicted in blue on Figure 4.6, which shows the cells' distribution across the range of preferred response and tuning modulations. We cannot distinguish whether the lack of an effect of hand position in the baseline shifted cells is due to the arm impinging on the receptive field, the small sample size, some other factor, or a combination of these possibilities.

4.4.8 Effect of the Hand on Response Variability

Previous studies have shown reductions in response variability during reaching in premotor cortex (Churchland et al., 2010) and oculomotor preparation in FEF (Purcell et al. 2012). The reduction in oculomotor response variability has been shown to also propagate back to visual neurons in area V4, which show a similar reduction prior to a saccade (Steinmetz & Moore, 2010). If near-hand attention is mediated by feedback from fronto-parietal reaching and grasping networks (Culham et al., 2003), we would expect to find a similar reduction in response variability in V2 neurons when a sustained reach places the hand nearby. To control for changes in firing rate, we first mean-matched response rates in the Hand-Near and Hand-Away conditions (as per Churchland et al., 2010) and then computed their Fano factors (spike count variance/mean spike count). Figure 4.5a shows the Fano factor distribution in the Hand-Near compared to the Hand-Away condition across the population of 38 neurons included in the dataset (in red). The Fano factor of the preferred orientation response (Figure 4.5b) significantly declined (Z = -8.68, p < 0.001) in the Hand-Near condition (Mean: 0.96 ± 0.11 SEM), compared to the Hand-Away condition (Mean: 1.52 ± 0.31 SEM). Response variability also significantly declined in the baseline shifted cells ($Z = -8.76$, $p < 0.001$, Figure 4.5a and b in blue) in the Hand-Near condition (Mean: 0.61 ± 0.086) compared to the Hand-Away condition (Mean: 0.85 ± 0.13). This reduction in response variability within near-hand space is consistent with Fano factor reductions seen due to spatial attention and/or motor feedback (Churchland et al., 2010; Purcell, Heitz, Cohen, & Schall, 2012; Steinmetz & Moore, 2010).

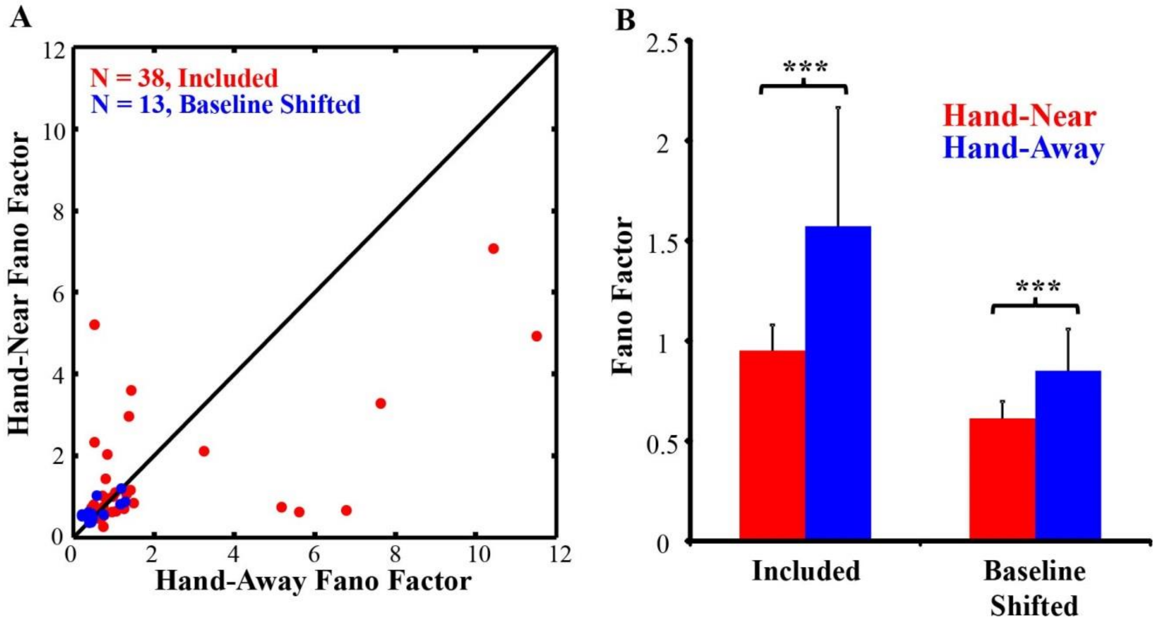

Figure 4.5: Changes in response variability. A) The Fano factor in the Hand-Near and Hand-Away conditions are plotted for the population of neurons included in the dataset (n = 38, in red) and baseline shifted neurons (n = 13, in blue). B) In both populations response variability was significantly reduced when the hand was present.

4.4.9 Relationship Between Changes in Response Rates and Orientation Tuning

We investigated the relationship between changes in preferred response and orientation tuning and found different patterns of activity (Figure 4.6). While the upper right quadrant contains the majority of cells, which exhibited both increased response and sharpened tuning when the hand was near, there was no significant relationship between preferred response modulation and tuning index modulation across the population of cells (*F* = 0.26, *p* = 0.614). The bi-orientation cells, as discussed previously, produced negative tuning index modulations in the Hand-Near condition due to increasing responsivity to the secondary preferred orientation. Thus they are predominantly found on the left hand side of the distribution (black dots). Finally, the baseline shifted cells are plotted in blue, depicting where they fall amongst the rest of the population.

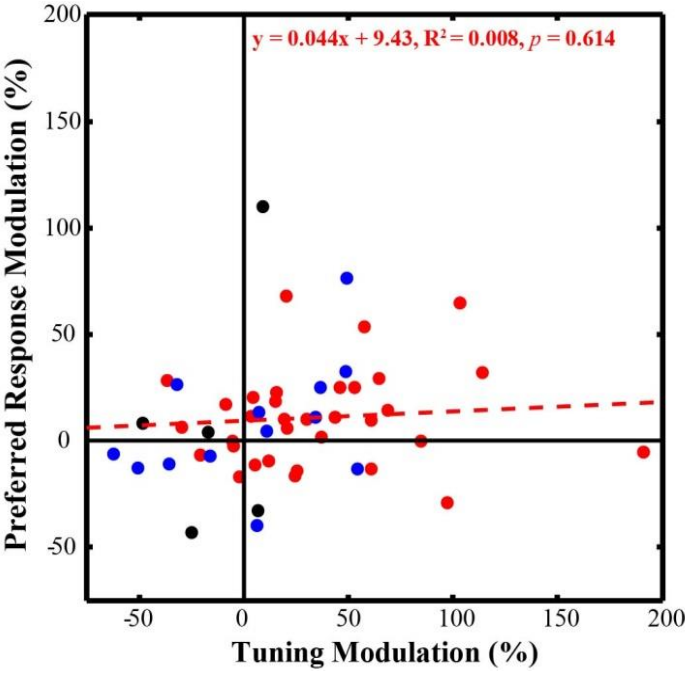

Figure 4.6: Response modulation versus sharpened tuning. We plotted the tuning modulation (x-axis) against the preferred modulation (y-axis) for each unit. While the majority of the neurons fall within the upper right quadrant, the population of single orientation tuned neurons (in red) did not show a significant relationship between modulation in the preferred response and changes in the tuning index. Bi-orientation neurons are shown in black and baseline shifted neurons in blue for comparison.

4.4.10 Effect of Hand Position on Fitted Tuning Curves

Of the 38 neurons used in the previous analysis, we removed the 5 bi-orientation tuned cells as they would not be fit by a unimodal von Mises function. We then used the von Mises function to fit the remaining 33 neurons. Two additional neurons were poorly fit (as per the nlinfit function due to ill-conditioned Jacobians) and thus were removed from the population. Figure 4.7a depicts the population tuning curves in both the Hand-Near and Hand-Away. The shaded area between the two curves highlights how tuning sharpens when the hand is present, with increased responsivity around the preferred orientation and decreased responsivity at orthogonal orientations, consistent with the previous results. Kappa is the concentration parameter from the fit that describes the tuning bandwidth: the larger the kappa, the sharper the tuning. From each cell's individual curve fits, we have plotted the kappa in the Hand-Near versus Hand-Away conditions in Figure 4.7c. Consistent with the population tuning curve and the raw data analyses, the majority of cells (Figure 4.7c, red dots) fall above the line of unity. Kappa significantly increased by 17% (+0.114 ± 0.085SEM, $Z = 2.49$, $p = 0.013$, Figure 4.7d) in the Hand-Near (Mean: 0.79 ± 0.07 SEM) compared to the Hand-Away (Mean: 0.67 ± 0.09 SEM) condition. The population amplitude (a), a multiplicative scaling factor that represents the scaling of the response above baseline, was not significantly different in the two hand conditions (Hand-Near: 11.2 ± 1.3 SEM; Hand-Away: 11.6 ± 1.4 SEM, $Z = -0.53$, $p = 0.60$). Thus there was no evidence in support of gain modulation. In addition, the preferred orientation across the population did not significantly differ between Hand-Away and Hand-Near conditions (Mean Difference: -7.09º ± 10.6 º SEM, $Z = -0.20$, $p = 0.85$).

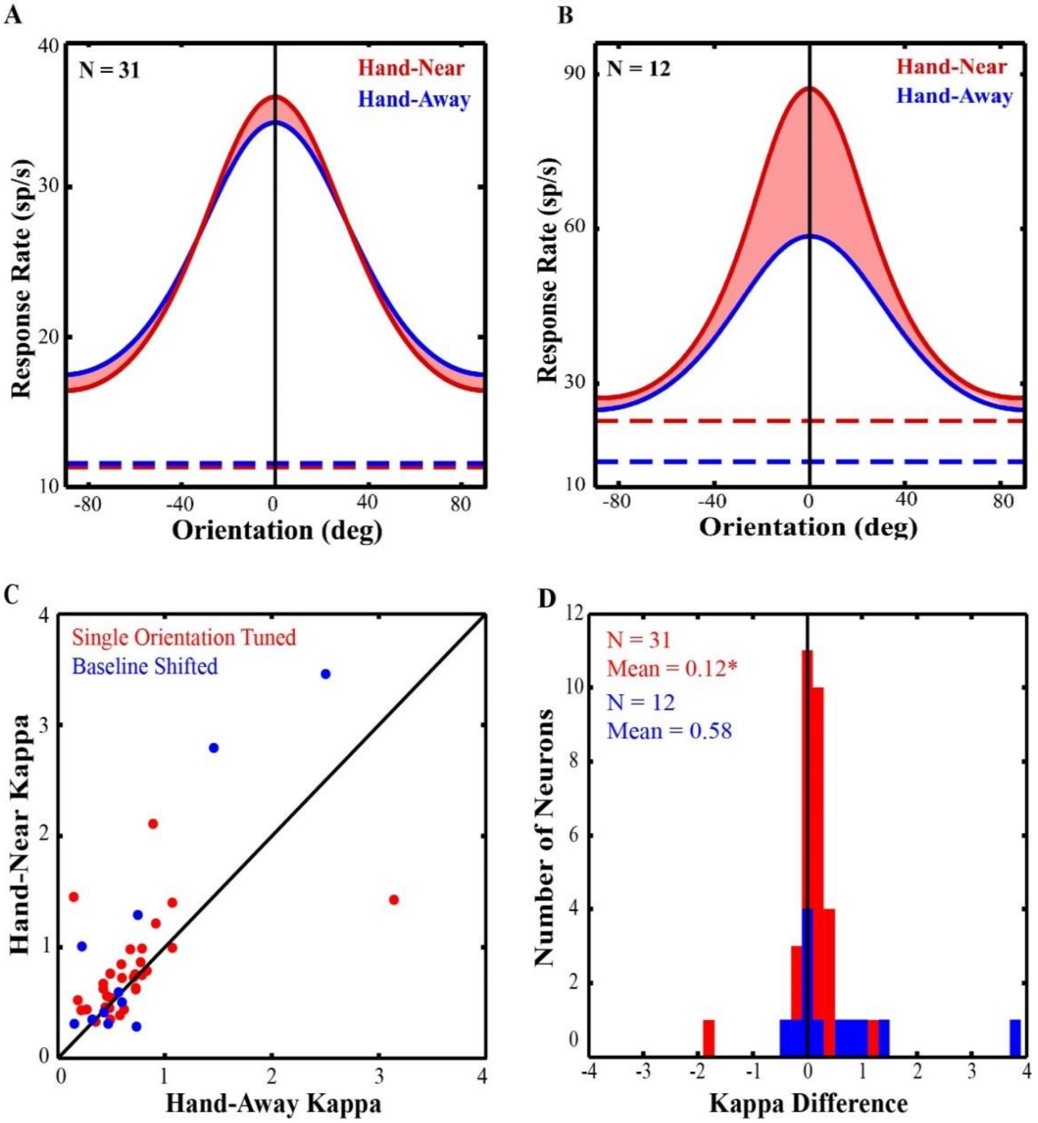

Figure 4.7: Curve fit data. The population averages of the tuning curve fits are depicted with the preferred directions aligned to vertical (0º). Baseline firing rates are indicated by the dashed lines. The shaded area between the curves for the Hand-Near (red) and Hand-Away (blue) conditions represents the change in kappa (bandwidth) between the conditions. Panel A represents neurons tuned for one orientation (n = 31) and panel B, neurons that had a significant baseline shift between the Hand-Near and Hand-Away conditions (n = 12). Panel C shows that the majority of the neurons included in the dataset fall above the line of unity, producing a significant sharpening in tuning bandwidth (panel D). The baseline shifted neurons did not show a significant change in kappa.

Of the 14 baseline shifted cells, 12 were fit with von Mises functions (Figure 4.7b) and 2 were removed as they were poorly fit. In this population there was a trend (*p* = 0.09) for an increase in kappa in the Hand-Near (Mean: 1.32 ± 0.42 SEM) over the Hand-Away (Mean: 0.738 ± 0.12 SEM) condition (Figure 4.7c and d, in blue). Amplitudes were not significantly different (*p* = 0.233) between Hand-Near (Mean: 17.2 ± 2.9SEM) and Hand-Away (Mean: 20.9 ± 3.9SEM) conditions. Furthermore, there was no significant shift in preferred orientation between conditions (Mean Difference: 6.0º ± 3.6 º SEM, *p* = 0.17), Similar to the results with the raw data, there were no significant differences in this population of baseline shifted cell, though the trend for sharpened tuning may be due to a lack of statistical power due to the small sample size.

4.4.11 Relationship Between Orientation Selectivity and the Orientation of the Hand

While classic spatial attention does not differentially modulate preferred and non-preferred stimulus response, such an effect has previously been seen with feature-based attention (Treue & Martinez-Trujillo, 1999). The feature-similarity gain model (Treue & Martinez-Trujillo, 1999) states that the strongest enhancement occurs when the attended feature is also the neuron's preferred stimulus, decreasing as the difference between the two gets larger. We would expect that if the feature similarity gain model was responsible for the sharpened tuning seen in the current study, then because the task-relevant touch bar was vertical, neurons preferring vertical orientations should have the greatest enhancement while neurons preferring horizontal orientations should have the least enhancement.

A similar effect would occur with far surround suppression. More recently, there has been a description of 'far surrounds' distinct from 'near surrounds' for visual neurons in areas V1 and V2 (e.g. Okamoto, Naito, Sadakane, Osaki, & Sato, 2009; Shushruth, Ichida, Levitt, & Angelucci,, 2009). The near surround is based on feedforward and horizontal connections, whereas the far surround is based on feedback from extrastriate areas (Shushruth et al., 2009). While the distance between the touch bar and the receptive field is large enough that the hand was not within the classical near surround of the V2 neurons, the hand may have fallen within the far surround. The effect of far surround stimulation has been shown to enhance orientation selectivity in area V1 in the cat (Okamoto et al., 2009), when large gratings covered from the center to the far surround. The hand and/or touch bar in our paradigm would be a much weaker stimulus as it only covers a portion of the far surround, but if a similar effect occurred in V2 in the monkey, then we would once again expect that the magnitude of the sharpened tuning would be strongest when the cell's preferred direction was near vertical.

So the potential effects of far surround suppression and feature-based attention would be the same in the current paradigm: the hand/touch bar are vertically oriented in the surround and would have the greatest effect on cells that preferred that orientation and the least effect on cells that preferred horizontal. Instead we found no significant relationship between the neurons' vertical offsets *[abs(90º-preferred orientation)]* and kappa (tuning bandwidth) for the main population (regression analysis, n = 31; F = 0.06, *p* = 0.81) or the baseline shifted population (n = 12; ; F = 0.51, *p* = 0.49). Therefore, near-hand modulation of visual processing was not dependent on the orientation of the touch bar, either through feature-based attention or far surround suppression.

4.4.12 Qualitative Analysis of Full Population

To determine if the presence of the hand had any effect on all the neurons regardless of responsivity and selectivity, we performed the following analysis. As a proportion of the neurons were not significantly visually responsive or orientation selective, we had to first estimate a preferred orientation. For each neuron, all trials (Hand-Near and Hand-Away) were averaged and the peak response was selected as that neuron’s preferred orientation. We then aligned the preferred orientations to produce population averages for Hand-Near and Hand-Away conditions. These population averages were then fit using the von Mises function. These results are depicted in Figure 4.8. Across the population of all V2 neurons (n=93), including cells that were not visually responsive or tuned for orientation, there was no evidence of gain modulation as the amplitude did not differ appreciably between the Hand-Near (9.84) and Hand-Away (9.66) conditions. However, there was still a qualitative sharpening of orientation tuning, as kappa, the concentration parameter, showed an almost 20% increase in the Hand-Near condition (Hand-Near = 0.429, Hand-Away = 0.359). This pattern of results is similar to that seen in the previous analyses, and may likely be driven by the visually responsive, orientation selective neurons.

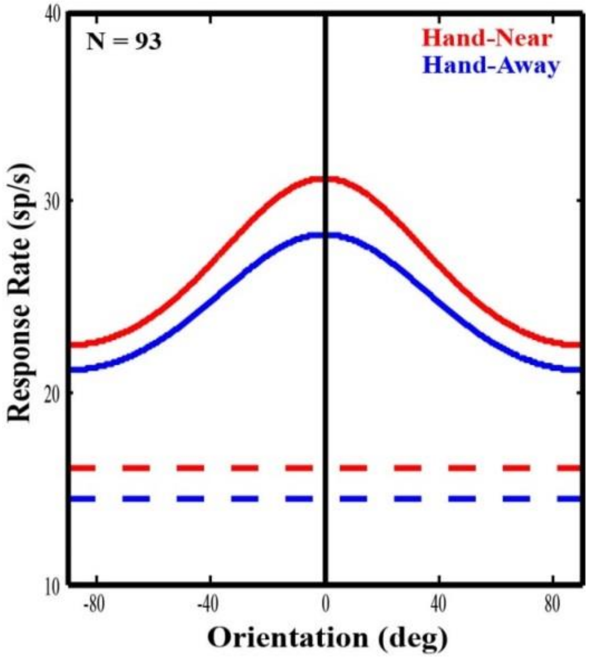

Figure 4.8: Effect of hand position across the full population. All neurons regardless of responsivity were aligned to the orientation of their maximum response, averaged with each hand condition and then fit with von Mises functions. The curve fits and baseline rates are depicted for qualitative comparison. Curve amplitude did not differ appreciably between conditions (Hand-Near = 9.84, Hand-Away = 9.66). There was however, a qualitative sharpening of tuning which showed an almost 20% increase in the Near-Hand condition (0.429) over that in the Hand-Away (0.359) condition.

4.5 Discussion

Previous studies on hand-related attention have focused on behavioral benefits only (Abrams et al., 2008; Bekkering & Neggers, 2002; Brown et al., 2008; Craighero et al., 1999; Deubel et al., 1998; di Pellegrino & Frassinetti, 2000; Fagioli et al., 2007; Reed et al., 2006; Schendel & Robertson, 2004); this study provides the first neurophysiological evidence that a nearby hand affects neuronal responses in an early visual processing area. Our results show that hand position, like gaze position, alters visual processing, but they also show that the mechanisms for these two phenomena are somewhat different. The responses of area V2 neurons were preferentially enhanced to the preferred orientation over the orthogonal orientation (Figure 4.7a) and produced sharpened orientation tuning. These results are not completely consistent with current models of spatial attention or feature-similarity gain. Instead, the results suggest a novel effector-based mechanism which improves sensitivity in early visual processing areas of a feature relevant for that effector, i.e. orientation for reaching and grasping with the hand. Further, we showed that a maintained reach and grasp reduced the variability of V2 neuronal responses to nearby task-irrelevant visual stimuli, a result consistent with attentional deployment near the hand. We hypothesize that this reduction in response variability indicates feedback from parietal areas involved in the fronto-parietal motor network, proprioception and/or encoding of peripersonal space. These hand-specific tuning properties may be functionally advantageous because sharpened orientation tuning would allow for more accurate grasping of nearby objects.

4.5.1 Proposed Neural Mechanism

Prior studies of spatial attention (McAdams & Maunsell, 1999; McAdams & Reid, 2005; Siedemann & Newsome, 1999) have shown that visual neurons undergo gain modulation when attended. However, the results of the present study on hand attention do not show gain modulation. In the main population (without bi-orientation cells), while the preferred response significantly increased in the Hand-Near condition, the orthogonal response significantly decreased. This was also evident in the population tuning curves (Figure 4.7a). Thus hand attention sharpened orientation selectivity instead of increasing the gain of the responses across all orientations. Similar effects on direction selectivity have been found in area MT neurons with feature-based attention (Treue & Martinez,-Trujillo, 1999). But feature-based attention is dependent on congruency between the attended feature, in this case the vertically oriented touch bar and hand, and the preferred orientation of the cell. Instead, we found no relationship between the orientation of the touch bar and the orientation of the visual stimulus within the RF. Therefore the effects of the hand on visual processing were not driven by feature-based attention either.

A third potential mechanism is based on suppressive surrounds. When a preferred stimulus is presented in the RF and a matching stimulus is presented in the surround, that neuronal response is suppressed by the stimulus in the surround (Akasaki, Sato, Yoshimura, Ozeki, & Shimegi, 2002; DeAngelis, Freeman, & Ohzawa, 1994; Li & Li, 1994; Walker, Ohzawa, & Freeman, 1999, 2000). This surround suppression is thought to be driven by feedforward and horizontal connections. Additionally, a far surround dependent on feedback from extrastriate areas has been described in areas V1 and V2 (e.g. Shushruth et al., 2009). In V1, orientation tuning can be enhanced when a large oriented stimulus covers a cell's classical receptive field and its far surround (Orban, Kato, & Bishop, 1979; Chen et al., 2005; Xing, Shapley, Hawken, & Ringbach, 2005; Okamoto et al., 2009). While the hand and touch bar were placed outside the near surround, it is possible they fell within the far surround. However, it is unlikely that the sharpened orientation tuning seen in the Hand-Near condition in the current experiment is due to surround suppression. Surround effects are dependent on the similarity between the stimulus in the surround and the preferred orientation of the cell, but the results of our regression analysis showed no such relationship.

Orientation tuning improved in the Hand-Near over the Hand-Away condition, but this effect was not subserved by spatial attention (gain modulation), feature-based attention, or surround suppression. Therefore near hand attention is dependent on a novel mechanism wherein general orientation selectivity is enhanced in the space near the hand. The mechanism operates by enhancing the preferred responses while inhibiting the non-preferred, which results in sharper tuning.

4.5.2 Proposed Neural Circuitry

As hand-related visual enhancement differs in effect from current models of spatial and feature-based attention, it would need to be served by separate neural circuitry. It has been proposed (Rizzolatti et al. 1987) and demonstrated (Moore & Fallah, 2001, 2004; Moore et al., 2003) that recurrent feedback from the oculomotor system modulates visual attention and early visual responses. Reductions in neuronal variability due to movement preparation have been shown to occur in areas PMv (Churchland et al., 2010) and FEF (Purcell et al., 2012). The reduction in response variability found in FEF coincides with reductions in response variability in area V4 prior to a saccade (Steinmetz & Moore, 2010). Based on these studies, and given that behavioral studies have shown visual enhancement with both sustained and active arm movements (Abrams et al., 2008; Bekkering & Neggers, 2002; Brown et al., 2008; Craighero et al., 1999; Deubel et al., 1998; di Pellegrino & Frassinetti, 2000; Fagioli et al., 2007; Festman, Adam, Pratt, & Fischer, 2013; Hannus et al., 2005; Langerak, La Mantia, & Brown, 2013; Reed et al., 2006; Schendel & Robertson, 2004; Symes et al., 2008), we hypothesize that reductions in V2 neuronal variability in the current study could also reflect feedback from fronto-parietal reaching and grasping networks that would influence subsequent feedforward orientation processing in a recurrent network. In fact, a recent study (Gutteling et al., 2013) showed that temporary inactivation of aIPS (a parietal region associated with grasping movements) using TMS eliminated an increased sensitivity to orientation seen when a grasping versus a pointing movement was planned.

Areas in posterior parietal cortex both receive visual input to guide actions (sensorimotor integration) as well as providing feedback to extrastriate visual areas (Borra et al., 2008; Passarelli et al., 2011; Prime, Vesia, & Crawford, 2008; Rizzolatti & Matelli, 2003). For example, neurons in the anterior intraparietal area (AIP) are associated with grasping movements and exhibit selectivity for the type, shape, size and orientation of objects that are to be grasped (Murata et al., 2000; Monaco et al., 2013). The inferior parietal lobule, which includes area AIP, also has feedback connections with extrastriate visual areas (Rizzolatti & Matelli, 2003) that are thought to be crucial for tactile object recognition. Additionally, area V6A neurons are selective for the orientation of the hand (Fattori et al. 2009), are involved in grasping (Fattori et al., 2010), and have direct connections with area V2 (Passarelli et al., 2011). Therefore, feedback from parietal areas involved with control of the hand should be able to provide the signal that improves orientation selectivity in early visual processing.

These parietal areas receive visual, proprioceptive and motor efference information that could be used to guide (Kalaska, 1988; Vesia, Yan, Sergio, & Crawford, 2010) the spatial focus for reach-related visual enhancement. First of all, motor efference signals from active motor circuitry, such as motor and premotor cortices, encode the end point of a reach. Secondly, proprioceptive processing in somatosensory cortex uses information from the joints, tendons and muscles to determine the location of the arm in space. Thirdly, the visual system encodes the position of a visible arm. For example, vision of a fake arm affects neurons in area 5 that encode the position of the arm (Graziano, Cooke, & Taylor, 2000). Thus area 5 encodes arm position both by vision and proprioception. It is possible that any of these sources could provide the spatial information necessary to guide hand-related attention as the brain regions involved in each are all integrated into the parietal portion of the reaching and grasping network (Buneo &

Andersen, 2006, 2012; Grea et al., 2002; Pisella et al. 2000). It would be through this integration that reciprocal connections from the parietal areas in the reaching and grasping network may drive hand-related attention. The broader spatial resolution of the motor system would be ideal to improve visual processing of the workspace near the hands, including nearby task-irrelevant stimuli and potential reach targets. In the current study the arm is visible and the reach is sustained meaning that visual, proprioceptive and motor efference information is all available. To determine the relative strength of each of these factors in deploying near-hand attention, future studies will need to be conducted with an occluded arm to isolate proprioception from vision of the hand, a fake arm to isolate the contribution of visual information, and with passive arm placement versus active reaching to disambiguate motor efference feedback.

Other investigations also show that planned hand movements improve visual processing (Craighero et al., 1999; Fagioli et al., 2007; Symes et al., 2008). Specifically, orientation selection was improved when participants were to grasp the visual target (oriented bars) as opposed to when they were to point to the target (Bekkering & Neggers, 2002; Gutteling et al., 2011; Hannus et al., 2005). These studies suggest a link between maintaining the plan for hand movement and altered visual processing near the endpoint of the movement. Such a mechanism parallels motor plans in the oculomotor system deploying attention to the endpoint of the planned saccade (Moore & Fallah, 2001, 2004) and enhancing visual responses in area V4 (Moore & Armstrong, 2003). Having separate parallel effector-based mechanisms for deploying spatial attention has the advantage that the effectors can more easily be decoupled for movement. That is, we can grab an object while looking elsewhere. In fact, the parietal occipital junction (POJ) has been implicated in reaching to a peripheral target (Prado et al. 2005), and damage to the posterior parietal cortex results in optic ataxia, an inability to accurately reach to peripheral targets (Milner & Goodale, 1995; Carey, Coleman, & Della Sala, 1997; Jackson, Newport, Mort, & Husain, 2005). Thus posterior parietal cortex has separate representations for the spatial locations of gaze and reach targets (Jackson et al., 2009). These parallel effector-based systems could not only maintain separate target locations but may also provide the signals to improve visual processing of each target.

Note that the full range of the near-hand effect has not yet been determined. The spatial extent of these parietal feedback connections would likely be similar to the spatial extent of the far surround in area V2 (Shushruth et al., 2009), which is also dependent on feedback from extrastriate areas. The spatial extent of the hand effect on orientation selectivity found in this study varied between 8.3 – 14.9 degrees of visual angle, based on the spacing between the hand and the receptive field borders and the size of the receptive fields themselves. Alternatively, feedback from parietal cortex may not be spatially limited but instead extend throughout the ipsilateral visual field. Determining the spatial extent of the near-hand effect may provide further insight into the underlying circuitry.

4.5.3 Oculomotor-Driven Spatial Attention

Prior research and the current results suggest that improved visual processing in near-hand space is due to attentional prioritization of the space near the hand, and propose a neural mechanism based upon feedback from parietal areas involved in visual guidance of hand movements. However, similar results may have been found as a result of oculomotor-driven spatial attention. That is not likely due to the following factors. First of all, the stimulus in the receptive field is task-irrelevant: there is no need for the animals to attend to the oriented rectangle as they make no responses or judgments based upon it. Spatial attention may have been allocated to the touch bar for the animals to make accurate reaches in their visual periphery. However, the orientation stimuli only appear after the touch bar has been grasped. As there was no other location or stimulus requiring attention, oculomotor-driven attention *may* have been allocated to one of these locations during the task. If the animals had learned to attend to the oriented rectangle in order to judge the timing of the reward, this attentional allocation would have occurred whether the bar was grasped or not and there would be no modulation between the Hand-Near and Hand-Away conditions. If instead, oculomotor-driven spatial attention was allocated to the touch bar when the hand grasped it, attention would have been allocated away from the oriented stimulus and the recorded neuronal receptive fields, which would result in lower response rates and poorer orientation selectivity in the Hand-Near versus Hand-Away conditions as seen in biased competition (e.g. Desimone & Duncan, 1995). Instead, we see increased orientation selectivity when the hand was present; a result opposite to any likely allocation of oculomotor-driven spatial attention.

4.5.4 Attentional Control, Task Design, and Future Studies

Thus, this experimental paradigm does not specifically control for the locus of attention beyond requiring gaze fixation. An alternative would have been to use an attentional paradigm such as spatial cueing (e.g. Posner, 1980) that controls for spatial attention by allocating attention towards and away from a receptive field independent of hand position. While this type of manipulation is useful for determining whether the hand modifies behavior above and beyond that of spatial attention, it would also confound the effects of spatial and hand attention. In an effort to avoid this, the current paradigm was developed to specifically eliminate cues that would allocate spatial attention to the receptive field stimuli. This allowed for investigating hand attention without the confusion of spatial attention modulations also being involved. So it must be noted that the results of hand attention in this study cannot be directly related to spatial attention. While previous studies in humans have suggested that spatial cueing operates independently of hand attention in speeded reaction time studies (Abrams et al., 2008; Reed et al., 2006), future studies will be needed to determine how they interact on neurons in visual processing areas.

The experimental paradigm used in the current study also sought to dissociate the eyes and the hand and thus did not have the animal reach to the visual stimulus that was presented in the neuronal receptive field. It is known that when reaching, the eyes move to the reach target prior to the hand arriving (Ballard et al., 1992; Biguer et al., 1982; Fisk & Goodale 1985; Neggers & Bekkering, 2000, 2001, 2002; Prablanc et al., 1979). Since spatial attention is allocated to the target region of an oculomotor plan (Moore & Armstrong, 2003; Moore & Fallah, 2001, 2004; Müller et al., 2005), even though the eye movement output is inhibited, (i.e. with continued fixation) the plan to move the eyes, and thus the shifting of spatial attention, would still occur if a reach was made to the stimulus in the RF. This would again mean that in the Hand-Near condition the results would be confounded with those of spatial attention. By placing the touch bar outside of the RF, it ensures that when a reach occurs, spatial attention is not allocated to the experimental visual stimulus (the oriented bar within the RF). A limitation of this design is that only the effects of a maintained reach have been determined. Since we suggest that improved orientation selectivity near the hand would be useful in guiding the hand for more accurate grasps, it would be important to also determine the temporal aspects of near hand attention that unfold before and during an active reach to a target in the receptive field. With the results of this study as a template, future studies could investigate hand attention during a dynamic reach.

4.5.5 Summary and Conclusion

In conclusion, we find that when a hand is nearby, neurons in area V2 exhibit sharpened orientation selectivity and reduced response variability. It was not dependent on the relationship between the orientation of the touch bar and the oriented rectangle suggesting it was a general improvement in orientation selectivity instead of feature-based attention or far surrounds suppression. These factors are advantageous for guiding subsequent or on-going hand movements. We propose that parietal areas involved in grasping and encoding peripersonal space are likely involved in deploying near-hand attention, although future work is necessary to support this hypothesis.

Chapter 5. General Summary and Conclusions

Information in this chapter is adapted from two additional published manuscripts:

Citation: Perry, C. J., & Fallah, M. (2015). Feature integration and object representations along the dorsal stream visual hierarchy. *Frontiers in Computational Neuroscience*, *8*, 1-17.

This manuscript was prepared by Carolyn J Perry, and revised and edited by Carolyn J Perry and Dr. Mazyar Fallah.

Citation: Perry, C. J., Amarasooriya, P., & Fallah, M. (2016). An eye in the palm of your hand: Alterations in visual processing near the hand, a mini-review. *Frontiers in Computational Neurosience, 10*, 1-8.

This manuscript was prepared by Carolyn J Perry and Prakash Amarasooriya. It was revised and edited by Carolyn J Perry and Dr. Mazyar Fallah.

5.1 Chapter Two and Three Summary of Results

While previous work has indicated the presence of object representations in the dorsal pathway, very little is known about their influence on motion processing, where they might occur, and the neural mechanisms that may underlie object-mediated enhanced visual processing in the dorsal pathway.

Building on the finding that colour can be combined with motion features to produce object-based effects in the dorsal pathway (Mitchell et al., 2003; Reynolds et al., 2003; Valdés-Sosa et al., 1998, 2000; Wannig et al., 2007), and that the integration of colour did not affect direction computations in area MT but did significantly speed motion processing (Perry & Fallah, 2012), we wanted to determine if the combination of dorsal stream features also produced object representations that would in turn speed motion processing. Our findings suggest that it is the co-processing of dorsal stream features (direction and speed) that allows for improved direction perception. In addition, our findings suggest that speed can also be integrated into an object representation as an independent feature, beyond direction computations in area MT, and in turn speed processing. Independent simply meaning that even though speed and direction are combined and coprocessed to improve direction perception, surface speed can then become an object feature independent of other motion features such as direction. The formation of an object in this case further speeds motion processing over that seen when colour and direction are combined (chapter two, Perry et al., 2014). We also determined that both speed and contrast are automatically integrated into a dorsal stream object representation but that colour requires active, top-down task demands that link the colour to the direction of each surface (chapter three).

5.2 Possible Framework for Object-Mediated Enhancement in Dorsal Pathway Visual Processing and Future Directions

Based on this research, we have proposed a possible neural mechanism for the improved speed of motion processing and also a possible location for dorsal stream object representations (Perry & Fallah, 2014). One of the key findings across these studies (Perry & Fallah, 2012; Perry et al., 2014; and chapter three) involves the affect that different surface features have on direction discriminations (i.e. Direction Repulsion) and processing time. Differences in surface speed make direction discriminations more veridical, but surfaces that are different colours or contrasts have no effect on direction discriminations. This gives us a fundamental piece of information as to when feature integration may occur and consequently, at what point an object representation may be formed in the dorsal pathway. Prior research has found that colour affects motion processing as early as area MST (Tchernikov & Fallah, 2010), but gives no indication as to how early in the processing hierarchy feature integration and object representations may occur. In the ventral stream, early object representations may occur as soon as V2 (Zhou et al., 2000) and it is possible that the same is true in the dorsal pathway. The results surrounding direction discriminations suggest that because colour and contrast do not affect direction repulsion, this information is not utilized by the dorsal pathway prior to the computation of global motion direction in area MT (i.e. global motion direction processing does not work off of object representations but relies on the processing of motion features). However, surfaces that are different colours or contrasts do significantly reduce processing time. This suggests that colour and contrast information *is* utilized by the dorsal pathway, and that the integration of these features with dorsal pathway direction information allows for significant reductions in processing time beyond direction computations in MT. In addition, even though speed and direction are combined prior to MT direction computations and thus improve direction discriminations, likely through multidimensional tuning (see Figure 2.3), we suggest that because surfaces differentiated by speed also significantly reduce processing time, speed is also a feature integrated into a dorsal stream object representation, but independently of direction (Figure 5.1).

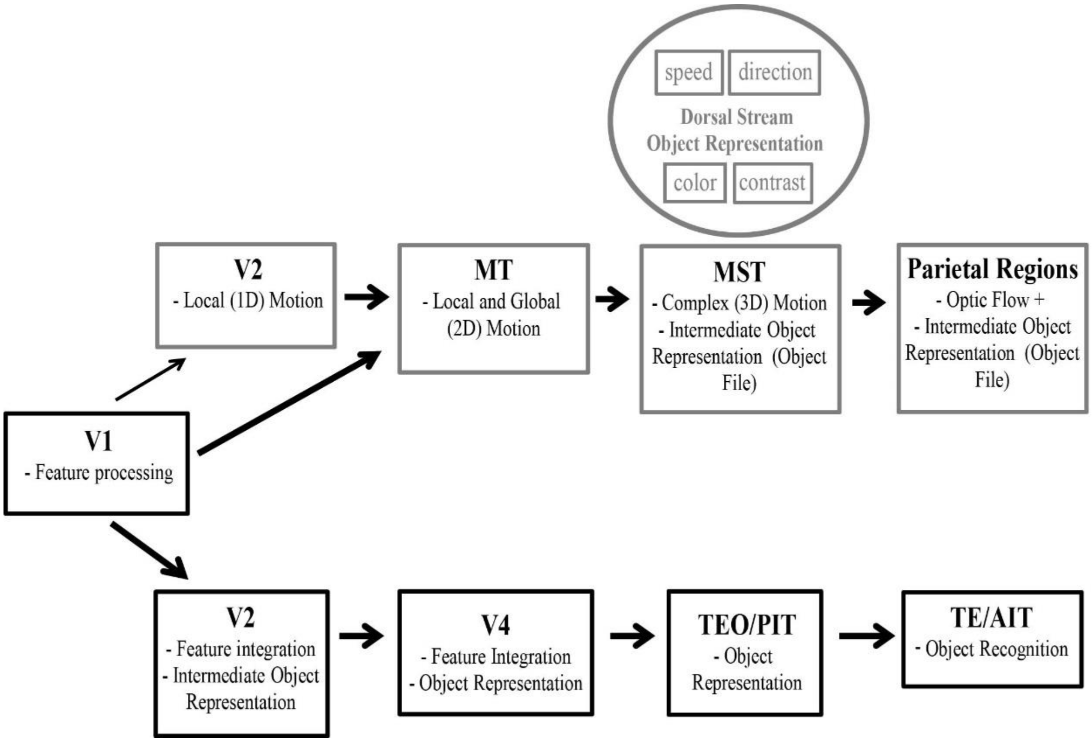

Figure 5.1: Possible object representation location model (adapted from Perry & Fallah, 2014). Visual processing along the ventral stream is depicted along with known object representations starting in area V2. We also depict visual processing along the dorsal stream with the hypothetical stages which process dorsal stream object files/representations. As visual processing progresses along the dorsal pathway stimulus parameters are calculated and this information is provided to area MT. In MT, information regarding speed, direction and spatial frequency are co-processed forming multidimensional selectivity. After local and global motion processing circuits in MT, an intermediate object representation is formed that incorporates independent motion features (such as speed and direction) and ventral stream features (such as color and contrast, with other features such as shape and size to be determined). This intermediate object representation is in place prior to decision making circuitry that represents motion or guides action.

If the combination of speed and direction (i.e. velocity) that improves direction discrimination, were to be the feature integrated into a dorsal stream object representation, we would have expected processing time to be no different than when the surfaces were the same speed, as in both cases there is only one feature distinguishing the surfaces from each other (velocity and direction respecitively). Importantly, independent features that make the surfaces more distinct from each other (i.e. differentiate the surfaces along additional feature dimensions other than just direction), appear to be necessary to facilitate speeded processing time downstream of direction computations in area MT (for a summary see Figure 3.8).

Secondly, had direction discrimination *and* processing time been improved across all features tested, we would not have been able to as accurately pinpoint the underlying neural mechanism possibly driving the improvements in processing time. In a serial model, there are a number of processes involved in computing the direction of two superimposed surfaces (see Figure 5.2 for a breakdown). The effects that different features have on these processes allows us to infer both the location of the dorsal pathway object representation, and the processing stage which is affected. Knowing which processing stage is affected, in turn allows us to suggest a possible neural mechanism that may be driving decreases in processing times. Because segmentation of the surfaces and switching attention from one surface to the next does not account for the large decreases in processing time (Caputo & Casco, 1999; Raymond, Shapiro, & Arnell, 1992, 1995) seen in these experiments, by process of elimination, this would suggest that the time it takes to process the direction of each surface (D1 and D2 in Figure 5.2) likely underlies changes in processing time. Of the three processes necessary for direction computation (as shown in Figure 5.2B), only the “information accumulation/decision making” process occurs after global motion direction processing in MT.

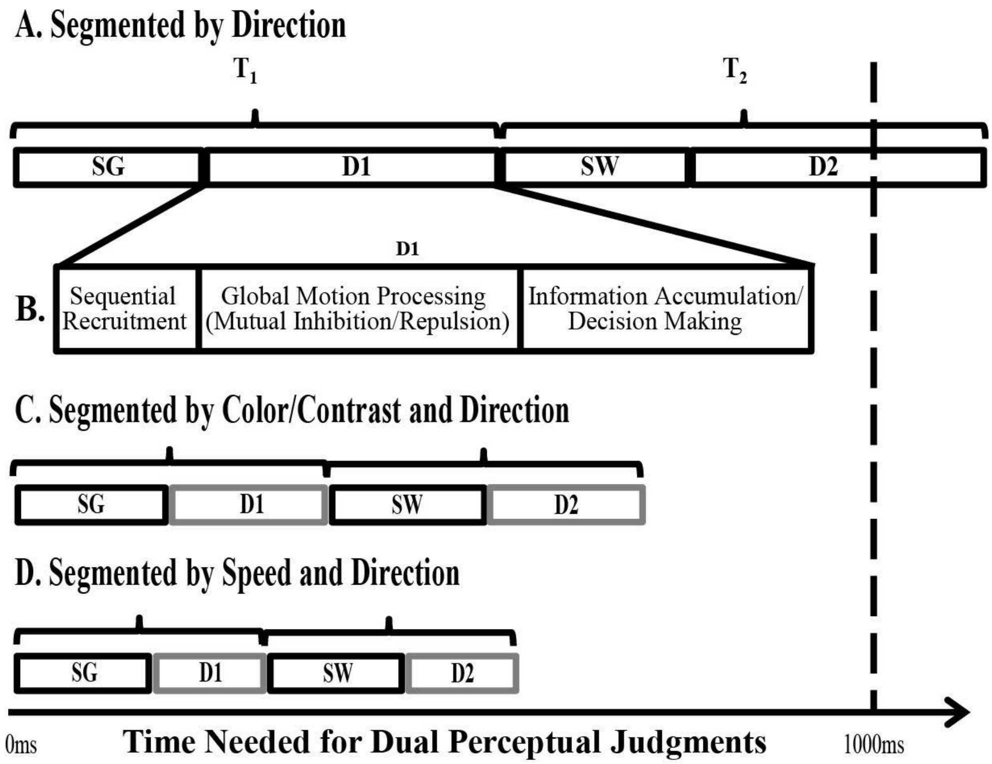

Figure 5.2: Stages required for direction judgments of two superimposed objects (adapted from Perry & Fallah, 2014). Based on the experimental paradigm described in Chapters Two and Three. SG = time needed for *Segmentation* of the 2 fields of dots into two surfaces, based on different directions of motion, SW = time needed to *Switch* processing from one surface to the other, D1 and D2 = the time needed to process the *Directions* of each superimposed surface (includes sequential recruitment, global motion computation, information accumulation and decision making; shown in detail in **B**). **(A)** When the two surfaces differ only in direction, the time needed to complete all the stages involved in the task takes more than 1000ms on average (Perry & Fallah, 2012). **(B)** Depicts the processes needed to determine the direction of motion of one surface (D1). **(C)** When the surfaces differ in color or contrast as well as direction, processing time significantly decreases to less than 1000ms (Perry & Fallah, 2012). **(D)** When the surfaces differ in speed as well as direction, the time needed to process both directions is reduced further. As the initial segmentation (SG) and attentional switch time (SW) do not appreciably decrease with additional distinguishing features, we propose that the time needed to complete the task decreases as a result of speeded decision making processes (D1 and D2 – see text for details) and correspondingly, in (B) and (C), D1 and D2 are depicted as requiring less time than in (A).

As mentioned above, that colour and contrast do not affect direction discrimination but do affect processing time suggests that the improvements in processing time seen in the colour and contrast conditions would not occur prior to (sequential recruitment) or at the global motion direction processing stage. By process of elimination then, we hypothesize that the integration of colour, contrast, and speed into a dorsal stream object representation, occurs at some point after direction processing in area MT, and allows for speeded information accumulation/decision making processes that result in a decrease in processing time.

We have suggested that the integration of features, that differentiate superimposed surfaces along more feature dimensions than just direction, and result in the presence of object representations downstream of direction processing in area MT, would allow for object-based selection mechanisms to speed decision making (Perry & Fallah, 2014). Based on the accumulator model (Palmer et al., 2005) we suggest that areas downstream of area MT, that are known to accumulate information necessary for decision making (Huk & Shadlen, 2005; Hussar & Pasternak, 2013; Shadlen & Newsome, 1996, 2001; Zaksas & Pasternak, 2006), would use object-based selection to reduce the interference between the processing of each surface and in turn reduce the time needed to process each surface (see Figure 3.7). We propose that this occurs because the presence of the second feature (colour, speed, contrast) that creates an object representation, allows one surface to be selected and processed while the other is essentially ignored, leading to a reduction in the noise (i.e. the information accumulation for the ignored surface direction) on the rise to a decision threshold. This reduction in noise results in a steeper slope to a decision threshold, or a decrease in the time needed to process that surface (see Figure 3.7B vs. 3.7A).

To further examine the components of the model suggested in this dissertation, future investigations should include testing additional features that are processed exclusively in the ventral pathway to see if our model can be generalized for cross stream feature integration. For example, comparing superimposed surfaces in which each surface is composed of different form elements rather than dots (i.e. a surface of squares versus a surface of triangles), to superimposed surfaces of the same coloured dots (as in our Unicolour conditions). In addition, testing spatial frequency, in a manner similar to Kim and Wilson (1996), with the addition of a staircase paradigm, would allow for conclusions to be drawn regarding the model of feature processing and object representations of dorsal stream features suggested above. We have also suggested that the presence of object representations allows for each surface to be selected and processed with little interference from the other surface. This would be similar to processing the surfaces in a serial manner. This part of the model then, could be tested by comparing direction discriminations and processing time in surfaces that were superimposed and in surfaces that were presented serially. Location of the object representation could be tested neurophysiologically with recordings from area MT, MST, and further downstream in LIP. Colour would not be expected to alter direction processing in area MT, however, the signals that give rise to pursuit motion in MST should be modulated by surface colour, and further on, the rise to decision thresholds in LIP should be steeper when superimposed surfaces contain a second distinguishing feature. Lastly, investigating whether an object representation exists at all in the dorsal pathway could be accomplished in patients with visual agnosia who have damage to the ventral pathway. If object representations were to only exist within the ventral pathway, then damage to ventral regions should eliminate the speeded processing seen in the research presented here.

5.3 Chapter Four Summary of Results

Although there is a growing body of literature that seeks to investigate all of the possible visual enhancements seen near the hand, there is a dearth of neurophysiological research more directly addressing the possible neural underpinnings of these enhancements. Work in both patient (Brown et al., 2008; di Pellegrino & Frassinetti, 2000; Schendel & Robertson, 2004) and normal populations (Abrams et al., 2008; Davoli & Brockmole, 2012; Dufour & Touzalin, 2008; Garza, Strom, Wright, Roberts, & Reed, 2013; Lloyd, Azañón, & Poliakoff, 2010; Reed et al., 2006, 2010; Weidler & Abrams, 2013) has suggested that enhanced visual processing near the hand may be due to an attentional prioritization of the space near the hand. More recently, it has been suggested that action-relevant object features (such as orientation) may be preferentially selected due to grasp-related motor preparation (Guetteling et al., 2011). To more directly test this hypothesis, Gutteling and colleagues (2013) showed that TMS of AIP eliminates improved orientation sensitivity seen during grasping but not pointing action preparation. We wanted to further investigate the neural underpinnings of this result and to test the hypothesis that feedback from fronto-parietal motor control networks involved with reaching and/or grasping may be involved in enhanced orientation processing near the hand. We recorded neuronal activity from an early visual area V2, known to be selective for orientation. Importantly, consistent with previous work in human populations (Bekkering & Neggers, 2002; Gutteling et al., 2011, 2013; Hannus et al., 2005), we did find that orientation processing was improved when the hand was nearby. However, the pattern of improvement suggested the enhancement was not due to either known oculomotor driven spatial attention or feature-based attentional selection mechanisms (chapter four). In addition, we found that neuronal response variability in V2 neurons decreased when the hand was nearby, a result that, within the oculomotor system, has been known to be propagated back to V4 from area FEF during saccade preparation.

5.4 Possible Framework for Action-Modulated Enhancements of Visual Processing Near the Hand and Future Directions

We hypothesize that, along with previous work (Bekkering & Neggers, 2002; Gutteling et al., 2011, 2013; Hannus et al., 2005; Reed et al., 2006), these results suggest that improved orientation processing near the hand is driven by an effector-specific mechanism that is separate from oculomotor-driven spatial attention or feature-based attention (Perry et al., 2015, 2016). As well, within the oculomotor system, a decrease in response variability in FEF prior to a saccade was shown to propagate backwards to neurons in area V4 (Steinmetz & Moore, 2010). We therefore suggest that the improvements in orientation processing seen in an early visual area (V2) are driven by feedback from fronto-parietal regions that control reaching and/or grasping as we also see a reduction in response variability when the hand is present. The work by Gutteling and colleagues (2013) suggests that area AIP could mediate this feedback, but it is possible that other fronto-parietal regions, such as V6A, could also mediate feedback to early visual processing regions.

More recently (Abrams & Weidler, 2014; Goodhew, Edwards, Ferber, & Pratt, 2015) have suggested that altered visual processing near the hand is due specifically to enhanced magnocellular input. However, not much later, Goodhew (Goodhew & Clarke, 2016) revised this viewpoint to suggest that either M cell or P cell input could be enhanced based on the attentional demands of the task. As orientation is a feature that can be processed by both the M cell and P cell mediated pathways, the current study cannot speak to these theories directly. However, when one speaks of enhancing select inputs from all the possible inputs in a visual display, one is inherently speaking about attentional selection. What remains unknown is *how* this visual input is enhanced. We suggest that regardless of whether it is M cell or P cell input that is enhanced, the enhancement is driven by feedback mechanisms, similar to those that are already well established within the oculomotor system. In addition, it is often assumed that attending to the space surrounding the hand will necessarily invoke patterns of responses that are indicative of oculomotor-driven or visual spatial attention. The work in chapter four shows that this is not necessarily the case. The enhancement in orientation tuning in V2 neurons, when the hand was nearby, did not mimic the attentional enhancements seen with oculomotor-driven spatial attention (see Figure 5.3). Finally, we suggest that separate attentional mechanisms for both oculomotor-driven and hand-driven selection, that enhance processing of stimuli at the endpoints for eye movements and hand movements would be especially beneficial in cases where the eyes and hands are involved in tasks that are occurring at different spatial locations.

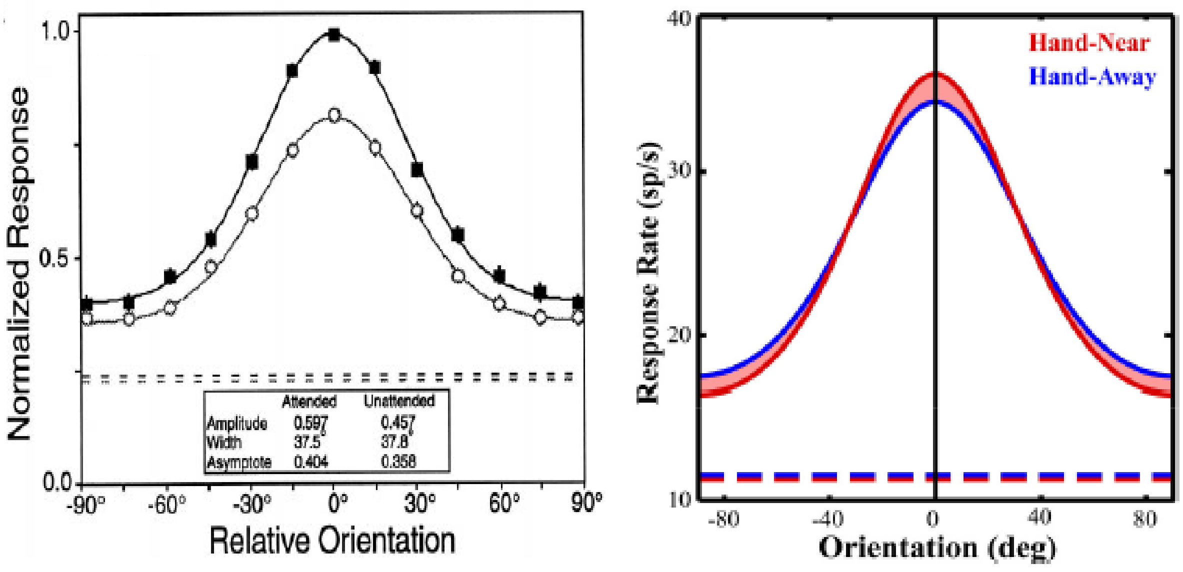

Figure 5.3: Orientation tuning in visual-spatial and hand attention. (Adapted from McAdams & Maunsell, 1999, on the left, and Perry et al., 2015, on the right). The normalized neuronal response rate is shown in both instances, for 13 and 8 orientations respectively. On the left, neuronal responses undergo gain modulation without a change in tuning curve width indicating no sharpening of orientation tuning with attention (black line and squares). On the right, responses at the preferred orientation (the orientation with the greatest response) undergo a gain modulation not seen at the orthogonal orientation (±90°) indicating a sharpening of the tuning curve.

Future neurophysiological work should seek to confirm the hypotheses set forth in the work in chapter four. It would be interesting to test the M versus P cell debate using a paradigm similar to the one presented in chapter four but with stimuli that were processed more exclusively in one pathway or the other. In addition, to more directly compare the results from chapter four with oculomotor-driven spatial attention effects on orientation tuning in V2 neurons, it would be helpful to test both using the same paradigm, in the same experiment as repeated measures conditions across all neurons. This would also help to confirm that there exist separate mechanisms for oculomotor-driven and hand-driven selection. Finally, to determine more directly if feedback from fronto-parietal reaching and grasping control regions underlies enhanced processing near the hand, a similar experiment to that used by Moore and Fallah (2001, 2004) could help in this regard. Instead of stimulating regions that drive saccadic eye movements (FEF) to determine if there is a change in contrast sensitivity at the end point of a planned saccade, stimulation of regions that are associated with the control of reaching and grasping could be stimulated to determine if there is a similar enhancement of orientation processing as seen in the work presented here (chapter four).

5.5 Conclusions

The research contained within this dissertation has sought to shed new light on functions associated with the dorsal pathway and how they selectively enhance visual processing of stimuli in our environment. We have shown that the formation of objects in the dorsal pathway can significantly reduce the time needed to process visual stimuli and have suggested that object-based selection may reduce the noise in the accumulation of information needed for decision making processes. It should be noted that while the known stages of motion processing in the dorsal pathway allow us to discuss possible mechanisms, associated with speeded decision-making, and object representation location, further research is needed to test these hypotheses more directly. Furthermore, we have shown that visual processing of stimuli near the hand are enhanced in a pattern not associated with known mechanisms of spatial or feature-based attentional selection. We suggest that feedback from dorsal pathway fronto-parietal regions, associated with the control of reaching and grasping movements, selectively enhance the processing of action-relevant object features, such as orientation, as a means of improving the accuracy of arm and hand movements. Future studies will be needed to test this hypothesis more directly and to fill-out the underlying neural mechanisms of hand-related enhanced visual processing more fully. With these two dorsal-pathway-mediated enhancements in visual processing, I am positive my niece will have great success learning how to accurately catch a Frisbee!

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Chapter 7. Appendices

7.1 Appendix A: Informed Consent Form

INFORMED CONSENT FORM
DEPARTMENT OF KINESIOLOGY, YORK UNIVERSITY: (416) 736 2100, EXT. 77215

PARTICIPANTS NAME & CODE:____
STUDY TITLE:____

Our research team is interested in how we process the visual world around us. Our research aims to understand how different regions of the brain, that process different object features, interact to produce objects we see.

The lab is run by Dr. Mazyar Fallah. You can contact Dr. Fallah by email: mfallah@yorku.ca or by phone (416) 736 2100, ext. 20555 if you have any questions. The research has been reviewed and approved by the Human Participants Review Sub-committee of York University within the context of York University's research ethics review guidelines, and conforms to the standards of the Canadian Tri-Council Research Ethics guidelines. If you have any questions about this process, or about your rights as a participant in the study, please contact Ms. Alison Collins-Mrakas, Research Ethics, 277 York Lanes, York University (telephone: 416-736-5914 or email acollins@yorku.ca). There are no evident risks inherent in participating in this research.

To record where you move your eyes, you will be fitted with a light-weight head band which holds two small infrared cameras. These cameras will be positioned in front and below your eyes. You should feel no discomfort. You will be asked to look at visual targets displayed on the screen in front of you, and may also be asked to respond by pressing buttons on a keyboard, button box, or mouse. This is NOT a test of your individual abilities. The experiment will take place in a darkened room.

Your participation in the study is completely voluntary and you may choose to stop participating at any time. Your decision not to volunteer will not influence the nature of your relationship with York University, either now or in the future, and you will still be eligible to receive the promised credit for agreeing to be in the project. The estimated duration of the experiment is about an hour; you are free to take breaks between blocks of trials. All information you supply during the research will be held in confidence and unless you specifically indicate your consent, your name will not appear in any report or publication of the research. Your data will be safely stored in a locked facility and only research staff will have access to this information. Confidentiality will be provided to the fullest extent possible by law.

I have been informed about the nature and procedures of the study, and understand it in full. I know that I may withdraw from it at any time. I agree to serve as a participant in the study. I know that any concerns or comments regarding my participation in the study can be addressed to the ethics committee at York University.

______________________________________ ____
Signature of Participant Signature of Witness

______________________________ ____
Date Name and Position of Witness

7.2 Appendix B: Ethics Approval

YORK
UNIVERSITÉ
UNIVERSITY

Certificate #:	**2014 - 035**
Initial Approval:	**01/29/14-01/29/15**
Amendments:	**Amendment Approved: 09/29/15** **2nd Amendment Approved: 03/04/16**
Renewals:	**03/04/16**
Current Approval Period:	**03/04/16-03/04/17**

OFFICE OF RESEARCH ETHICS (ORE)
5th Floor, Kaneff Tower

4700 Keele St.
Toronto ON
Canada M3J 1P3
Tel 416 736 5914
Fax 416 736-5512
www.research.yorku.ca

ETHICS RENEWAL / AMENDMENT APPROVAL

To: **Professor Mazyar Fallah**
Department of Kinesiology and Health Science
Faculty of Health
mfallah@yorku.ca

From: Alison M. Collins-Mrakas, Sr. Manager and Policy Advisor, Research Ethics
(on behalf of Denise Henriques, Chair, Human Participants Review Committee)

Date: Friday, March 04, 2016

Title: **Brain Mechanisms of Selection and Object Processing**

Risk Level: ☒ Minimal Risk ☐ More than Minimal Risk

Level of Review: ☒ Delegated Review ☐ Full Committee Review

With respect to your research project entitled, **"Brain Mechanisms of Selection and Object Processing"**, the committee notes that, as there are no substantive changes to either the methodology employed or the risks to participants in and/or any other aspect of the research project, a renewal of approval re the proposed amendment(s) to the above project is granted.

Any further changes to the approved protocol must be reviewed and approved through the amendment process by submission of an amendment application to the HPRC prior to its implementation.

Ongoing research – research that extends beyond one year – must be renewed prior to the expiry date.

Any adverse or unanticipated events in the research should be reported to the Office of Research ethics (ore@yorku.ca) as soon as possible.

For further information on researcher responsibilities as it pertains to this approved research ethics protocol, please refer to the attached document, **"RESEARCH ETHICS: PROCEDURES to ENSURE ONGOING COMPLIANCE".**

Should you have any questions, please feel free to contact me at: 416-736-5914 or via email at: acollins@yorku.ca.

Yours sincerely,

Alison M. Collins-Mrakas M.Sc., LLM
Sr. Manager and Policy Advisor,
Office of Research Ethics

RESEARCH ETHICS: PROCEDURES to ENSURE ONGOING COMPLIANCE

Upon receipt of an ethics approval certificate, researchers are reminded that they are required to ensure that the following measures are undertaken so as to ensure on-going compliance with Senate and TCPS ethics guidelines:

1. **RENEWALS:** Research Ethics Approval certificates are subject to annual renewal. **It is the responsibility of researchers to ensure the timely submission of renewals.**
    a. As a courtesy, researchers will be reminded by ORE, in advance of certificate expiry, that the certificate must be renewed. Please note, however, it is the expectation that researchers will submit a renewal application prior to the expiration of ethics certificate(s).
    b. **Failure to renew an ethics approval certificate** (or to notify ORE that no further research involving human participants will be undertaken) **may result in suspension of research cost fund and access to research funds may be suspended/ withheld**.

2. **AMENDMENTS:** Amendments must be reviewed and approved **PRIOR** to undertaking/making the proposed amendments to an approved ethics protocol;

3. **END OF PROJECT**: ORE must be notified when a project is complete;

4. **ADVERSE EVENTS**: Adverse events must be reported to ORE as soon as possible;

5. **POST APPROVAL MONITORING:**
    a. More than minimal risk research may be subject to post approval monitoring as per TCPS guidelines;
    b. A spot sample of minimal risk research may similarly be subject to Post Approval Monitoring as per TCPS guidelines.

FORMS: As per the above, the following forms relating to on-going research ethics compliance are available on the Research website:

a. Renewal
b. Amendment
c. End of Project
d. Adverse Event

7.3 Appendix C: Offprints of Relevant Articles

Perry, Tahiri, & Fallah 2014

Journal of Vision (2014) 14(2):10, 1–8 http://www.journalofvision.org/content/14/2/10 1

Feature integration within and across visual streams occurs at different visual processing stages

Carolyn J. Perry
School of Kinesiology and Health Science, Centre for Vision Research, York University, Ontario, Canada

Abdullah Tahiri
School of Kinesiology and Health Science, York University, Toronto, Ontario, Canada

Mazyar Fallah
School of Kinesiology and Health Science, Centre for Vision Research, Departments of Biology and Psychology, York University, Ontario, Canada
Canadian Action and Perception Network, Canada

Direction repulsion is a perceptual illusion in which the directions of two superimposed surfaces are repulsed away from the real directions of motion. The repulsion is reduced when the surfaces differ in dorsal stream features such as speed. We have previously shown that segmenting the surfaces by color, a ventral stream feature, did not affect repulsion but instead reduced the time needed to process both surfaces. The current study investigated whether segmenting two superimposed surfaces by a feature coprocessed with direction in the dorsal stream (i.e., speed) would also reduce processing time. We found that increasing the speed of one or both surfaces reduced direction repulsion. Since color segmentation does not affect direction repulsion, these results suggest that motion processing integrates speed and direction prior to forming an object representation that includes ventral stream features such as color. Like our previous results for differences in color, differences in speed also decreased processing time. Therefore, the reduction in processing time derives from a later processing stage where both ventral and dorsal features bound into the object representations can reduce the time needed for decision making when those features differentiate the superimposed surfaces from each other.

Introduction

An object in the visual system is a representation of bound features from within and across the two visual streams (ventral and dorsal). However, it is not known at which stage of visual processing these features are bound together. Neurons within the middle temporal area (MT) possess the ability to process both local (component) and global (pattern/plaid) motion (Britten, Shadlen, Newsome, & Movshon, 1992; Recanzone, Wurtz, & Schwarz, 1997) and are able to determine global motion direction apart from other randomly moving stimuli. This suggests that the inputs to MT are integrated in order to determine the global motion of several moving objects. Binding these features together makes area MT suitable for determining the motion directions of multiple objects within the same spatial location (Adelson & Movshon, 1982; Stoner & Albright, 1992, 1996) and in turn allows for the segmentation of a visual scene into objects and surfaces (Snowden, Treue, Erickson, & Andersen, 1991).

In spite of these characteristics that allow MT to process superimposed global motion, this type of motion has been shown to produce a perceptual illusion known as direction repulsion (Braddick, Wishart, & Curran, 2002; Curran & Benton, 2003; Hiris & Blake, 1996; Marshak & Sekuler, 1979; Mather & Moulden, 1980). In this case, the directions of motion of two superimposed surfaces are misjudged perceptually. Observers perceive the directions of motion as being further away from each other, for example, repulsed from 4° to 20° away from each surface's real direction (Braddick et al., 2002; Marshak & Sekuler, 1979). In the classic direction repulsion paradigm, the surfaces are identical except for the direction in which they are moving. This means that, first, the local motion of the dots in each surface must be calculated before they can be segmented into two surfaces and then the overall direction of each surface can be processed and a decision threshold reached. However, the addition of a

Citation: Perry, C. J., Tahiri, A., & Fallah, M. (2014). Feature integration within and across visual steams occurs at different visual processing stages. *Journal of Vision*, *14*(2):10, 1-8, http://www.journalofvision.org/content/14/2/10, doi:10.1167/14.2.10.

doi: 10.1167/14.2.10 Received August 11, 2013; published February 13, 2014 ISSN 1534-7362 © 2014 ARVO

second surface feature, making the surfaces more distinct from one another, should provide additional information that could be used to reduce the competition between the surfaces' directions and attenuate the repulsion. And, in fact, this is what occurs when the surfaces are different speeds (Curran & Benton, 2003; Marshak & Sekuler, 1979), or, in the case of superimposed gratings, when the surfaces are different spatial frequencies (Kim & Wilson, 1996). Stereoscopic viewing, producing a real depth difference between the two surfaces, does not reduce direction repulsion however (Hiris & Blake, 1996). This is thought to be because superimposed surfaces are already perceived as being at different apparent depths (Hiris & Blake, 1996) and therefore stereoscopic depth cannot be used as an additional feature to aid in segmenting the surfaces.

Speed and direction, along with spatial frequency and depth, are all constituents of motion processing that occurs within the dorsal stream. Previously (Perry & Fallah, 2012), we tested whether the integration of a ventral stream feature, such as color, could also alter direction perception. Color is a motion-irrelevant feature, and neurons in area MT are not known to be color sensitive (Maunsell & Van Essen, 1983). In order for color to alter direction perception, color information from the ventral stream would have to be integrated (or bound) to the surface before or at the time of motion processing in area MT. We found that segmenting two superimposed surfaces by color did not alter direction repulsion but, surprisingly, did significantly decrease processing time. This shows that color is not bound to motion before global direction processing in area MT occurs. However, color does affect processing time suggesting that color may affect decision-making in areas downstream of area MT (Huk & Shadlen, 2005; Hussar & Pasternak, 2013; Shadlen & Newsome, 1996, 2001; Zaksas & Pasternak, 2006). Therefore, color and motion are bound after global motion processing in area MT.

Based on those findings, we hypothesized that all segmentation cues bound to an object should speed up decision making about features of that object. Ventral stream features such as color showed just such an effect (Perry & Fallah, 2012). In the current study, we investigated whether speed segmentation cues would also reduce processing time. This is important to determine as motion processing in area MT is based on the conjunction of speed and direction, and thus the features are potentially linked before being integrated into the object's representation. We expect that, due to the conjunction, differences in speed will affect direction repulsion. However, that by itself should not reduce processing time. If we find that differences in surface speeds also produce reductions in processing time, then it suggests that speed information is also treated as a feature independent of direction at a later stage of decision making, similar to the effects of color differences. Alternatively, no changes in processing time would occur if velocity (the conjunction of speed and direction) is the feature bound into the object representation used by the decision-making circuitry.

Methods

Participants

Twelve naive participants (ages 18–23, 5 female) completed the 3/6:unicolor paradigm and an additional set of 12 participants (ages 18–39, 10 female) completed the 6/6:unicolor paradigm. All participants provided informed consent, had normal or corrected-to-normal visual acuity and none tested positive for color blindness using Ishihara color plates. Ethics approval was provided by the York University Human Participants Review Committee.

Procedure

Experiments were performed in a darkened, quiet room. Participants sat 57 cm from a computer monitor (21 in. Viewsonic, 1028 × 1024 resolution, 60 Hz) with their head positioned and stabilized on a headrest (Headspot, UHCOtech, Houston, TX). Participants wore a head-mounted infrared eye tracker (Eyelink II, SR Research Ltd., 500 Hz, Mississauga, ON, Canada) monitoring the left eye. Superimposed random dot kinetograms (RDKs) were created using MATLAB (MathWorks, Natick, MA) and experimental control was maintained using Presentation (Neurobehavioral Systems, Berkeley, CA) software.

Each trial commenced with the participant fixating a white cross (Figure 1) centered on a black screen. 200 ms later a circular aperture appeared in the lower right quadrant containing two superimposed surfaces containing 100% coherent RDKs (white: 122 cd/m^2, dot size = 0.04°, aperture size = 5°, dot density = 1.54 dots/degree^2). The experimental paradigm is the same as used previously (Perry & Fallah, 2012) except that instead of varying surface color we varied surface speed in the current study. In the 6/6:unicolor condition both surfaces moved at 6°/s. In the 3/6:unicolor condition, one surface of dots moved at 3°/s and the other at 6°/s.

The surfaces moved in 12 directions relative to both the vertical and horizontal axes (±2°, 6°, and 10° from either up or down and left or right). All directions appeared with equal frequency creating differences between the two directions that ranged from 70° and 100°. If fixation was broken before or during stimulus presentation, the trial was aborted and randomly

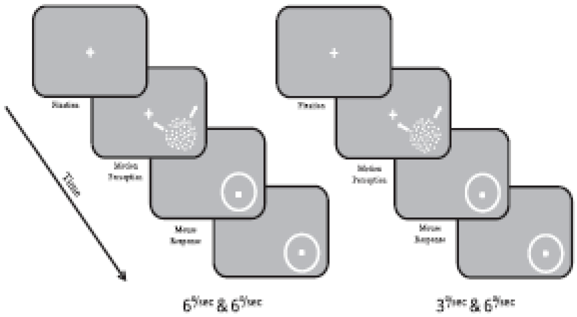

Figure 1. Experimental paradigm. In each condition, a trial is initiated with the appearance of a fixation point in the middle of the screen. When fixation has been maintained for 200 ms, the superimposed RDKs are then presented in the lower right quadrant of the screen. Once the stimulus has disappeared, a circular outline (the response circle) is presented at the same location as the stimulus. Participants made two clicks on the response circle indicating the directions in which the two surfaces were moving. In the 6/6:unicolor condition, the surfaces both move at 6°/s and in the 3/6:unicolor condition one surface moves at 3°/s and the other at 6°/s.

replaced. After the stimulus disappeared, a circular outline (the response circle) replaced the aperture. The participant was required to make two mouse clicks on the response circle indicating the directions in which the two surfaces were moving.

Stimulus duration was varied using a staircase design (Perry & Fallah, 2012). A block consisted of eight trials at a given stimulus duration (initial duration: 2000 ms). If performance (the ability to get both directions correct) in a given block was ≥87.5% (7/8) the stimulus duration in the next block was decreased. When performance fell below this threshold, indicating the stimulus duration was not long enough to correctly determine both directions, stimulus duration in the subsequent block was increased. The staircase had two stages. In the first, stimulus duration increased or decreased by 500 ms step sizes. Upon reaching a double reversal, stage two commenced in which the step size was 100 ms. The staircase ended when a second double reversal occurred. This allowed us to estimate the time needed to correctly process both directions of motion to within ±50 ms.

Data analysis

Correct responses were defined to allow for repulsion as in the previous study (Perry & Fallah, 2012): responses that fell within a range that extended from halfway between the two directions to 45° away from each real direction. A correct trial was defined as being any trial in which the participant determined both directions of motion within the ranges described above. Direction repulsion was calculated as the perceived direction minus the real direction of motion, so that positive values were indicative of direction repulsion. Means were calculated for both direction repulsion and processing time and independent t tests were used to assess any statistical differences between the conditions. When comparing the data to the 3/3:unicolor condition from the previous study, one-way ANOVAs with Tukey post hoc tests to control for multiple comparisons were utilized. The data was analyzed using MATLAB and SPSS (SPSS Inc., IBM, Armonk, NY).

Results

Previous work has found that increasing the strength of surface segmentation, using features processed within the dorsal stream, improved perception of direction (Kim & Wilson, 1996; Marshak & Sekuler, 1979). However, we previously determined that increasing the strength of surface segmentation using a ventral stream feature did not affect direction perception but instead reduced processing time (Perry & Fallah, 2012). In this study we wanted to determine if increasing the strength of surface segmentation using a dorsal stream feature would similarly reduce processing time in addition to improving direction perception. From the results, we can then determine when different features are bound together.

Direction repulsion

To determine how a difference in speed, 3/6:unicolor, affects direction repulsion compared to equal speeds, 6/6:unicolor and 3/3:unicolor from the previous study (Perry & Fallah, 2012), we performed a one-way ANOVA and post hoc Tukey HSD tests. We found a significant effect of surface speeds on direction repulsion (Figure 2A, $F(2,33) = 4.51$, $p = 0.019$). Increasing the speed of both surfaces, in the 6/6:unicolor condition (DR: 10.10° ± 0.74 *SEM*), significantly reduced direction repulsion when compared to the 3/3:unicolor condition (DR: 13.93 ± 1.38 *SEM*, $p = 0.027$), consistent with increased speed of motion reducing direction repulsion (Braddick et al., 2002). If there were no additional effect of speed segmentation on the attenuation of direction repulsion, then the repulsion in the 3/6 condition should fall between the repulsion in the 3/3 and 6/6 conditions, as the sum of the repulsion produced by one 3°/s surface (13.93°/2 = 6.97°) and one 6°/s surface (10.10°/2 = 5.05°) estimates a 12.02° repulsion. However, the repulsion in the 3/6 condition (10.47°) was significantly less from that seen in the 3/

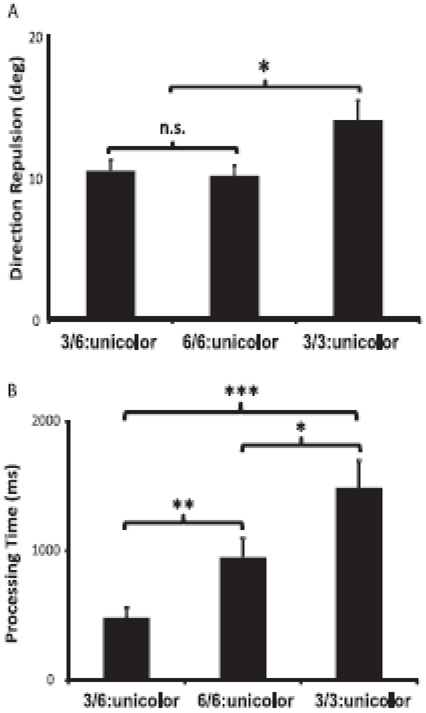

Figure 2. Direction repulsion and processing time. These graphs combine results from the current study and Perry & Fallah, 2012. (A) Direction repulsion in the 3/6:unicolor (10.47° ± 0.74 *SEM*) and 6/6:unicolor (10.10° ± 0.74 *SEM*) conditions was not significantly different. Repulsion in these two conditions was significantly less than in the 3/3:unicolor (13.93° ± 1.38 *SEM*) condition. (B) Processing time in the 3/6:unicolor (483 ms ± 80.09 *SEM*) condition was significantly less than in the 6/6:unicolor (950 ms ± 132.57 *SEM*) and the 3/3:unicolor (1488 ms ± 208.5 *SEM*) conditions. Errors bars represent *SEM*.

3:unicolor (previous study) condition (DR: 13.93° ± 1.38 *SEM*, $p < 0.05$) and was nearly identical to that in the 6/6 condition (10.10°, Figure 2A, $p = 0.961$). Therefore, speed segmentation likely provided additional attenuation of direction repulsion above that produced by an increase in the speed of one surface. Next we addressed the question of interest: Does speed segmentation affect processing time?

Processing time

When we compared the time needed to process both surfaces correctly (processing time, Figure 2B) in the 6/6:unicolor and 3/6:unicolor conditions, we found that speed segmentation afforded a significant, $t(22) = 3.013$, $p = 0.006$, advantage. The average time needed in the 6/6:unicolor condition, 950 ms (±132.57 *SEM*), was reduced by nearly 500 ms (467 ms) when the surfaces were different speeds (3/6:unicolor = 483 ms ± 80.10 *SEM*). When compared to the results from our previous study, we found a significant effect of surface speed on processing time, $F(2,33) = 11.23$, $p < 0.001$). Segmenting the surfaces by increasing the speed of one surface (3/6:unicolor condition) significantly reduced processing time by approximately 1000 ms when compared to the slower speed 3/3:unicolor condition (1488 ms, ±208.54 *SEM*, $p < 0.001$). However, increasing the speed of both surfaces (6/6:unicolor condition) reduced that benefit by half from about 1000 ms to approximately 500 ms, ($p = 0.042$). Therefore, task-irrelevant speed segmentation cues reduce the processing time needed for direction judgments.

Discussion

Direction repulsion

Using the same experimental paradigm as used previously (Perry & Fallah, 2012) we were able to determine how the speed of the surfaces affect direction repulsion under a number of conditions: two matching speeds (3/3:unicolor, 6/6:unicolor), and a speed segmentation condition where the speeds differed (3/6:unicolor). Consistent with previous literature, we found in the current study that differences in surface speed attenuated direction repulsion (Curran & Benton, 2003; Marshak & Sekuler, 1979). Also consistent with prior research (Braddick et al., 2002; Curran & Benton, 2003), we found that increasing the speed of both surfaces (6/6:unicolor) similarly reduced direction repulsion, likely due to increases in speed strengthening the representation of motion information (Maunsell & Van Essen, 1983; Palmer, Huk, & Shadlen, 2005). With the addition of speed differences or increase in the speed of both surfaces, attention of direction repulsion reached its limit: approximately 10° for two direction judgments (Braddick et al., 2002) or about 4° for a single direction judgment (Curran & Benton, 2003). In comparison, differences in surface color do *not* attenuate direction repulsion (Perry & Fallah, 2012). Therefore, direction repulsion is modulated by features processed within the dorsal stream, such as speed and spatial frequency, but not by features processed within the ventral stream, such as color. This suggests that direction repulsion occurs prior to color and motion being bound into an object representation. Thus, it is likely that direction repulsion is driven by a local circuit in area MT prior to forming an object representation that includes ventral stream information.

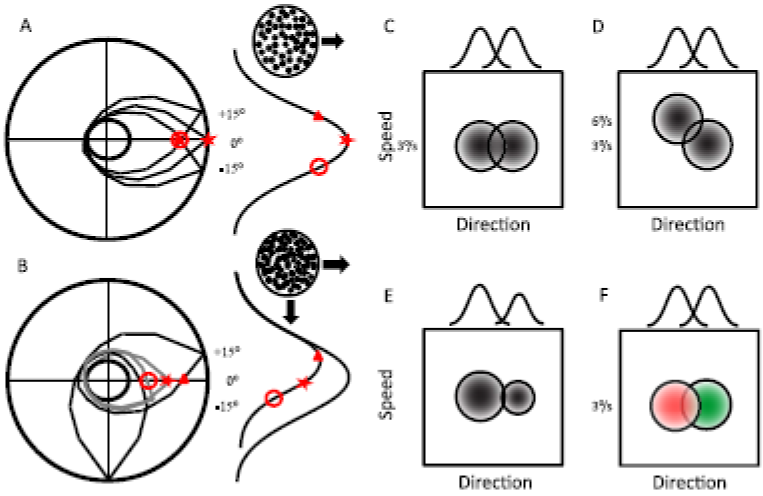

Figure 3. Uni- and multidimensional mutual inhibition. (A) Depicts individual neurons and population tuning curves for rightward motion. (B) The addition of a second surface suppresses the neuronal responses and shifts the population tuning away from the real direction due to inhibition whose strength is based on the overlap between the tuning curves. (C–F) Multidimensional tuning curves for speed and direction. Above each polar plot is a depiction of the direction tuning overlap for comparison. The greater the size of the overlapping region, the greater the mutual inhibition. (C) When all motion features are identical except for direction, multidimensional tuning is reduced to direction alone, or is unidimensional. (D) Segmenting the surfaces by an additional motion feature (such as speed) changes the population of neurons engaged in mutual inhibition, thus diminishing the area of overlap and reducing direction repulsion. Note that the overlap in the direction dimension (curves above) is no different than when the speeds are the same (C). (E) Attention to one of the surfaces suppresses the influence of the second surface. This reduction in gain of one surface shrinks the population response underlying that surface, which in turn reduces the overlap between the two causing a reduction in direction repulsion. (F) The addition of a ventral stream (color) feature difference, unlike speed, did not influence direction repulsion, and thus was not a feature dimension in the mutual inhibition circuit.

Neural circuitry: Direction repulsion

Direction repulsion was originally described as arising from mutual inhibition (Marshak & Sekuler, 1979; Mather & Moulden, 1980) where the neurons responding to one direction inhibit the neurons responding to the other direction. The amount of mutual inhibition also varied by the difference in directions, with repulsion decreasing as the difference increased (Marshak & Sekuler, 1979; Mather & Moulden, 1980). We propose a mutual inhibition circuit wherein each direction inhibits the other based on the overlap in tuning between the neurons representing each direction (Figure 3). Figure 3A depicts a population of area MT neurons with preferred directions of −15°, 0°, and +15° all of which respond to rightward motion (0°). The population tuning curve to the right of the polar plot depicts how the responses are integrated to determine the direction of motion (peak population response). When a second surface is added moving downwards (270°), the responses to that direction proportionally inhibit the first direction's responses based on the amount of overlap in the tuning curves. The population tuning curve is reduced but more importantly, the peak direction is shifted away; that is, it is repulsed (Figure 3B). This model is supported by the following aspects. First, as the angular difference between the directions increases, the overlap in tuning decreases which reduces the repulsion as was previously found (Marshak & Sekuler, 1979; Mather & Moulden, 1980). Second, direction tuning, like orientation tuning, is wider at oblique angles and sharper on the cardinal axes (Coletta, Segu, & Tiana, 1993; Gros, Blake, & Hiris, 1998; Hiris & Blake, 1996). When one direction is on a cardinal axis, the range of angles that produce repulsion is more limited (Marshak & Sekuler, 1979; Mather & Moulden, 1980) compared to when both directions are oblique (Braddick et al., 2002; Perry & Fallah, 2012).

We further propose that the mutual inhibition circuit is based not only on the overlap of direction tuning between neurons, but more so on the overlap of multidimensional tuning across conjunctions of motion features such as speed, spatial frequency, and direction selectivity (Albright, 1984; Lagae, Raiguel, & Orban, 1993; Maunsell & Van Essen, 1983; Perrone & Thiele, 2001). When other motion features are identical between the two surfaces, the multidimensional tuning is reduced to directionality alone (Figure 3C). However, adding a second distinguishing motion feature, such as speed, would reduce the overlap between the multidimensional tuning curves, thus reduce mutual inhibition and direction repulsion (Figure 3D). As speed and spatial frequency are features that form conjunctions with direction tuning in the dorsal stream, this model supports the reduction in direction repulsion seen with differences in speed (current study; Marshak & Sekuler, 1979) or spatial frequency (Kim & Wilson, 1996). Finally, this model also describes the effects that attending to one surface has on direction repulsion. Attention to speed or luminance changes in one superimposed surface reduced direction repulsion but dividing attention across both surfaces did not (Chen, Meng, Matthews, & Qian, 2005). The authors suggest that the results when attending to one surface can be explained based on feature-similarity gain (Martinez-Trujillo & Treue, 2004; Treue & Maunsell, 1999) in which attention enhances the representation of the attended feature and simultaneously reduces the influence of the unattended feature. Since the features in question are dorsal stream features coprocessed by directionally selective cells in area MT, the effect of attending to one surface while suppressing the other would be to reduce the gain of the suppressed surface and thus reduce the overlap for mutual inhibition (Figure 3E). This would produce the attenuation in direction repulsion that was seen (Chen et al., 2005). Finally, as color differences did not reduce direction repulsion, color is not a feature dimension used by the mutual inhibition circuitry. The multidimensional tuning for mutual inhibition works on dorsal stream, not ventral stream, features (Figure 3F).

Processing time

Having previously found that color segmentation did not affect direction discrimination but did increase the speed of processing, we investigated whether speed segmentation also reduces the processing time needed to make direction discriminations. There is a time cost associated with the integration of features over the processing of single features (Bartels & Zeki, 2006; Bodelón, Fallah, & Reynolds, 2007). Also, adding additional features increases the perceptual load, which generally slows processing (Lavie, 1995) Thus, further segmenting the surfaces by adding irrelevant features, such as speed or color differences, requires binding and should take longer than processing direction alone. However, we have found that there is a substantial advantage to be had by integrating features when the end result is to increase segmentation between superimposed surfaces. Using differences in surface speed (current study) and color (Perry & Fallah, 2012) we have shown that the time needed to process the direction of two superimposed surfaces can be reduced by over 500 ms. Therefore, the integration of features within the dorsal stream (speed and direction), where features are often coprocessed by neurons (Gross, Bender, & Rocha-Miranda, 1969; Holcombe & Cavanagh, 2001; Maunsell & Van Essen, 1983), and binding of features between the ventral and dorsal streams (color and direction) both produce a significant advantage in how quickly the information is processed.

While increasing the speed of one surface to 6°/s produces speed segmentation (vs. 3°/s), increasing both surfaces' speeds to 6°/s does not. If in the speed segmentation (3/6:unicolor) condition, the reduction in processing time is solely due to increasing the speed of the one surface, then increasing the speed of both surfaces should reduce processing time further, or if processing time is already at its lower limit, produce the same processing time advantage. Instead, we found that increasing both surfaces' speeds to 6°/s reduced the processing advantage. Differences in speed provide a greater advantage to direction judgments than just moving at faster speeds. Note that there was still a (smaller) advantage for the matched faster speeds (6/6:unicolor) over the matched slower speeds (3/3:unicolor). An equivalent increase in speed raised the response rates of area MT neurons (Maunsell & Van Essen, 1983) presumably increasing the strength of the motion representation. As others have shown reduced reaction times from increasing stimulus strength by luminance (Pins & Bonnet, 1996) or motion coherence (Palmer et al., 2005), increasing motion strength by increasing surface speed should also reduce reaction times. Our results show how reduced processing time would underlie these faster reaction times.

Neural circuitry: Processing time

We propose that the large decrease in processing time that occurs with increases in surface segmentation by additional features is most likely due to speeding up decision making (see Perry & Fallah, 2012). Motion direction is processed in area MT (Albright, 1984; Mikami, Newsome, & Wurtz, 1986; Newsome & Pare, 1988; Salzman, Murasugi, Britten, & Newsome, 1992) and passed forward to frontal and parietal areas, which can accumulate the direction information in order to reach a decision threshold (Huk & Shadlen, 2005; Hussar & Pasternak, 2013; Shadlen & Newsome, 1996, 2001; Zaksas & Pasternak, 2006). When two surfaces are identical except for direction of motion, each surface's direction information interferes with the processing of the other surface's direction, creating a "noisy walk" toward the decision threshold (accumulator model, Palmer et al., 2005). By introducing differences in color (Perry & Fallah, 2012) or speed (current study), the objects become more distinct from each other, providing additional features through which the direction information can be separated. Filtering out the input from the other surface would reduce the noise in the walk to threshold, increasing the slope of information accumulation. Thus, the decision threshold would be reached sooner resulting in decreased processing time.

Conclusion

Irrelevant speed segmentation cues reduce the processing time required to make direction judgments. Color segmentation cues also reduce the processing time required to make direction judgments (Perry & Fallah, 2012). However, only speed affects direction processing as measured by changes in magnitude of direction repulsion, an illusion linked to a local mutual inhibition circuit within area MT. Therefore, motion processing integrates speed and direction prior to global motion processing. The output of global motion processing feeds forward to decision-making areas, where color segmentation cues, as well as speed, reduce processing time. Therefore, by this stage the object representation includes ventral (color) and dorsal (speed and direction) information. Thus, the integration of features within and across the streams occurs at different stages of processing along the visual hierarchy.

Keywords: feature integration, direction repulsion, motion transparency, processing speed

Acknowledgments

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Commercial relationships: none

Corresponding author: Carolyn J. Perry.
Email: carolynperry08@gmail.com.
Address: School of Kinesiology and Health Science, Centre for Vision Research, York University, Ontario, Canada.

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Hand placement near the visual stimulus improves orientation selectivity in V2 neurons

Carolyn J. Perry,^{1,2,3} Lauren E. Sergio,^{2,3} J. Douglas Crawford,^{2,4,5} and Mazyar Fallah^{1,2,3,5}
^{1}*Visual Perception and Attention Laboratory, School of Kinesiology and Health Science, York University, Toronto, Ontario, Canada;* ^{2}*Centre for Vision Research, York University, Toronto, Ontario, Canada;* ^{3}*School of Kinesiology and Health Science, York University, Toronto, Ontario, Canada;* ^{4}*Department of Psychology, York University, Toronto, Ontario, Canada; and* ^{5}*Canadian Action and Perception Network, York University, Toronto, Ontario, Canada*

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Perry CJ, Sergio LE, Crawford JD, Fallah M. Hand placement near the visual stimulus improves orientation selectivity in V2 neurons. *J Neurophysiol* 113: 2859–2870, 2015. First published February 25, 2015; doi:10.1152/jn.00919.2013.—Often, the brain receives more sensory input than it can process simultaneously. Spatial attention helps overcome this limitation by preferentially processing input from a behaviorally-relevant location. Recent neuropsychological and psychophysical studies suggest that attention is deployed to near-hand space much like how the oculomotor system can deploy attention to an upcoming gaze position. Here we provide the first neuronal evidence that the presence of a nearby hand enhances orientation selectivity in early visual processing area V2. When the hand was placed outside the receptive field, responses to the preferred orientation were significantly enhanced without a corresponding significant increase at the orthogonal orientation. Consequently, there was also a significant sharpening of orientation tuning. In addition, the presence of the hand reduced neuronal response variability. These results indicate that attention is automatically deployed to the space around a hand, improving orientation selectivity. Importantly, this appears to be optimal for motor control of the hand, as opposed to oculomotor mechanisms which enhance responses without sharpening orientation selectivity. Effector-based mechanisms for visual enhancement thus support not only the spatiotemporal dissociation of gaze and reach, but also the optimization of vision for their separate requirements for guiding movements.

attention; peripersonal space; reaching; vision

A GROWING BODY OF HUMAN PSYCHOPHYSICAL evidence shows that visual processing is altered near the hand. In blindsight, simply placing the hand in the blind field near to visual stimuli improves detection and size perception (Brown et al. 2008; Schendel and Robertson 2004). In extinction, patients fail to attend to a second stimulus presented in the contralesional hemifield, but, when the hand is placed within the affected field, detection of the second stimulus is improved (di Pellegrino and Frassinetti 2000). An improvement in detection near the hand, especially in cases involving extinction, would suggest that attention is deployed to near-hand space much like how the oculomotor system deploys spatial attention (Moore et al. 2003). Studies using classic spatial attention paradigms have shown this to be true. In a spatial cueing paradigm, reaction times to targets near the hand were facilitated, regardless of cue location (Reed et al. 2006). In another study involving visual search, inhibition of return and attentional blink paradigms, the presence of the hand slowed the shifting of attention between visual items (Abrams et al. 2008). These studies suggest that improved visual processing near the hand is linked to attentional prioritization of the space near the hand.

These behavioral studies suggest that attentional prioritization occurs in "near-hand space," when movements are sustained. However, there is currently no neurophysiological evidence to support these findings, and the neuronal mechanisms underlying this enhancement are as yet unknown. To determine if and how a nearby hand affects early visual processing, we recorded from neurons in macaque area V2, an early visual area shown to be modulated by attention (Luck et al. 1997; Motter 1993), selective for orientation (Motter 1993), a feature necessary for accurate reaching (Fattori et al. 2009; Murata et al. 2000; Raos et al. 2004) and is directly connected with fronto-parietal reaching and grasping networks to guide the hand (Gattass et al. 1997; Passarelli et al. 2011). We measured the responses of V2 neurons to oriented rectangles when the animals maintained their grasp on a touch bar, placing their hand near to but outside the neuron's receptive field (RF) (Fig. 1, Hand-Near). As we wanted to be able to dissociate the effects of oculomotor driven spatial attention from those of near-hand attention, we separated the grasp target (touch bar) from the visual stimulus in the RF. Eye movements precede arm movements toward a reach target (Ballard et al. 1992; Biguer et al. 1982; Fisk and Goodale 1985; Neggers and Bekkering 2000, 2001, 2002; Prablanc et al. 1979) and the oculomotor system deploys spatial attention (Moore and Armstrong 2003; Moore and Fallah 2001, 2004; Müller et al. 2005). Thus, if the visual stimulus was also the reach target, oculomotor-driven spatial attention would be deployed to the reach target and would at the least confound and at the most completely mask modulation due to the nearby hand. To avoid this, we did not make the visual stimulus the reach target, but placed the hand nearby to take advantage of the spatial extent of attention afforded by the nearby hand.

Prior studies of spatial attention (McAdams and Maunsell 1999; Moran and Desimone 1985; Motter 1993; Treue and Martinez-Trujillo 1999) have used "Attend-In" and "Attend-Away" paradigms to compare the neuronal modulation when a spatial location is attended vs. when attention is located elsewhere. In Attend-In conditions, a cue, presented prior to the visual target, is used to allocate attention to a certain spatial location. In Attend-Away conditions, the cue allocates attention to a location away from where the target is presented. Under these circumstances, neuronal responses undergo a gain

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Address for reprint requests and other correspondence: C. J. Perry, 357 Bethune College, 4700 Keele St., Toronto, ON, Canada M3J 1P3 (e-mail: carolynperry08@gmail.com).

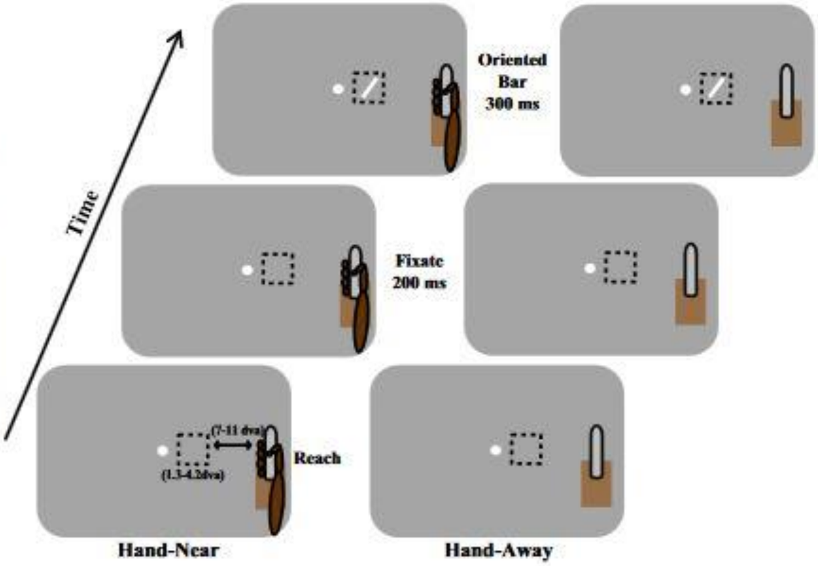

Fig. 1. Experimental paradigm. In a Hand-Near block, the animal grasps a vertically orientated touch bar placed outside the receptive field (RF, dashed box) at which time a fixation point appears. Two hundred milliseconds later, an oriented bar is displayed within the RF for 300 ms. In a Hand-Away block, the touch bar apparatus remains visible, but no reach is made by the animal. Reward is given for maintaining fixation and grasp (Hand-Near) or simply maintaining fixation (Hand-Away). The *bottom left* panel shows the variation in RF diameter [1.3–4.2 degrees of visual angle (dva)] and also the distance between the right edge of the RF and the edge of the fingers (7–10.7 dva). This figure represents a depiction and is not drawn to scale or matched for the color and contrast of the experimental apparatus or the animal.

modulation when the spatial location is attended. We modified this paradigm so that the presence of the hand acted in a similar manner as the spatial cue in those studies. We hypothesized that, if the hand is the center of an attentional field, as suggested by prior research (Abrams et al. 2008; Brown et al. 2008; di Pellegrino and Frassinetti 2000; Reed et al. 2006; Schendel and Robertson 2004), neuronal responses in "Hand-Near" and "Hand-Away" conditions should be similar to the neuronal responses seen in Attend-In and Attend-Away conditions, respectively. As the relationship between oculomotor-driven spatial attention and the effect of hand position on early visual responses is unknown, the stimuli measuring V2 neurons' orientation selectivity were task irrelevant. If the task had instead required attending to and making judgments of the stimuli within the RFs, the effects of spatial attention would have confounded neuronal responses associated with hand attention. This task design is similar to real-life situations where you are reading a paper and reach, without looking, to pick up your cup of coffee: would orientation processing improve when the hand is near the cup? Across the population, we found that, in the Hand-Near condition, orientation tuning sharpened. This suggests that the mechanisms of near-hand attention are different than gain modulation seen with oculomotor-driven spatial attention. In addition, we found that the presence of a nearby hand reduced the variability of neuronal responses. Together, these results show that orientation selectivity is improved near the hand, which could increase the accuracy of subsequent reaches and grasps in the peripersonal workspace.

MATERIALS AND METHODS

Electrophysiology

Two adult female rhesus monkeys were each implanted with a head-holding device and a recording chamber positioned over left V2 using stereotaxic coordinates. Placement was confirmed by assessing RF size and eccentricity, topographic organization and feature selectivity (Gattass et al. 1981; Hubel and Livingstone 1987; Levitt et al. 1994; Roe and Ts'o 1995). A microdrive (3-NRMD-A2, Crist Instruments) was used to advance a tungsten electrode (FHC). Neuronal data were acquired and stored using a Multichannel Acquisition Processor (Plexon). Single neurons were isolated online using Rasputin software (Plexon). RFs were mapped with a manually controlled flashing oriented bar that could be varied in orientation, size, and position. The diameter of the RF varied across neurons but ranged between 1.3 and 4.2 degrees of visual angle ("dva"; mean = 1.8, SD = 0.5). Note that the experiment was carried out if a RF was plotted; orientation selectivity was not tested at this point. This allowed for including neurons that only developed orientation selectivity in the presence of the hand. Neurons were isolated offline using Offline Sorter (Plexon) for subsequent analyses. All experimental and surgical procedures complied with animal care guidelines, as defined by the CACC (Canadian Animal Care Committee) and York University's Animal Care Committee. The study and all associated protocols were approved by York University's Animal Care Committee.

Stimuli and Task

Experimental control was maintained using Cortex software (http://dally.nimh.nih.gov/). Eye gaze was tracked using an infrared eye tracker (ISCAN model ETL-200, 240 Hz). Stimuli were presented on a computer monitor (Viewsonic G225f, 1,024 × 768 resolution, 60 Hz) that was placed 36 cm from the monkey. This distance allowed the animal to comfortably reach with its right hand to a vertically oriented touch bar immediately adjacent to the front of the monitor (Fig. 1) which was present throughout the experiment and positioned outside of the visual RF. The distance from the right edge of the RF to the touch bar ranged between 5.6 cm (8.8 dva) and 7.9 cm (12.5 dva). As the monkeys would grasp the touch bar by wrapping their fingers around it, the distance to the fingers (1.8 dva wide) ranged between 7 and 10.7 dva (see Fig. 1). This minimum distance of 7 dva reduced the possibility of the hand encroaching upon the RF and modulating baseline firing rates, even if hand-mapping underestimated the size of the RF center. With this spacing, visual stimulation within the RF was identical across both conditions (Hand-Away and Hand-Near). The experiments were conducted in a darkened room illuminated by the ambient light from the computer monitor. The hand and touch bar were low contrast but visible to the animals.

In a Hand-Near block, once the animal had grasped the touch bar, each trial began with the appearance of a fixation point (Fig. 1, *left*). When the animal maintained fixation within a 2 dva window for 200 ms, a task-irrelevant oriented rectangle was presented for 300 ms in the center of the RF. The rectangle varied in orientation (0, 22.5, 45, 67.5, 90, 112.5, 135, and 157.5°) and size (based on the size of the RF). If fixation and grasp of the touch bar were maintained throughout this period, the animal received a reward (Monkey A: juice, Monkey B: fruit). In a Hand-Away block (Fig. 1, *right*), the touch bar apparatus remained in place, but the animal did not reach and grasp the touch bar. Trials again commenced with the appearance of the fixation point. Each orientation was tested 10–20 times in each hand condition.

We used this paradigm as it replicates the hand position of studies in which a sustained reach placed the hand near visual stimuli and showed improved visual processing and attentional prioritization of near-hand space (Abrams et al. 2008; Brown et al. 2008; Reed et al. 2006). This links the current research to previous neurophysiological work on spatial attention, with "Hand-Near" and "Hand-Away" substituting for "Attend-In" and "Attend-Away" (McAdams and Maunsell 1999; Moran and Desimone 1985; Motter 1993; Treue and Martinez-Trujillo 1999).

Data Analysis

We computed baseline rates from −175 to 0 ms prior to the onset of the oriented rectangle and stimulus response rates from 0 to 300 ms after stimulus onset. From these we computed the following measures.

Orientation tuning index. To quantify possible changes in tuning between Hand-Near and Hand-Away conditions, we computed an orientation tuning index (OTI): R_{pref}/R_{orth} in each condition, where R is the response rate of the neuron for preferred or orthogonal orientation. The preferred orientation was the orientation that produced a maximal response, and the orthogonal orientation was 90° to the preferred orientation. In contrast to curve-fitting, this index, based on response rates, avoids the use of interpolated data when determining changes in tuning.

Response modulation. We quantified the effect of hand position by computing a number of modulation indexes. First, we computed the percent change of firing rate based on whether a reach had occurred or not: $[(HN - HA)/HA] \times 100$, where HN represents the average response in the Hand-Near condition, and HA represents the average response rate in the Hand-Away condition. We similarly computed the percent change in the response rate to the preferred direction only: $[(HN_{Pref} - HA_{Pref})/HA_{Pref}] \times 100$. Finally, we computed the modulation of the tuning indexes to determine whether changes in tuning occurred between the Hand-Near and Hand-Away conditions: $[(OTI_{HN} - OTI_{HA})/OTI_{HA}] \times 100$. Significant shifts were tested using the Wilcoxon signed-rank test.

Curve fitting. We fit the orientation tuning data for unimodally oriented neurons with a von Mises (vM) function, a circular form of the Gaussian function, used for orientation selectivity (Kohn and Movshon 2004). The function takes the form:

$$vM(\theta) = ae^{\kappa \cos(\theta - p)} + m$$

where a is the multiplicative scaling factor, κ is the concentration or bandwidth of tuning, θ is the orientation at that point in the tuning curve, p is the preferred orientation, and m is the baseline rate. Fits were performed in Matlab with the ***nlinfit*** function (based upon least squares estimation). For each neuron, fits were computed for Hand-Near and Hand-Away conditions separately. Two neurons in the main population and two neurons in the baseline shifted population were removed from further analysis due to poor fits. For these neurons, ***nlinfit*** did not converge to a solution (ill-conditioned Jacobians), and they were rejected from further analysis (similar to Kohn and Movshon 2004). Significant shifts in the fit parameters were tested using the Wilcoxon signed-rank test.

Fano factors. To quantify response variability we computed Fano factors (FF = spike count variance/mean spike count; Chang et al. 2012; Cohen and Maunsell 2009; McAdams and Maunsell 1999; Mitchell et al. 2007) in the HN_{pref} and HA_{pref} conditions. To eliminate the possibility that changes in the FF were influenced by neuronal firing rates, we mean-matched response rates in the HN_{pref} and HA_{pref} conditions and then compared the FFs in each using a Wilcoxon signed-rank test.

RESULTS

Inclusion and Exclusion Criteria

Neurons were only included for further analysis if they had a significant visual response over baseline (*t*-test). As we wanted to test the effect of the hand on orientation tuning, we then limited our analysis to neurons exhibiting significant orientation tuning (one-way ANOVA, e.g., Jansen-Amorim et al. 2011; Motter 1993) in either the Hand-Near or Hand-Away condition. The only difference between the conditions was the presence or absence of the hand on the touch bar. To eliminate the possibility that the hand or arm visually encroached on the classic RF, neurons were excluded if they showed a significant modulation in the baseline firing rate between Hand-Near and Hand-Away conditions (*t*-test). Eliminating cells from analysis that had a significant shift in their baseline firing rate also removed the possibility that responses were altered due to other variables, such as arousal. Of 93 neurons from which data were obtained, 41 were removed as they were not orientation tuned in either the Hand-Near or Hand-Away conditions (26) or did not have a significant visual response above baseline to the oriented bars (15 neurons). Fifty-two neurons were orientation selective. Although studies have shown that spatial attention can increase baseline responses in area V2 (Luck et al. 1997), 14 cells (baseline-shifted neurons) were analyzed separately as they had a significant baseline modulation between the Hand-Near and Hand-Away conditions, which could also reflect the animal's arm impinging on the RF center. The remaining 38 neurons became the main population for analysis. Note that, of the 52 orientation-selective neurons, 15 were only orientation selective in the Hand-Near condition. These cells would have been missed if we only tested neurons that exhibited orientation selectivity during the mapping of the RF.

Gaze Position

To ensure that gaze position did not shift dependent on hand placement, we calculated the difference between the average horizontal eye position shift between the baseline period and the presentation of the stimulus for each included neuron's experimental session and computed any potential shifts between the Hand-Near and Hand-Away conditions. There was no significant shift [$F(1,27) = 0.34$, $P = 0.568$] of the eye position toward the hand [Hand-Near − Hand-Away = -0.002 ± 0.001 (SE) dva]. This indicates that the presence or absence of the hand did not influence gaze position. There was, however, a significant shift of gaze toward the RF during stimulus presentation [$F(1,27) = 7.73$, $P = 0.010$]. This suggests that the onset of the stimulus was salient enough to slightly (0.046 dva) draw the eyes toward the RF, regardless of the hand position. This indicates that the hand was not the target of a saccade and an oculomotor-driven shift in attention.

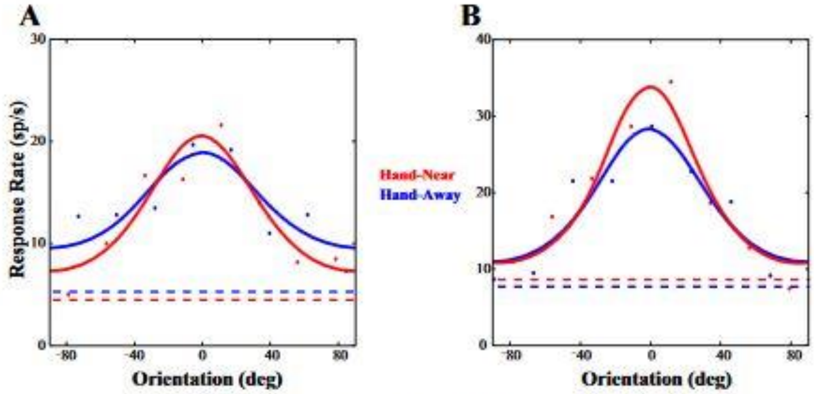

Fig. 2. Example cells. The data from two cells fitted with von Mises functions are shown. *A*: this neuron shows responses that are increased at the preferred orientation and reduced at the orthogonal orientation, resulting in a sharpening of tuning. *B*: while showing a larger increase response at the preferred orientation, this neuron instead had no modulation at the orthogonal orientation. sp/s, Spikes per second. Dashed lines represent baseline firing rates.

Neuronal Analysis

Figure 2 shows the tuning curves of two example neurons. *Neuron A* depicts a neuron whose responses increased slightly at the preferred orientation but sharpened during the Hand-Near condition (Fig. 2*A*) due to a reduction in response to the orientations on the flank of the tuning curve. *Neuron B* instead showed an increase in response to the preferred orientation, with no corresponding change in response at the orthogonal orientation (Fig. 2*B*). While spatial attention classically results in a proportional increase to responses across the tuning curve, neither *neuron A* nor *B* show this pattern of response.

Effect of Hand Position on Preferred and Orthogonal Responses

Figure 3*A* plots the distribution of neuronal responses to the preferred orientation in the Hand-Near vs. the Hand-Away condition. Points that lie above the line of unity indicate cells in which the response rate to the preferred orientation in the Hand-Near condition was greater than in the Hand-Away condition. More of the neurons lie above the line of unity than below (red and black dots). Across the population ($n = 38$), the response to the preferred orientation significantly increased ($Z = 2.12$, $P = 0.034$) by 10.76% (±4.69 SE) in the Hand-

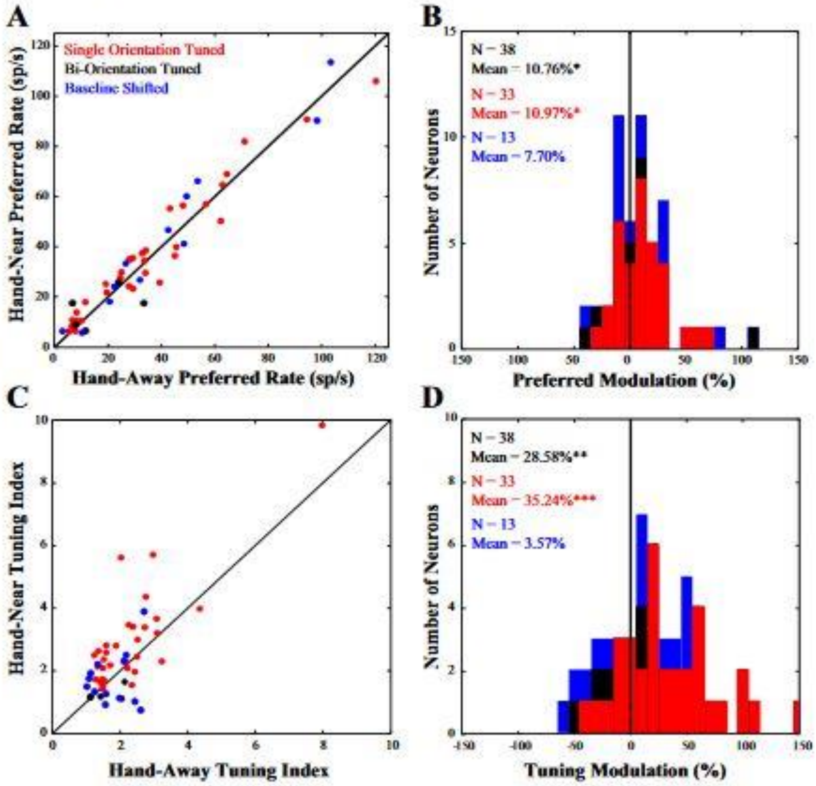

Fig. 3. Modulation of preferred rate and tuning. *A*: the response of each neuron to the preferred orientation in the Hand-Away (*x*-axis) condition is plotted against the response of each neuron in the Hand-Near (*y*-axis) condition. The diagonal line on the plot represents the line of unity; the majority of points fall above this line, indicating an increased response to the preferred orientation when the hand was nearby. *B*: we quantified this change in response by computing a modulation index and found that the presence of the hand significantly increased neuronal response to the preferred orientation (seen as a shift of the population to the right of zero). *C*: the tuning index of each neuron in the Hand-Away condition (*x*-axis) is plotted against the tuning index in the Hand-Near condition (*y*-axis). Again more units fall above the line of unity. *D*: we used the same modulation index to quantify tuning modulation and found that the presence of the hand significantly sharpened tuning. Data in red represent all neurons in the dataset that were tuned for a single orientation. Data in black represent neurons that were tuned for two orientations, and data in blue are neurons that were excluded from the main analysis, as they showed a significant baseline shift between the Hand-Near and Hand-Away conditions.

Near vs Hand-Away condition (Fig. 3B). In contrast, the population showed no significant increase in the response rate at the orthogonal orientation with the Hand-Near [$Z = 1.50$, $P = 0.133$, mean: $-3.69 \pm 6.69\%$ (SE)]. It is important to note that previous studies of classic spatial attention have shown little to no effect on neuronal responses to irrelevant stimuli when attention is directed outside of the RF (e.g., Moran and Desimone 1985). Finding enhanced responses when grasping a touch bar outside of the RF is not only surprising but also provides neurophysiological evidence that attention is deployed to near-hand space. Based on the distance between the touch bar and the stimulus in the RF, near-hand-related visual enhancement appears to operate with a larger spatial focus than oculomotor-driven spatial attention. In addition, hand position preferentially enhances responses at the preferred orientation and not at the orthogonal orientation.

Effect of the Hand on Orientation Tuning

Multiplicative gain modulation, proportional increases across stimulus selectivity (McAdams and Maunsell 1999), is a mechanism commonly used to describe how spatial attention affects the responses of visual neurons. That is, multiplicative gain modulation increases responses across the tuning curve without changing the shape of the tuning curve. If, similar to spatial attention, the presence of the hand enhances early visual processing through gain modulation, there should be no change in the OTI ($\mathrm{OTI} = R_{\mathrm{Pref}}/R_{\mathrm{Orth}}$). Plotting the tuning index in the Hand-Near vs the Hand-Away condition (Fig. 3C, red and black dots) shows that the majority of the neurons fall above the line of unity. Tuning is significantly sharpened by 28.58% [± 7.71 SE, $Z = 3.30$, $P = 0.001$; Fig. 3D] across the population ($n = 38$). Thus, unlike classic spatial attention which does not affect tuning, hand-related attention sharpened orientation selectivity by almost 30%.

Effect without Biorientation Tuned Cells

Previous work (Anzai et al. 2007) has found that up to 20% of V2 neurons show enhanced responses at two orthogonal orientations (i.e., are biorientation tuned). These types of cells have been shown to be used to determine contours and occlusion (Rubin 2001). Figure 4 shows the responses of an example biorientation tuned neuron. While the polar plot (*panel A*) doubles up the orientation information, it clearly shows the crossed axes of the two preferred orientations. *Panel B* shows the same data plotted as an 180° tuning curve. When the hand is present (Hand-Near), the major axis of orientation (e.g., the longer one in the Hand-Away condition) is little changed. However, the response to the minor axis increases. The responses to the orientations in between these two axes are suppressed and drop below baseline. Changes in tuning, then, are hard to determine in biorientation cells as any increase in response in the lesser of the two preferred orientations would reduce the tuning index because the OTI reflects tuning to a single orientation. As tuning indices do not accurately reflect biorientation cells, we reexamined our population and found five biorientation cells (~13%). We then removed them from our cell population and performed the analyses again. Due to the small sample size ($n = 5$), we did not analyze the biorientation tuned cells on their own; however, they are depicted separately (black dots and bars in Figs. 3 and Fig. 6).

With the biorientation cells removed, the single orientation population ($n = 33$) still produced an increase in response when the hand was present (Fig. 3B, red bars). Responses at the preferred orientation were significantly ($Z = 2.53$, $P = 0.011$) increased by 10.97% (± 3.86 SE) in the Hand-Near vs Hand-Away condition (Fig. 5B). Responses to the orthogonal orientation were now significantly decreased in the presence of the hand [$-9.41 \pm 5.76\%$ (SE), $Z = 2.17$, $P = 0.030$]. The presence of the hand not only improves responses to the preferred orientation, but also decreases responses to the orthogonal orientation. This was masked by the biorientation cells in the whole population because the biorientation cells also preferred the orthogonal orientation. Consistent with these results, the tuning index showed a greater decrease with the hand present when the biorientation cells are removed (Fig. 3D, red bars). Tuning was sharpened by 35.24% (± 8.03 SE, $Z = 3.76$, $P < 0.001$) in Hand-Near vs Hand-Away, an increase from that seen across the full population (28.58%).

Effect of Hand Position on Baseline Shifted Cells

Although studies have shown that spatial attention can increase baseline responses in area V2 (Luck et al. 1997), 14 neurons that had a significant baseline shift between the Hand-Near and the Hand-Away condition were not included in the main analysis. This was done to ensure that the effect of hand position was not being driven by the arm encroaching on the visual RF. We now analyzed the baseline-shifted neurons to determine whether their responses were similar to the rest of the population. None of the cells were biorientation tuned. It should be noted, however, that one cell within this population was removed as an extreme outlier (preferred modulation = 387%, orthogonal modulation = 742%). In the presence of the

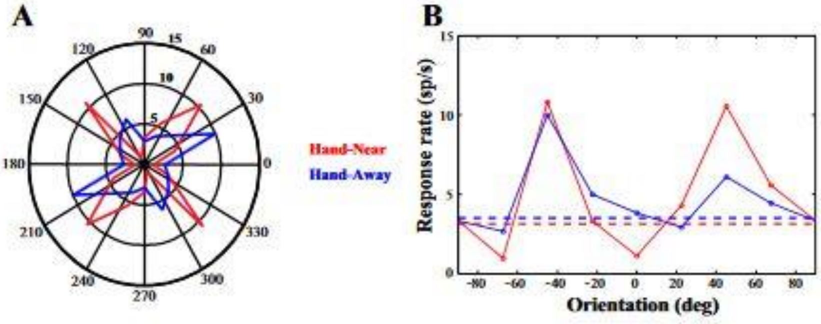

Fig. 4. Example biorientation tuned cell. Polar (*A*) and 180° (*B*) plots for the same example neuron are shown. The firing rate in the polar plot is depicted as the distance away from the center, and the responses to each orientation are mirrored 180° to depict a circular tuning plot. In the Hand-Near condition, there is an increased response along the minor axis (orthogonal orientation) with no change in the major axis (preferred orientation), compared with the Hand-Away condition. *B*: also, with the hand present, responses to orientations between the two axes are suppressed below baseline.

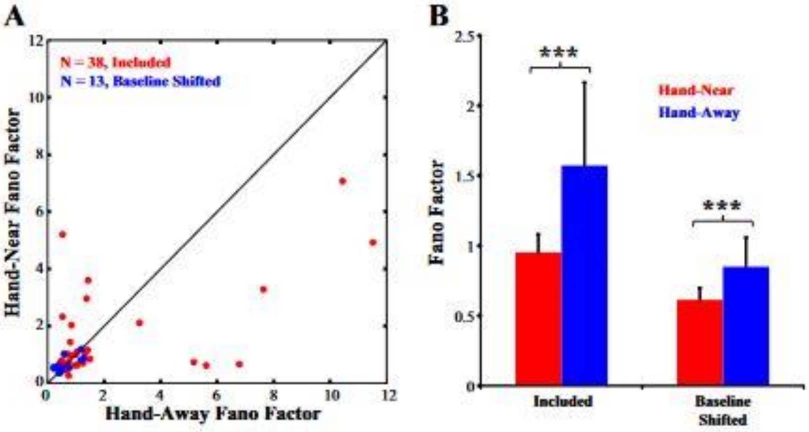

Fig. 5. Changes in response variability. *A*: the Fano factor in the Hand-Near and Hand-Away conditions are plotted for the population of neurons included in the dataset (n = 38, in red) and baseline shifted neurons (n = 13, in blue). *B*: in both populations, response variability was significantly reduced when the hand was present. ***Significant difference, Hand-Near vs. Hand-Away.

hand, the remaining baseline shifted cells ($n = 13$) were not significantly modulated by hand position in their responses to the preferred [mean: 7.70 ± 7.71% (SE), $P = 0.267$] or the orthogonal orientations [mean: 20.16 ± 14.87% (SE), $P = 0.414$]. Nor was there a significant modulation of the tuning index [mean: 3.57 ± 11.11% (SE), $P = 0.787$]. Figure 3 shows the distribution of the baseline shifted cells in blue with the rest of the population (red) and biorientation cells (black). The baseline shifted cells are also depicted in blue in Fig. 6, which shows the cells' distribution across the range of preferred response and tuning modulations. We cannot distinguish whether the lack of an effect of hand position in the baseline shifted cells is due to the arm impinging on the RF, the small sample size, some other factor, or a combination of these possibilities.

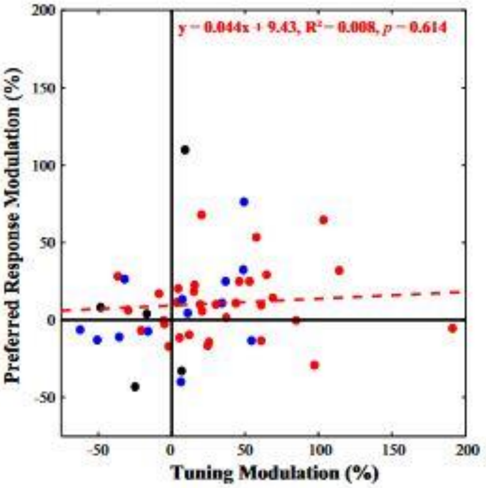

Fig. 6. Response modulation vs. sharpened tuning. We plotted the tuning modulation (x-axis) against the preferred modulation (y-axis) for each unit. While the majority of the neurons fall within the *top right* quadrant, the population of single orientation tuned neurons (in red) did not show a significant relationship between modulation in the preferred response and changes in the tuning index. Biorientation neurons are shown in black, and baseline shifted neurons in blue for comparison.

Effect of the Hand on Response Variability

Previous studies have shown reductions in response variability during reaching in premotor cortex (Churchland et al. 2010) and oculomotor preparation in frontal eye field (FEF) (Purcell et al. 2012). The reduction in oculomotor response variability has been shown to also propagate back to visual neurons in area V4, which show a similar reduction prior to a saccade (Steinmetz and Moore 2010). If near-hand attention is mediated by feedback from fronto-parietal reaching and grasping networks (Culham et al. 2003), we would expect to find a similar reduction in response variability in V2 neurons when a sustained reach places the hand nearby. To control for changes in firing rate, we first mean-matched response rates in the Hand-Near and Hand-Away conditions (as per Churchland et al. 2010) and then computed their FF (spike count variance/mean spike count). Figure 5*A* shows the FF distribution in the Hand-Near compared with the Hand-Away condition across the population of 38 neurons included in the dataset (in red). The FF of the preferred orientation response (Fig. 5*B*) significantly declined ($Z = -8.68$, $P < 0.001$) in the Hand-Near condition (mean: 0.96 ± 0.11 SE), compared with the Hand-Away condition (mean: 1.52 ± 0.31 SE). Response variability also significantly declined in the baseline shifted cells ($Z = -8.76$, $P < 0.001$, Fig. 5 in blue) in the Hand-Near condition (mean: 0.61 ± 0.086) compared with the Hand-Away condition (mean: 0.85 ± 0.13). This reduction in response variability within near-hand space is consistent with FF reductions seen due to spatial attention and/or motor feedback (Churchland et al. 2010; Purcell et al. 2012; Steinmetz and Moore 2010).

Relationship Between Changes in Response Rates and Orientation Tuning

We investigated the relationship between changes in preferred response and orientation tuning and found different patterns of activity (Fig. 6). While the *top right* quadrant contains the majority of cells, which exhibited both increased response and sharpened tuning when the hand was near, there was no significant relationship between preferred response modulation and tuning index modulation across the population of cells ($F = 0.26$, $P = 0.614$). The biorientation cells, as discussed previously, produced negative tuning index modulations in the Hand-Near condition due to increasing responsivity to the secondary preferred orientation. Thus they are predominantly found on the left-hand side of the distribution (black dots). Finally, the baseline shifted cells are plotted in blue, depicting where they fall among the rest of the population.

Effect of Hand Position on Fitted Tuning Curves

Of the 38 neurons used in the previous analysis, we removed the 5 biorientation tuned cells as they would not be fit by a unimodal von Mises function. We then used the von Mises function to fit the remaining 33 neurons. Two additional neurons were poorly fit (as per the *nlinfit* function due to ill-conditioned Jacobians) and thus were removed from the population. Figure 7*A* depicts the population tuning curves in both the Hand-Near and Hand-Away. The shaded area between the two curves highlights how tuning sharpens when the hand is present, with increased responsivity around the preferred orientation and decreased responsivity at orthogonal orientations, consistent with the previous results. κ is the concentration parameter from the fit that describes the tuning bandwidth: the larger the κ, the sharper the tuning. From each cell's individual curve fits, we have plotted the κ in the Hand-Near vs. Hand-Away conditions in Fig. 7*C*. Consistent with the population tuning curve and the raw data analyses, the majority of cells (Fig. 7*C*, red dots) fall above the line of unity. κ significantly increased by 17% (+0.114 ± 0.085 SE, $Z = 2.49$, $P = 0.013$, Fig. 7*D*) in the Hand-Near (mean: 0.79 ± 0.07 SE) compared with the Hand-Away (mean: 0.67 ± 0.09 SE) condition. The population amplitude (a), a multiplicative scaling factor that represents the scaling of the response above baseline, was not significantly different in the two hand conditions (Hand-Near: 11.2 ± 1.3 SE; Hand-Away: 11.6 ± 1.4 SE, $Z = -0.53$, $P = 0.60$). Thus there was no evidence in support of gain modulation. In addition, the preferred orientation across the population did not significantly differ between Hand-Away and Hand-Near conditions [mean difference: −7.09 ± 10.6° (SE), $Z = -0.20$, $P = 0.85$].

Of the 14 baseline shifted cells, 12 were fit with von Mises functions (Fig. 7*B*) and 2 were removed as they were poorly fit. In this population, there was a trend ($P = 0.09$) for an increase in κ in the Hand-Near (mean: 1.32 ± 0.42 SE) over the Hand-Away (mean: 0.738 ± 0.12 SE) condition (Fig. 7, *C* and *D*, in blue). Amplitudes were not significantly different ($P = 0.233$) between Hand-Near (mean: 17.2 ± 2.9 SE) and Hand-Away (mean: 20.9 ± 3.9 SE) conditions. Furthermore, there was no significant shift in preferred orientation between conditions [mean difference: 6.0 ± 3.6° (SE), $P = 0.17$]. Similar to the results with the raw data, there were no significant differences in this population of baseline shifted cell, although the trend for sharpened tuning may be due to a lack of statistical power due to the small sample size.

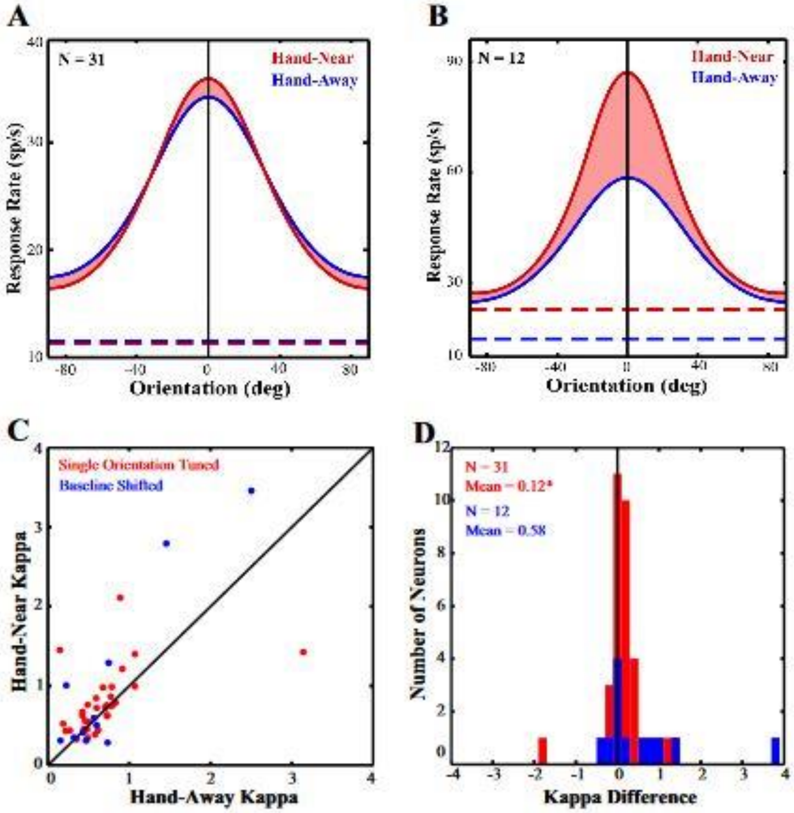

Fig. 7. Curve fit data. The population averages of the tuning curve fits are depicted with the preferred directions aligned to vertical (0°). Baseline firing rates are indicated by the dashed lines. The shaded area between the curves for the Hand-Near (red) and Hand-Away (blue) conditions represents the change in κ (bandwidth) between the conditions. *A*: neurons tuned for one orientation ($n = 31$). *B*: neurons that had a significant baseline shift between the Hand-Near and Hand-Away conditions ($n = 12$). The majority of the neurons included in the dataset fall above the line of unity (*C*), producing a significant sharpening in tuning bandwidth (*D*). The baseline shifted neurons did not show a significant change in κ.

Relationship Between Orientation Selectivity and the Orientation of the Hand

While classic spatial attention does not differentially modulate preferred and nonpreferred stimulus response, such an effect has previously been seen with feature-based attention (Treue and Martinez-Trujillo 1999). The feature-similarity gain model (Treue and Martinez-Trujillo 1999) states that the strongest enhancement occurs when the attended feature is also the neuron's preferred stimulus, decreasing as the difference between the two gets larger. We would expect that, if the feature similarity gain model was responsible for the sharpened tuning seen in the current study, then because the task-relevant touch bar was vertical, neurons preferring vertical orientations should have the greatest enhancement, while neurons preferring horizontal orientations should have the least enhancement.

A similar effect would occur with far surround suppression. More recently, there has been a description of "far surrounds" distinct from "near surrounds" for visual neurons in areas V1 and V2 (e.g., Okamoto et al. 2009; Shushruth et al. 2009). The near surround is based on feedforward and horizontal connections, whereas the far surround is based on feedback from extrastriate areas (Shushruth et al. 2009). While the distance between the touch bar and the RF is large enough that the hand was not within the classical near surround of the V2 neurons, the hand may have fallen within the far surround. The effect of far surround stimulation has been shown to enhance orientation selectivity in area V1 in the cat (Okamoto et al. 2009), when large gratings covered from the center to the far surround. The hand and/or touch bar in our paradigm would be a much weaker stimulus, as it only covers a portion of the far surround, but if a similar effect occurred in V2 in the monkey, then we would once again expect that the magnitude of the sharpened tuning would be strongest when the cell's preferred direction was near vertical.

So the potential effects of far surround suppression and feature-based attention would be the same in the current paradigm: the hand/touch bar are vertically oriented in the surround and would have the greatest effect on cells that preferred that orientation and the least effect on cells that preferred horizontal. Instead we found no significant relationship between the neurons' vertical offsets [abs(90°-preferred orientation)] and κ (tuning bandwidth) for the main population (regression analysis, $n = 31$; $F = 0.06$, $P = 0.81$) or the baseline shifted population ($n = 12$; $F = 0.51$, $P = 0.49$). Therefore, near-hand modulation of visual processing was not dependent on the orientation of the touch bar, either through feature-based attention or far surround suppression.

Qualitative Analysis of Full Population

To determine if the presence of the hand had any effect on all of the neurons, regardless of responsivity and selectivity, we performed the following analysis. As a proportion of the neurons were not significantly visually responsive or orientation selective, we had to first estimate a preferred orientation. For each neuron, all trials (Hand-Near and Hand-Away) were averaged, and the peak response was selected as that neuron's preferred orientation. We then aligned the preferred orientations to produce population averages for Hand-Near and Hand-Away conditions. These population averages were then fit using the von Mises function. These results are depicted in Fig. 8. Across the population of all V2 neurons ($n = 93$), including cells that were not visually responsive or tuned for orientation, there was no evidence of gain modulation as the amplitude did not differ appreciably between the Hand-Near (9.84) and Hand-Away (9.66) conditions. However, there was still a qualitative sharpening of orientation tuning, as κ, the concentration parameter, showed an almost 20% increase in the Hand-Near condition (Hand-Near = 0.429, Hand-Away = 0.359). This pattern of results is similar to that seen in the previous analyses and may likely be driven by the visually responsive, orientation selective neurons.

DISCUSSION

Previous studies on hand-related attention have focused on behavioral benefits only (Abrams et al. 2008; Bekkering and Neggers 2002; Brown et al. 2008; Craighero et al. 1999; Deubel et al. 1998; di Pellegrino and Frassinetti 2000; Fagioli et al. 2007; Reed et al. 2006; Schendel and Robertson 2004); this study provides the first neurophysiological evidence that a nearby hand affects neuronal responses in an early visual processing area. Our results show that hand position, like gaze position, alters visual processing, but they also show that the mechanisms for these two phenomena are somewhat different. The responses of area V2 neurons were preferentially enhanced to the preferred orientation over the orthogonal orientation (Fig. 7*A*) and produced sharpened orientation tuning. These results are not completely consistent with current models of spatial attention or feature-similarity gain. Instead, the results suggest a novel effector-based mechanism which improves sensitivity in early visual processing areas of a feature relevant for that effector, i.e., orientation for reaching and grasping with the hand. Furthermore, we showed that a maintained reach and grasp reduced the variability of V2 neuronal responses to

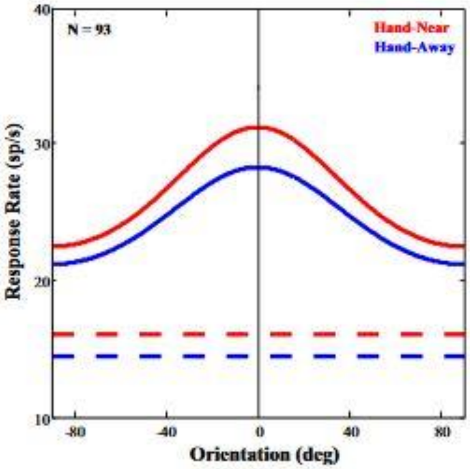

Fig. 8. Effect of hand position across the full population. All neurons, regardless of responsivity, were aligned to the orientation of their maximum response, averaged with each hand condition and then fit with von Mises functions. The curve fits and baseline rates are depicted for qualitative comparison. Curve amplitude did not differ appreciably between conditions (Hand-Near = 9.84, Hand-Away = 9.66). There was, however, a qualitative sharpening of tuning which showed an almost 20% increase in the Near-Hand condition (0.429) over that in the Hand-Away (0.359) condition.

nearby task-irrelevant visual stimuli, a result consistent with attentional deployment near the hand. We hypothesize that this reduction in response variability indicates feedback from parietal areas involved in the fronto-parietal motor network, proprioception and/or encoding of peripersonal space. These hand-specific tuning properties may be functionally advantageous because sharpened orientation tuning would allow for more accurate grasping of nearby objects.

Proposed Neural Mechanism

Prior studies of spatial attention (McAdams and Maunsell 1999; McAdams and Reid 2005; Seidemann and Newsome 1999) have shown that visual neurons undergo gain modulation when attended. However, the results of the present study on hand attention do not show gain modulation. In the main population (without biorientation cells), while the preferred response significantly increased in the Hand-Near condition, the orthogonal response significantly decreased. This was also evident in the population tuning curves (Fig. 7*A*). Thus hand attention sharpened orientation selectivity instead of increasing the gain of the responses across all orientations. Similar effects on direction selectivity have been found in area middle temporal neurons with feature-based attention (Treue and Martinez-Trujillo 1999). But feature-based attention is dependent on congruency between the attended feature, in this case the vertically oriented touch bar and hand, and the preferred orientation of the cell. Instead, we found no relationship between the orientation of the touch bar and the orientation of the visual stimulus within the RF. Therefore, the effects of the hand on visual processing were not driven by feature-based attention either.

A third potential mechanism is based on suppressive surrounds. When a preferred stimulus is presented in the RF and a matching stimulus is presented in the surround, that neuronal response is suppressed by the stimulus in the surround (Akasaki et al. 2002; DeAngelis et al. 1994; Li and Li 1994; Walker et al. 1999, 2000). This surround suppression is thought to be driven by feedforward and horizontal connections. Additionally, a far surround dependent on feedback from extrastriate areas has been described in areas V1 and V2 (e.g., Shushruth et al. 2009). In V1, orientation tuning can be enhanced when a large oriented stimulus covers a cell's classical RF and its far surround (Chen et al. 2005; Okamoto et al. 2009; Orban et al. 1979; Xing et al. 2005). While the hand and touch bar were placed outside the near surround, it is possible they fell within the far surround. However, it is unlikely that the sharpened orientation tuning seen in the Hand-Near condition in the current experiment is due to surround suppression. Surround effects are dependent on the similarity between the stimulus in the surround and the preferred orientation of the cell, but the results of our regression analysis showed no such relationship.

Orientation tuning improved in the Hand-Near over the Hand-Away condition, but this effect was not subserved by spatial attention (gain modulation), feature-based attention, or surround suppression. Therefore, near-hand attention is dependent on a novel mechanism wherein general orientation selectivity is enhanced in the space near the hand. The mechanism operates by enhancing the preferred responses while inhibiting the nonpreferred, which results in sharper tuning.

Proposed Neural Circuitry

As hand-related visual enhancement differs in effect from current models of spatial and feature-based attention, it would need to be served by separate neural circuitry. It has been proposed (Rizzolatti et al. 1987) and demonstrated (Moore and Fallah 2001, 2004; Moore et al. 2003) that recurrent feedback from the oculomotor system modulates visual attention and early visual responses. Reductions in neuronal variability due to movement preparation have been shown to occur in areas ventral premotor (Churchland et al. 2010) and FEF (Purcell et al. 2012). The reduction in response variability found in FEF coincides with reductions in response variability in area V4 prior to a saccade (Steinmetz and Moore 2010). Based on these studies, and given that behavioral studies have shown visual enhancement with both sustained and active arm movements (Abrams et al. 2008; Bekkering and Neggers 2002; Brown et al. 2008; Craighero et al. 1999; Deubel et al. 1998; di Pellegrino and Frassinetti 2000; Fagioli et al. 2007; Festman et al. 2013; Hannus et al. 2005; Langerak et al. 2013; Reed et al. 2006; Schendel and Robertson 2004; Symes et al. 2008), we hypothesize that reductions in V2 neuronal variability in the current study could also reflect feedback from fronto-parietal reaching and grasping networks that would influence subsequent feedforward orientation processing in a recurrent network. In fact, a recent study (Gutteling et al. 2013) showed that temporary inactivation of the anterior intraparietal sulcus (a parietal region associated with grasping movements) using transcranial magnetic stimulation eliminated an increased sensitivity to orientation seen when a grasping vs. a pointing movement was planned.

Areas in posterior parietal cortex both receive visual input to guide actions (sensorimotor integration) as well as providing feedback to extrastriate visual areas (Borra et al. 2008; Passarelli et al. 2011; Prime et al. 2008; Rizzolatti and Matelli 2003). For example, neurons in the anterior intraparietal area are associated with grasping movements and exhibit selectivity for the type, shape, size and orientation of objects that are to be grasped (Monaco et al. 2014; Murata et al. 2000). The inferior parietal lobule, which includes the anterior intraparietal area, also has feedback connections with extrastriate visual areas (Rizzolatti and Matelli 2003) that are thought to be crucial for tactile object recognition. Additionally, area V6A neurons are selective for the orientation of the hand (Fattori et al. 2009), are involved in grasping (Fattori et al. 2010), and have direct connections with area V2 (Passarelli et al. 2011). Therefore, feedback from parietal areas involved with control of the hand should be able to provide the signal that improves orientation selectivity in early visual processing.

These parietal areas receive visual, proprioceptive and motor efference information that could be used to guide (Kalaska 1988; Vesia et al. 2010) the spatial focus for reach-related visual enhancement. First of all, motor efference signals from active motor circuitry, such as motor and premotor cortexes, encode the end point of a reach. Second, proprioceptive processing in somatosensory cortex uses information from the joints, tendons and muscles to determine the location of the arm in space. Third, the visual system encodes the position of a visible arm. For example, vision of a fake arm affects neurons in area 5 that encode the position of the arm (Graziano et al. 2000). Thus area 5 encodes arm position by both vision and proprioception. It is possible that any of these sources could provide the spatial information necessary to guide hand-related attention as the brain regions involved in each are all integrated into the parietal portion of the reaching and grasping network (Buneo and Andersen 2006, 2012; Grea et al. 2002; Pisella et al. 2000). It would be through this integration that reciprocal connections from the parietal areas in the reaching and grasping network may drive hand-related attention. The broader spatial resolution of the motor system would be ideal to improve visual processing of the workspace near the hands, including nearby task-irrelevant stimuli and potential reach targets. In the present study, the arm is visible and the reach is sustained, meaning that visual, proprioceptive and motor efference information is all available. To determine the relative strength of each of these factors in deploying near-hand attention, future studies will need to be conducted with an occluded arm to isolate proprioception from vision of the hand, a fake arm to isolate the contribution of visual information, and with passive arm placement vs. active reaching to disambiguate motor efference feedback.

Other investigations also show that planned hand movements improve visual processing (Craighero et al. 1999; Fagioli et al. 2007; Symes et al. 2008). Specifically, orientation selection was improved when participants were to grasp the visual target (oriented bars) as opposed to when they were to point to the target (Bekkering and Neggers 2002; Gutteling et al. 2011; Hannus et al. 2005). These studies suggest a link between maintaining the plan for hand movement and altered visual processing near the endpoint of the movement. Such a mechanism parallels motor plans in the oculomotor system, deploying attention to the endpoint of the planned saccade (Moore and Fallah 2001, 2004) and enhancing visual responses in area V4 (Moore and Armstrong 2003). Having separate parallel effector-based mechanisms for deploying spatial attention has the advantage that the effectors can more easily be decoupled for movement. That is, we can grab an object while looking elsewhere. In fact, the parietal occipital junction has been implicated in reaching to a peripheral target (Prado et al. 2005), and damage to the posterior parietal cortex results in optic ataxia, an inability to accurately reach to peripheral targets (Carey et al. 1997; Jackson et al. 2005; Milner and Goodale 1995). Thus posterior parietal cortex has separate representations for the spatial locations of gaze and reach targets (Jackson et al. 2009). These parallel effector-based systems could not only maintain separate target locations, but may also provide the signals to improve visual processing of each target.

Note that the full range of the near-hand effect has not yet been determined. The spatial extent of these parietal feedback connections would likely be similar to the spatial extent of the far surround in area V2 (Shushruth et al. 2009), which is also dependent on feedback from extrastriate areas. The spatial extent of the hand effect on orientation selectivity found in this study varied between 8.3 and 14.9 dva, based on the spacing between the hand and the RF borders and the size of the RFs themselves. Alternatively, feedback from parietal cortex may not be spatially limited, but instead extend throughout the ipsilateral visual field. Determining the spatial extent of the near-hand effect may provide further insight into the underlying circuitry.

Oculomotor-Driven Spatial Attention

Prior research and the present results suggest that improved visual processing in near-hand space is due to attentional prioritization of the space near the hand and propose a neural mechanism based upon feedback from parietal areas involved in visual guidance of hand movements. However, similar results may have been found as a result of oculomotor-driven spatial attention. That is not likely due to the following factors. First of all, the stimulus in the RF is task-irrelevant: there is no need for the animals to attend to the oriented rectangle as they make no responses or judgments based upon it. Spatial attention may have been allocated to the touch bar for the animals to make accurate reaches in their visual periphery. However, the orientation stimuli only appear after the touch bar has been grasped. As there was no other location or stimulus requiring attention, oculomotor-driven attention may have been allocated to one of these locations during the task. If the animals had learned to attend to the oriented rectangle to judge the timing of the reward, this attentional allocation would have occurred whether the bar was grasped or not and there would be no modulation between the Hand-Near and Hand-Away conditions. If instead, oculomotor-driven spatial attention was allocated to the touch bar when the hand grasped it, attention would have been allocated away from the oriented stimulus and the recorded neuronal RFs, which would result in lower response rates and poorer orientation selectivity in the Hand-Near vs. Hand-Away conditions, as seen in biased competition (e.g., Desimone and Duncan 1995). Instead, we see increased orientation selectivity when the hand was present, a result opposite to any likely allocation of oculomotor-driven spatial attention.

Attentional Control, Task Design, and Future Studies

Thus this experimental paradigm does not specifically control for the locus of attention beyond requiring gaze fixation. An alternative would have been to use an attentional paradigm such as spatial cueing (e.g., Posner 1980) that controls for spatial attention by allocating attention toward and away from a RF, independent of hand position. While this type of manipulation is useful for determining whether the hand modifies behavior above and beyond that of spatial attention, it would also confound the effects of spatial and hand attention. In an effort to avoid this, the current paradigm was developed to specifically eliminate cues that would allocate spatial attention to the RF stimuli. This allowed for investigating hand attention without the confusion of spatial attention modulations also being involved. So it must be noted that the results of hand attention in this study cannot be directly related to spatial attention. While previous studies in humans have suggested that spatial cueing operates independently of hand attention in speeded reaction time studies (Abrams et al. 2008; Reed et al. 2006), future studies will be needed to determine how they interact on neurons in visual processing areas.

The experimental paradigm used in the present study also sought to dissociate the eyes and the hand and thus did not have the animal reach to the visual stimulus that was presented in the neuronal RF. It is known that, when reaching, the eyes move to the reach target prior to the hand arriving (Ballard et al. 1992; Biguer et al. 1982; Fisk and Goodale 1985; Neggers and Bekkering 2000, 2001, 2002; Prablanc et al. 1979). Since spatial attention is allocated to the target region of an oculomotor plan (Moore and Armstrong 2003; Moore and Fallah 2001, 2004; Müller et al. 2005), even though the eye movement output is inhibited (i.e., with continued fixation), the plan to move the eyes, and thus the shifting of spatial attention, would still occur if a reach was made to the stimulus in the RF. This would again mean that, in the Hand-Near condition, the results would be confounded with those of spatial attention. By placing the touch bar outside of the RF, it ensures that, when a reach occurs, spatial attention is not allocated to the experimental visual stimulus (the oriented bar within the RF). A limitation of this design is that only the effects of a maintained reach have been determined. Since we suggest that improved orientation selectivity near the hand would be useful in guiding the hand for more accurate grasps, it would be important to also determine the temporal aspects of near-hand attention that unfold before and during an active reach to a target in the RF. With the results of this study as a template, future studies could investigate hand attention during a dynamic reach.

Summary and Conclusion

In conclusion, we find that, when a hand is nearby, neurons in area V2 exhibit sharpened orientation selectivity and reduced response variability. It was not dependent on the relationship between the orientation of the touch bar and the oriented rectangle, suggesting it was a general improvement in orientation selectivity instead of feature-based attention or far surrounds suppression. These factors are advantageous for guiding subsequent or on-going hand movements. We propose that parietal areas involved in grasping and encoding peripersonal space are likely involved in deploying near-hand attention, although future work is necessary to support this hypothesis.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: C.J.P., L.E.S., J.D.C., and M.F. conception and design of research; C.J.P. performed experiments; C.J.P. and M.F. analyzed data; C.J.P. and M.F. interpreted results of experiments; C.J.P. prepared figures; C.J.P. and M.F. drafted manuscript; C.J.P., L.E.S., J.D.C., and M.F. edited and revised manuscript; C.J.P., L.E.S., J.D.C., and M.F. approved final version of manuscript.

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Feature integration and object representations along the dorsal stream visual hierarchy

Carolyn Jeane Perry[1,2]* and Mazyar Fallah[1,2,3,4]

[1] Visual Perception and Attention Laboratory, School of Kinesiology and Health Science, York University, Toronto, ON, Canada
[2] Centre for Vision Research, York University, Toronto, ON, Canada
[3] Departments of Biology and Psychology, York University, Toronto, ON, Canada
[4] Canadian Action and Perception Network, York University, Toronto, ON, Canada

Edited by:
Antonio J. Rodríguez-Sánchez, University of Innsbruck, Austria

Reviewed by:
Da-Hui Wang, Beijing Normal University, China
Christopher Pack, McGill University, Canada

***Correspondence:**
Carolyn Jeane Perry, Visual Perception and Attention Laboratory, School of Kinesiology and Health Science, York University, 4700 Keele Street, Toronto, ON M3J 1P3, Canada
e-mail: carolynperry08@gmail.com

The visual system is split into two processing streams: a ventral stream that receives color and form information and a dorsal stream that receives motion information. Each stream processes that information hierarchically, with each stage building upon the previous. In the ventral stream this leads to the formation of object representations that ultimately allow for object recognition regardless of changes in the surrounding environment. In the dorsal stream, this hierarchical processing has classically been thought to lead to the computation of complex motion in three dimensions. However, there is evidence to suggest that there is integration of both dorsal and ventral stream information into motion computation processes, giving rise to intermediate object representations, which facilitate object selection and decision making mechanisms in the dorsal stream. First we review the hierarchical processing of motion along the dorsal stream and the building up of object representations along the ventral stream. Then we discuss recent work on the integration of ventral and dorsal stream features that lead to intermediate object representations in the dorsal stream. Finally we propose a framework describing how and at what stage different features are integrated into dorsal visual stream object representations. Determining the integration of features along the dorsal stream is necessary to understand not only how the dorsal stream builds up an object representation but also which computations are performed on object representations instead of local features.

Keywords: feature integration, dorsal pathway, object representation, motion processing, decision making

INTRODUCTION

Classically, visual processing from the retina onwards is described as following two general principles. One, the processing of different types of visual information is anatomically segregated into two visual streams, and two, each stream is comprised of hierarchical processing where each stage builds upon the previous stage, becoming increasingly more complex. In the ventral pathway this ultimately results in an ability to recognize objects in spite of changes in the surrounding environment or changes in certain object features (i.e., position, orientation, viewing angle, size, etc). In the dorsal pathway this hierarchical processing produces computations of complex motion of objects within the environment around us, either as we are stationary or moving through that environment. Because of this functional separation, there are many models of object representation in the ventral stream (see Peissig and Tarr, 2007 for a review) and many models of motion processing in the dorsal stream (for reviews see Burr and Thompson, 2011; Nishida, 2011), but motion processing research has been mostly devoid of investigations as to the nature or existence of object representations in the dorsal stream. In fact, the vision for action theory of dorsal stream function (Goodale and Milner, 1992; Goodale, 2008, 2013) would suggest that even though there might not be an internal representation of the object as a whole (see Farivar, 2009 for an alternative view), there are representations of features of an object that are relevant for action in real time. Evidence for this comes from spared functions in visual agnosia wherein damage to the ventral pathway eliminates the ability to recognize objects but spares scaling and orientation of the hand when grasping objects (Goodale et al., 1991, 1994; Milner et al., 2012). In addition, parietal regions of the dorsal pathway involved in reaching and grasping show selectivities for the orientation, shape and size of objects (Taira et al., 1990; Gallese et al., 1994; Murata et al., 2000; Fattori et al., 2005).

More recently, investigations into cross-talk between the two visual streams suggest that there are object representations in the dorsal stream (Schiller, 1993; Sereno and Maunsell, 1998; Tsutsui et al., 2001; Sereno et al., 2002; Peuskens et al., 2004; Durand et al., 2007; Lehky and Sereno, 2007; Wannig et al., 2007; Konen and Kastner, 2008; Tchernikov and Fallah, 2010; Perry and Fallah, 2012). It is important to note however, that this object representation would not necessarily be one that gives rise to object recognition, as in the ventral stream. For example, it has been shown that recognition of objects constructed from coherently moving dots (structure-from-motion) is severely impaired in visual agnosiacs (Huberle et al., 2012). These cross-talk studies suggest however, that the motion computations that occur within the dorsal stream can benefit from an intermediate object representation that includes different features of the object. This intermediate object representation would allow for selection of one moving object over others contained within the visual field as seen with flankers and crowding (Livne and Sagi, 2007; Malania et al., 2007; Sayim et al., 2008; Manassi et al., 2012; Chicherov et al., 2014), and superimposed surfaces (Valdes-Sosa et al., 1998; Rodríguez et al., 2002; Mitchell et al., 2003; Reynolds et al., 2003; Stoner et al., 2005; Fallah et al., 2007; Wannig et al., 2007).

In this review we will first give a brief overview of the hierarchical nature of feature processing in both the ventral and dorsal pathways. Various models of the ventral stream have been proposed wherein each integrates features to build up an object representation (scale invariant feature transform (SIFT): Lowe, 1987; Neocognitron: Fukushima, 1975; hierarchical model and X (HMAX): Riesenhuber and Poggio, 1999, and others. For review see Poggio and Ullman, 2013), often based on behavioral and neurophysiological studies (Cowey and Weiskrantz, 1967; Gross et al., 1971, 1972; Dean, 1976; Marr and Nishihara, 1978; Biederman, 1987; Biederman and Cooper, 1991). However, the dorsal stream has generally been relegated to models and algorithms that build up more complex motion representations, from the prior stage's processing (Marr and Ullman, 1981; Adelson and Bergen, 1985; Cavanagh and Mather, 1989; Taub et al., 1997; Krekelberg and Albright, 2005; Pack et al., 2006; Tsui and Pack, 2011; Mineault et al., 2012; Krekelberg and van Wezel, 2013; Patterson et al., 2014; for review see Burr and Thompson, 2011). This may be due to the fact that many behavioral and neurophysiological studies of the dorsal stream have used paradigms that are focused on individual motion features instead of object representations. While feature integration and object representations that lead to object based selection are fairly well understood concepts within the context of the ventral pathway, less is known about how and where these processes occur in the dorsal pathway. We will systematically review the studies that do shed light into which stages of the dorsal stream use object representations vs. motion features. Our aims are to provide a framework for object representations within the dorsal stream and propose where the anatomical locations of these representations may be. We find that motion features but not object representations are used up to global motion processing, as is found in area middle temporal (MT). The next stage of processing, area medial superior temporal (MST), relies on intermediate object representations based on smooth pursuit and glass pattern studies. Finally, intermediate object representations can be used by the decision making circuitry further down the dorsal stream (e.g., area lateral intraparietal (LIP)), which results in faster decisions. It should be noted that the review of literature presented here is strictly limited to those processes that are pertinent to the current discussion and thus is not by any means exhaustive.

HIERARCHICAL VISUAL PROCESSING

DORSAL PATHWAY

The dorsal visual pathway is specialized for motion processing. Much research has determined the hierarchical nature of motion processing wherein each stage builds upon the previous stage's output leading to understanding of the algorithms and connectivity to produce models of the different stages of motion processing (Marr and Ullman, 1981; Adelson and Bergen, 1985; Cavanagh and Mather, 1989; Taub et al., 1997; Krekelberg and Albright, 2005; Pack et al., 2006; Tsui and Pack, 2011; Mineault et al., 2012;

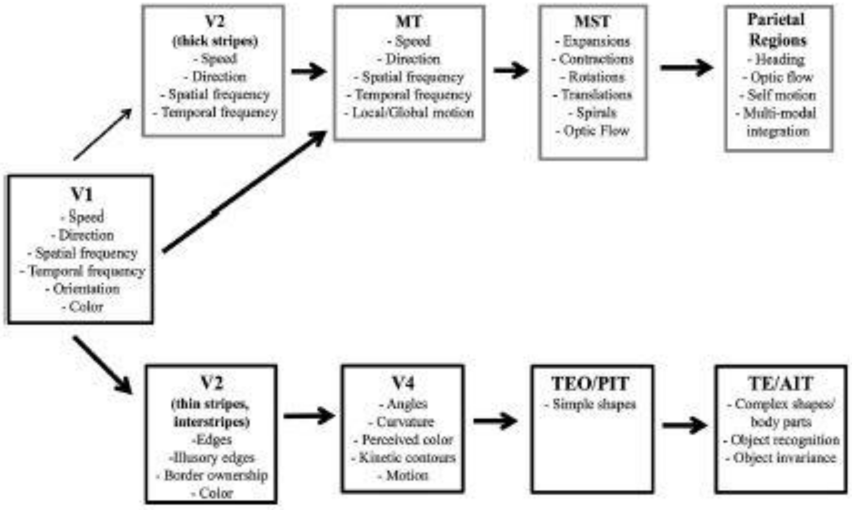

FIGURE 1 | Hierarchy of visual processing in ventral and dorsal streams. Gray boxes, from V2 on, depict select features processed at each region along the dorsal pathway. Black boxes, from V2 on, represent features processed along the ventral pathway.

Krekelberg and van Wezel, 2013; Patterson et al., 2014; for review see Burr and Thompson, 2011). It is important to note that these models focus on the transformation of motion information and not its integration into object representations. Although motion can produce form cues to be used in representing objects in the ventral stream, e.g., structure-from-motion (Johansson, 1973, 1976; Siegel and Andersen, 1988; Bradley et al., 1998; Grunewald et al., 2002; Jordan et al., 2006), object representation in the dorsal stream has not been historically focussed upon. This section briefly reviews the anatomical and functional hierarchy for motion processing (see **Figure 1** for an overview).

V1

Magnocellular cells in the retina and lateral geniculate nucleus (LGN) provide the input to motion processing in the dorsal pathway. These cells are sensitive to low luminance and also to lower spatial and higher temporal frequencies, but are not sensitive to color. They project to layer 4Cα in the primary visual cortex (V1). In V1complex cells are sensitive to the motion of oriented moving edges, bars or gratings (Hubel and Wiesel, 1968; Hubel et al., 1978; Adelson and Bergen, 1985) and show direction selectivity (Orban et al., 1986; Movshon and Newsome, 1996). Complex cells also show the combined spatiotemporal frequency tuning necessary for early speed selectivity (Orban et al., 1986; Priebe et al., 2006). In addition, it has been shown that V1 cells respond only to the local (or component) motion contained in complex patterns (Movshon and Newsome, 1996).

V2

Motion information, from layer 4B in V1, projects to the thick stripes in V2 (Hubel and Livingstone, 1987; Levitt et al., 1994). Although not traditionally thought to play a central role in motion processing, the thick stripes in V2 provide the second largest input to area MT (DeYoe and Van Essen, 1985; Shipp and Zeki, 1985; Born and Bradley, 2005) and it has recently been suggested that directional maps could first emerge in V2 (Lu et al., 2010; however, see Gegenfurtner et al., 1997 for an alternative view).

MT

While MT is the next stage of motion processing after V2, it also receives significant input directly from V1 (Felleman and Van Essen, 1991; Born and Bradley, 2005). MT cells are sensitive to many features associated with 2D motion such as direction (Maunsell and Van Essen, 1983; Albright, 1984; Lagae et al., 1993), speed (Maunsell and Van Essen, 1983; Lagae et al., 1993; Perrone and Thiele, 2001; Priebe et al., 2003; Brooks et al., 2011), and spatial frequency (Priebe et al., 2003; Brooks et al., 2011). The increase in receptive field size and the unique characteristics of MT cells allow for the processing of both local (component) and global (pattern/random dot kinetograms) motion (Pack and Born, 2001; gratings: Adelson and Movshon, 1982; Rodman and Albright, 1989; random dot kinetograms (RDKs): Britten et al., 1992; Snowden et al., 1992). This allows MT to both integrate the motion of multiple dots or incongruent motions created by edges within the same object, and also to separate multiple moving objects from each other. It is important to note that neurons in area MT have been shown to not be color selective (Maunsell and Van Essen, 1983; Shipp and Zeki, 1985; Zeki et al., 1991; Dobkins and Albright, 1994; Gegenfurtner et al., 1994).

MST

With the local and global 2D motion information from area MT, area MST has been implicated in processing complex, 3D motion and in the start of computations of optic flow and self-motion which are dependent on the analysis of 3D motion. Area MST has been anatomically divided into lateral (MSTl) and dorsal (MSTd) regions, where MSTl is thought to be intricately involved in computing the velocity signals of object trajectories used in the maintenance of pursuit eye movements (Tanaka et al., 1993; Ilg, 2008). In comparison, neurons in MSTd are selective for rotations and expansion/contraction motion (Saito et al., 1986), or their combination, aka spiral motion (Graziano et al., 1994; Mineault et al., 2012). MSTd neurons are also selective for optic flow (Duffy and Wurtz, 1991a,b). In fact MSTd neurons can take optic flow and compute the heading or direction of self-motion (Duffy and Wurtz, 1995; Gu et al., 2006).

Beyond MST

After MST, the dorsal pathway continues into the posterior parietal cortex. Motion processing therein involves more complicated optic flow and self-motion patterns, including the motion of objects while the viewer is also moving (Phinney and Siegel, 2000; Raffi and Siegel, 2007; Raffi et al., 2010; Chen et al., 2013; Raffi et al., 2014;). For example, cells in area 7a are tuned to distinguish between *types* of optic flow (Siegel and Read, 1997), and neurons in caudal pole of the superior parietal lobule (Brodmann area 5) (PEc) can combine optic flow information with signals regarding the position of the head and eye (Raffi et al., 2014).

VENTRAL PATHWAY

The ventral visual pathway processes form and color information in a hierarchical stream that builds up separately and then integrates into intermediate and full object representations (Marr and Nishihara, 1978; Biederman, 1987; Biederman and Cooper, 1991) ending with object recognition (Cowey and Weiskrantz, 1967; Gross et al., 1971, 1972; Dean, 1976). Thus, hierarchical models of the object representation and recognition focus on feature integration in the ventral stream (SIFT: Lowe, 1987; Neocognitron: Fukushima, 1975; HMAX: Riesenhuber and Poggio, 1999, and others. For review see Poggio and Ullman, 2013). This section briefly reviews the anatomical and functional hierarchy for building up an object in the ventral pathway (see **Figure 1** for an overview).

V1

Input to V1 in the ventral pathway comes mainly from the parvocellular layers of the LGN with additional magnocellular input (Ferrera et al., 1992, 1994). Parvocellular cells, sensitive to color, high contrasts, and high spatial and low temporal frequencies, project to layer 4Cβ of V1 which is subsequently divided into color blobs and form interblobs. Blobs are color selective but contrast and size invariant (Solomon et al., 2004; Solomon and Lennie, 2005), and untuned for orientation (Livingstone and Hubel, 1987;

Ts'o and Gilbert, 1988; Roe and Ts'o, 1999; Landisman and Ts'o, 2002; Shipp and Zeki, 2002). Interblobs are orientation selective for multiple stimulus types, i.e., edges, bars, gratings (Hubel and Wiesel, 1968; Hubel et al., 1978). Both blobs and interblobs process features without regard to objects, although feedback can produce object-based modulation (Roelfsema et al., 1998) and may be involved in representing objects (Fallah and Reynolds, 2001; Roelfsema and Spekreijse, 2001).

V2

While color processing (interstripes) changes little from that seen in V1, there is notable progression in form processing (thin stripes). V2 neurons are sensitive to the orientation of edges that are defined either by illusory contours or texture (von der Heydt et al., 1984; Peterhans and von der Heydt, 1989; von der Heydt and Peterhans, 1989). V2 cells also encode border ownership (Zhou et al., 2000) which is the first stage of assigning an oriented edge to an object representation. Thus contour-based object representation starts in V2.

V4

Neurons in V4 are tuned for hue that is unaffected by luminance and not limited to a set of colors along the cardinal color axes (red-green, blue-yellow) as seen in V1 (Conway and Livingstone, 2006; Conway et al., 2007). Center-surround interactions produce encoding of perceived color instead of physical color (Schein and Desimone, 1990). Thus, V4 is the first representation of perceived color which is the earliest stage at which color should be incorporated into an ecologically valid object representation.

Form processing in V4 combines multiple, spatially-adjacent, orientation responses seen in V1 and V2 to encode angles and curvatures (Pasupathy and Connor, 1999). These responses advance the nascent object representation from border ownership (Orban, 2008) to responses that are dependent on the placement of the curvature with respect to the center of the shape (Pasupathy and Connor, 2001).

Selection for the orientation of contours created between moving objects (kinetic contours) emerges in V4 (Mysore et al., 2006). Accordingly, a subset of V4 neurons are directionally selective (Ferrera et al., 1992, 1994; Li et al., 2013). Therefore, it should be noted that the intermediate object representations in area V4 can include motion features as well as color and shape.

IT cortex

Inferior temporal (IT) cortex has a range of object property complexity starting with simpler features posteriorly (PIT or TEO: Tanaka et al., 1991; Kobatake and Tanaka, 1994) that increase in complexity as processing moves anteriorly (AIT or TE) to represent objects and perform object recognition (Cowey and Weiskrantz, 1967; Gross et al., 1971, 1972; Dean, 1976). This includes complex shapes, combinations of color or texture with shape (Gross et al., 1972; Desimone et al., 1984; Tanaka et al., 1991), and body parts (faces or hands: see Gross, 2008 for a review). In addition, responses in IT cortex are position and size invariant (Sato et al., 1980; Schwartz et al., 1983; Rolls and Baylis, 1986; Ito et al., 1995; Logothetis and Pauls, 1995) and also invariant to changes in luminance, texture, and relative motion (Sáry et al., 1993). Combined, these characteristics make IT ideal for representing objects despite changes in the surrounding environment and retinal image.

FEATURE INTEGRATION IN THE DORSAL STREAM

Classically, as presented above, it is thought that the ventral pathway is involved in the creation of object representations and categorizations that allow for recognition, object-based selection and decision making processes. Comparatively, the early dorsal stream is most often thought to be specialized for motion processing. Growing evidence suggests however, that processing in the dorsal stream may also allow for object based selection and decision making, which is consistent with later dorsal stream involvement in visumotor guidance, e.g., vision for action (Goodale and Milner, 1992; Goodale, 2008, 2013). In the ventral stream, the object-file theory (Kahneman et al., 1992) has been supported by growing empirical evidence (Mitroff et al., 2005, 2007, 2009; Noles et al., 2005). Object-files collect, store and update information regarding specific objects over time. They are considered to be mid-level representations of objects that do not rely on higher-level object categorizations.

While motion processing studies have focused on individual motion features like direction or speed discriminations of a single moving stimulus, these motion computations could instead be working on intermediate object representations. We hypothesize that later dorsal stream processing occurs on intermediate object representations formed by feature integration instead of on independent motion features. Further we propose that the intermediate object representations also integrate ventral stream information such as color or form. Here we present evidence that support the presence of intermediate (or mid-level) object representations in the dorsal stream, resulting from both ventral and dorsal stream features being integrated into an object-file.

There are multiple ways to investigate the mechanism and timing of feature integration (Cavanagh et al., 1984; Kahneman et al., 1992; Croner and Albright, 1997; Mitroff et al., 2005; Bodelón et al., 2007; Perry and Fallah, 2012 among others). To study feature integration in the dorsal pathway, it is practical to utilize stimuli that activate motion processing regions. Area MT is well known to be involved in direction computations of moving stimuli including the global motion of RDKs (Britten et al., 1992; Snowden et al., 1992). The use of coherently moving, superimposed RDK's that produce the perception of two superimposed objects moving in different directions controls for spatial location, allowing for investigation of object properties (Valdes-Sosa et al., 1998; Rodríguez et al., 2002; Mitchell et al., 2003; Reynolds et al., 2003; Stoner et al., 2005; Fallah et al., 2007; Wannig et al., 2007). In addition, direction discrimination of two superimposed surfaces becomes more difficult as the presentation time decreases (Valdes-Sosa et al., 1998), suggesting that there is a limitation in speed of processing.

Using two superimposed RDKs does, however, create a perceptual illusion known as direction repulsion. Instead of the directions of the two superimposed surfaces being integrated, the directions are perceived as being repulsed away from the real directions of motion (Marshak and Sekuler, 1979; Mather and Moulden, 1980; Hiris and Blake, 1996; Braddick et al., 2002; Curran and Benton, 2003). This phenomenon can also be observed with superimposed gratings under conditions that produce motion transparency (Kim and Wilson, 1996). Direction repulsion is the result of inhibitory, repulsive interactions (Marshak and Sekuler, 1979; Mather and Moulden, 1980; Wilson and Kim, 1994; Kim and Wilson, 1996; Perry et al., 2014) between the directions of motion at the level of global motion processing in area MT (Wilson and Kim, 1994; Kim and Wilson, 1996; Benton and Curran, 2003). We will present studies on the integration of features into the dorsal stream wherein the direction repulsion paradigm is used to distinguish between perceptual alterations in the magnitude of direction repulsion and processing speeds needed to make the perceptual decisions (Perry and Fallah, 2012; Perry et al., 2014). The results provide insight into where features are integrated and when an intermediate object representation is likely to occur.

INTEGRATION OF COLOR

Color is a feature that is processed in the ventral stream through input from parvocellular cells.

Many neuronal studies have found that neurons in the dorsal pathway are not sensitive to color (Maunsell and Van Essen, 1983; Shipp and Zeki, 1985; Zeki et al., 1991; Dobkins and Albright, 1994; Gegenfurtner et al., 1994). In fact, ecologically speaking, color is an irrelevant feature when it comes to processing motion, as in the color of a ball should not matter when attempting to catch it. In spite of this, a number of studies have found that color does in fact alter different aspects of motion processing (Croner and Albright, 1997, 1999; Tchernikov and Fallah, 2010). This would suggest that there is integration of color with motion information in the dorsal stream.

We investigated the effects of color on direction repulsion (**Figure 2**) to determine whether cross-stream feature integration affects direction discrimination, which would support the use of intermediate object representations in motion processing. Two superimposed, coherently moving RDK's were presented, initially for 2000 ms. Each surface could move in one of 12 directions relative to either the vertical or horizontal axes, and both directions created angle differences between the two surfaces ranging between 70° and 110°. If participants correctly determined the directions of both surfaces $\geq 7/8$ times, the presentation time decreased, if participants failed to meet this criterion, the time increased. This process continued until participants completed a double reversal. The time needed to process both surfaces correctly (Presentation Time) was estimated to within ±50 ms. Direction repulsion was calculated as being the angle difference between the perceived directions of motion and the actual directions of the surfaces.

If segmenting the two superimposed surfaces by color (**Figure 2B**) reduced direction repulsion, compared to when both surfaces were the same color (**Figure 2A**), this would suggest that color information from the ventral stream is integrated into motion processing in the dorsal stream prior to or at the time that global motion processing is computed, e.g., the stage where mutual inhibition gives rise to repulsion.

Previous work found that when segmenting coherently moving dots of one color from distractor dots of a different color in the same RDK, color acts as a filter that allows for improvements in direction discriminations, behaviorally in humans and animals (Croner and Albright, 1997) and in the responses of area MT neurons (Croner and Albright, 1999). In this case, color would be gated earlier (in V2) allowing for the suppression of distractor colored input to MT. This effectively allows MT to process the coherently moving dots as if they were appearing alone and in turn improves direction computation. Thus when the distractor color is known, color filters can suppress input to motion processing, a finding that has been replicated in superimposed surfaces (Wannig et al., 2007). Based on these findings, we hypothesized that integrating the color with the motion of the two superimposed surfaces might also allow for the surfaces to be individually filtered by color and in turn reduce direction repulsion.

Surprisingly, when selecting between multiple moving surfaces that are different colors, direction discrimination is unchanged from that seen when both surfaces are the same color (**Figure 3A**). Therefore, the global motion processing of a moving RDK is not performed on intermediate object representations, but instead relies on processing the individual motion features. There is however, a large decrease (43% reduction) in the processing time needed to correctly determine both directions of motion. When both surfaces are the same color, processing both directions took almost 1500 ms, but when the surfaces were different colors, processing time was reduced to ~840 ms (**Figure 3B**; Perry and Fallah, 2012). We have suggested previously (Perry and Fallah, 2012; Perry et al., 2014) that it is most likely processing time is reduced through increasing the speed of the decision making process. **Figure 4A** depicts the steps necessary to perform the task of judging the directions of two superimposed surfaces, and the time needed for each step (Perry and Fallah, 2012). The superimposed dot fields are first segmented (SG) into two surfaces, and then the direction of one surface is processed (D1). This would include (**Figure 4B**) sequential recruitment (Nakayama and Silverman, 1984; McKee and Welch, 1985; Mikami et al., 1986), global motion processing, mutual inhibition (repulsion), and information accumulation for decision making (Shadlen and Newsome, 1996; Huk and Shadlen, 2005; Palmer et al., 2005; Zaksas and Pasternak, 2006; Hussar and Pasternak, 2013). Attention is switched (SW) to the second surface, and then the direction of the other surface is processed (D2). When both surfaces are the same color, correctly processing the direction of both surfaces takes more than 1000 ms (**Figure 4A**), but when the surfaces are segmented by color, the direction of both surfaces is correctly processed in under 1000 ms (**Figure 4C**; Perry and Fallah, 2012), a ~650 ms decrease in processing time. It could be that the time needed to segment (SG) the two surfaces is reduced when each surface is a different color. However, as segmentation is speeded by not more than 25 ms in texture-defined objects (Caputo and Casco, 1999) this is unlikely the sole mechanism underlying such a large decrease in processing time. Alternatively, switching

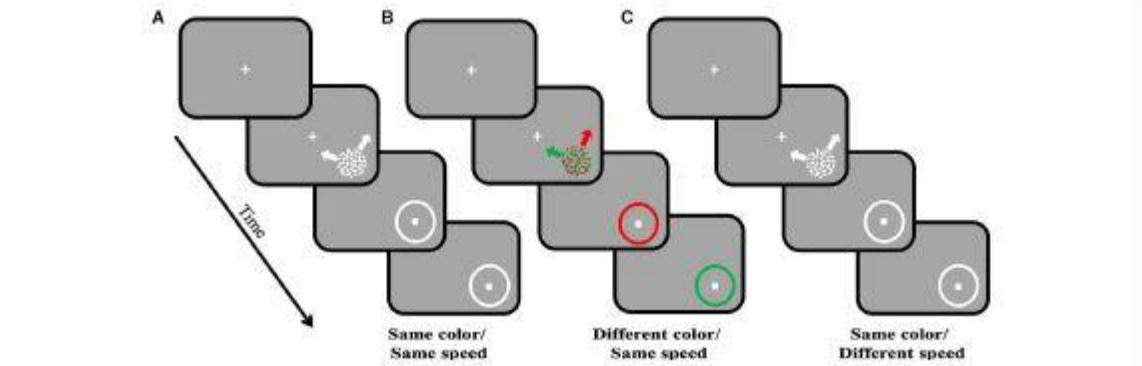

FIGURE 2 | Direction repulsion staircase paradigm. Each trial commences with the appearance of a centrally located fixation point. Once fixation is maintained for 200 ms, the visual stimulus, two superimposed, coherently moving in different directions, random dot kinetograms (RDK's), are presented in the lower right quadrant. In **(A)** the two surfaces are the same color and move at the same speed. In **(B)** the surfaces are the same speed but are different colors, and in **(C)** the surfaces are the same colors but different speeds. The two surfaces are presented for a variable amount of time (staircase procedure). Once they are removed, participants use a mouse to indicate the two directions of motion by clicking on the response circle, once for each direction. In **(B)** participants are required to give the direction for the indicated colored surface in order; the order is randomly assigned between trials. Initially the visual stimulus is presented for 2000 ms, and based on participant's ability to correctly determine both directions of motion, this time will either increase or decrease in successive blocks of trials. Once participants reach a double reversal of presentation times, the time needed to process both directions of motion can be estimated to within ±50 ms. Direction repulsion is calculated as the difference between the angle created by the two clicks on the response circle and the angle created by the two real directions of motion.

attention (SW) between the two surfaces may be speeded when each surface is a different color. Switching attention between serially presented objects in the same location (as in attentional blink) requires only a few hundred milliseconds (Raymond et al., 1992)—but can be attenuated by around 100 ms when targets and probes are less similar (Raymond et al., 1995). Again this mechanism is not sufficient by itself to produce the decrease in processing time. Therefore, there must be a reduction in the time needed to process each direction for such a large decrease in processing time to occur.

In order for color to reduce direction processing time (**Figure 4C**), color input would likely have to affect either the sequential recruitment or decision-making mechanisms including information accumulation (**Figure 4B**) since it does not affect global motion processing (the mutual inhibition circuit). First, MT needs to associate individual dots across two frames (sequential recruitment: Mikami et al., 1986) and pool that information across enough dots (Britten et al., 1992; Snowden et al., 1992) to determine the global motions of the two surfaces. If color worked on sequential recruitment processes, each dot would only need to be compared to dots of the same color across frames, reducing the possibilities by half, speeding up the process immensely. However, by acting as a color filter on sequential recruitment, this color filtering would also be expected to reduce the direction repulsion illusion as each set of colored dots would be processed individually as described earlier (Croner and Albright, 1997, 1999). Instead, there was no change in direction discrimination when two moving surfaces were superimposed (Perry and Fallah, 2012) which indicates that color could not be used to filter out the second surface and reduce the possibilities during sequential recruitment. Alternatively, the integration of color with motion could affect decision-making. Direction discriminations take the information from motion processing in area MT (Albright, 1984; Mikami et al., 1986; Newsome and Paré, 1988; Salzman et al., 1992), and pass it downstream, to areas like LIP, where it is accumulated and a decision threshold reached (Shadlen and Newsome, 1996; Huk and Shadlen, 2005; Zaksas and Pasternak, 2006; Hussar and Pasternak, 2013). If the two surfaces are identical except for their direction of motion, the direction of each surface interferes with the accumulation of direction information for the other surface (**Figure 5A**—Palmer et al., 2005). This interference results in a noisy walk to the decision threshold (accumulator model—Palmer et al., 2005). That is, a decision-making neuron accumulating information to make a decision of rightward motion, would treat input from directional cells preferring rightward motion as positive evidence towards reaching threshold, but input from cells preferring downward motion interferes reducing the accumulated evidence. This produces a noisy walk to threshold. More positive evidence would need to be accumulated before threshold is reached, which means more processing time is needed. With a second feature (color) added to each surface, the two sources of input can be distinguished and selected between. This selection can reduce or eliminate the input from the interfering surface, which reduces the noise in the walk towards the decision threshold, increasing the slope and thus reducing processing time (**Figure 5B**). Therefore, this requires that the accumulation of information for direction discrimination works on intermediate object representations in which color is integrated with motion. This intermediate object representation gives the advantage of allowing for competitive selection of objects (e.g., biased competition: Desimone and Duncan, 1995; Desimone, 1998; Reynolds et al., 2003; Fallah et al., 2007)

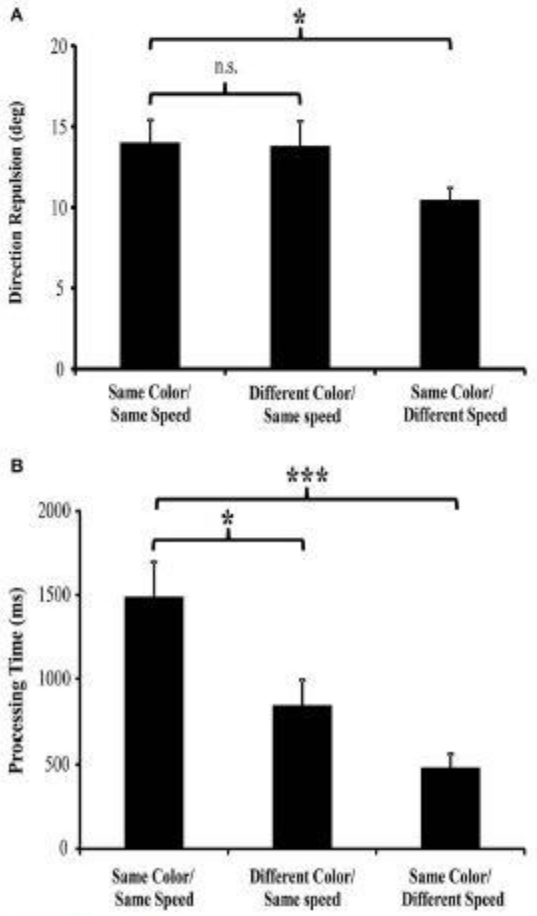

FIGURE 3 | Direction repulsion and processing time results (from Perry and Fallah, 2012; Perry et al., 2014). (A) There was no significant modulation of direction repulsion with the addition of color (Different Color/Same Speed: 13.79° ± 1.54 SEM) when compared to the Same color/Same speed (14.02° ± 1.39 SEM) condition. However, direction repulsion in the Same color/Different speed condition (10.47° ± 0.74 SEM) was significantly less than in the Same color/Same speed condition. **(B)** Processing time in both the Different color/Same speed (842 ms ± 209 SEM) and Same color/Different speed (483 ms ± 81 SEM) conditions was significantly less than in the Same color/Same speed (1488 ms ± 208 SEM) condition.

at later stages of dorsal stream computations such as decision making.

In summary, changes in processing time, due to speeded decision making processes (as proposed above), with no alteration in direction discrimination, suggest that color is integrated into dorsal stream intermediate object representations after global motion processing. This allows for decision-making processes to use those object representations to reach decision thresholds faster.

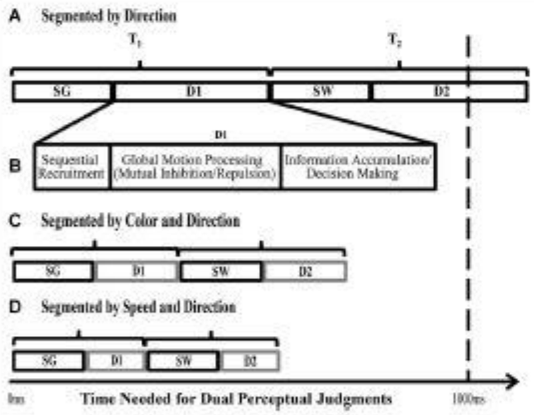

FIGURE 4 | Stages required for direction judgments of two superimposed objects. Based on the task described in **Figure 3**. SG = time needed for *Segmentation* of the two fields of dots into two surfaces, based on different directions of motion, SW = time needed to *Switch* processing from one surface to the other, D1 and D2 = the time needed to process the *Directions* of each superimposed surface (includes sequential recruitment, global motion computation, information accumulation and decision making; shown in detail in **(B)**. **(A)** When the two surfaces differ only in direction, the time needed to complete all the stages involved in the task takes more than 1000 ms on average (Perry and Fallah, 2012). **(B)** Depicts the processes needed to determine the direction of motion of one surface (D1). **(C)** When the surfaces differ in color as well as direction, processing time significantly decreases to less than 1000 ms (Perry and Fallah, 2012). **(D)** When the surfaces differ in speed as well as direction, the time needed to process both directions is reduced further. As the initial segmentation (SG) and attentional switch time (SW) do not appreciably decrease with additional distinguishing features, we propose that the time needed to complete the task decreases as a result of speeded decision making processes (D1 and D2—see text for details) and correspondingly, in **(B)** and **(C)** D1 and D2 are depicted as requiring less time than in **(A)** (adapted from Perry and Fallah, 2012).

INTEGRATION OF SPEED

Unlike with color, previous investigations of direction repulsion have shown that when two superimposed surfaces are of different speeds (Marshak and Sekuler, 1979; Curran and Benton, 2003; Perry et al., 2014) or different spatial frequencies (Kim and Wilson, 1996), direction discrimination improves; direction repulsion is attenuated. Given that spatial frequency, speed and direction are all co-processed within MT (Maunsell and Van Essen, 1983; Albright, 1984; Lagae et al., 1993; Perrone and Thiele, 2001), this is perhaps not surprising. Comparison of movement between two frames give us all three of these features. The spatial location of an object from one frame to the next can be used to calculate direction and speed, while spatial frequency can be extracted from the number of times an object appeared over a given distance. So this information comes in together as a single input and does not require integration; it is inherent based on the movement of the stimulus. Consistent with this, neurons in MT are simultaneously selective for multiple motion features, such as speed and direction. Consequently, a neurons response to one feature (direction for example) can be altered by the response of that same neuron to a different motion feature (such as speed), and as a

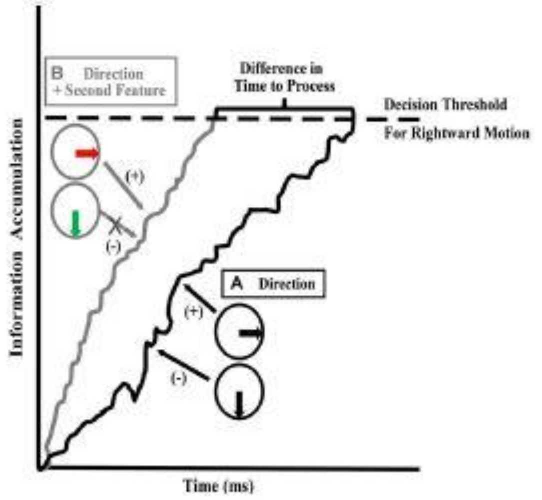

FIGURE 5 | Information accumulation and decision threshold. Hypothesized stage at which processing time is reduced. Areas downstream of MT accumulate motion information in order to arrive at a decision. The figure depicts information accumulation for the rightward direction. When accumulating evidence in support of the rightward direction (+), the evidence is reduced by noise created by the presence of the other surface (–). **(A)** When only direction (one feature) differs between the surfaces, interference between the directions of each surface creates a noisy walk: i.e., incongruent input that reduces the accumulated evidence for the rightward direction. This extends the time needed to reach the decision threshold. **(B)** When direction and a second feature such as color or speed differs between the surfaces, the second feature can be used to reduce the interference caused by the other surface (by allowing competitive selection to override the influence of the second surface) in the walk to threshold, thus reducing the time needed to reach a decision threshold.

result can be considered to be conjoined, i.e., the processing of one feature affects processing of a different feature (Maunsell and Van Essen, 1983; Albright, 1984; Lagae et al., 1993; Perrone and Thiele, 2001). Based on co-processing, motion processing is reflective then of the presented combination of conjoined features. This occurs without the need for a bound object representation. For example, perception of speed can be distorted under a number of different viewing conditions (Krekelberg et al., 2006a,b). A reduction in contrast reduces perceived speed in slow moving stimuli (Thompson, 1982) and increases perceived speed of fast moving stimuli (Thompson et al., 2006). Perceived speed is also dependent upon spatial frequency (Priebe et al., 2003). And finally the perception of direction is sensitive to motion processing conjunctions: direction discrimination becomes more accurate when superimposed surfaces are different speeds (Marshak and Sekuler, 1979; Curran and Benton, 2003; Perry et al., 2014) or different spatial frequencies (Kim and Wilson, 1996).

These examples suggest that direction computation occurs on conjoined dorsal stream features such as direction and speed or direction and spatial frequency information. Using the same paradigm as described in section Integration of color, but with surfaces that are segmented by differences in speed (**Figure 2C**), we tested whether speed, while conjoined with direction for discrimination, could also be used as a distinguishing feature in intermediate object representations like color is (Section Integration of color) and similarly speed up decision making circuitry (Perry et al., 2014). As with color (Perry and Fallah, 2012), we found that differences in the speeds of two superimposed surfaces decreased processing time (**Figure 3B**). In fact, processing time was lower than that seen when the surfaces were segmented by color (Speed-segmented: 483 ms vs. Color-segmented: 841 ms). It could be that velocity, conjoined speed and direction, is the signal that becomes a part of the object representation. If that were the case however, processing time would not be altered as velocity would comprise a single object feature and there would be no other independent feature for use by selection mechanisms to reduce the noise in the walk to threshold (**Figure 5**) and reach a decision threshold more quickly. Instead these results suggest that speed information is treated as an independent feature in an intermediate object representation that is used by decision making circuitry to speed processing times (**Figure 4D**; Perry et al., 2014) similar to the effect of color (Perry and Fallah, 2012). Independent in this case simply means that in spite of the fact that speed is co-processed with direction, and their conjunction attenuates direction repulsion during direction computations, speed *alone* can be utilized as a distinguishing feature to select between the object representations when accumulating information for the perceptual decision.

Unlike the effects of color integration, speed differences reduced direction repulsion which further supports that direction discrimination is modulated by other motion features that are conjoined (processed together) in the dorsal pathway. However, ventral stream features, such as color, do not affect motion until after global motion processing occurs. It has been suggested (Marshak and Sekuler, 1979; Mather and Moulden, 1980) that direction repulsion arises due to inhibitory interactions between populations of neurons, a theory recently formalized (**Figure 6**—adapted from Perry et al., 2014). In mutual inhibition, the responses of neurons to one direction are inhibited by the responses of neurons to a second direction (**Figures 6A,B**) and the amount of inhibition determines the magnitude of direction repulsion. As the angle between the two directions increases, direction repulsion diminishes (Marshak and Sekuler, 1979; Mather and Moulden, 1980) which suggests that mutual inhibition is dependent upon the overlap in tuning between the neurons responding to the two directions (**Figures 6A,B**). When the surfaces are identical except for direction (**Figure 7A**) mutual inhibition and direction repulsion is based solely on the overlap between the tuning curves. Since color is not integrated into motion until after this computation, differences in color do not change the overlap between the two populations and direction repulsion is unaffected (**Figure 7B**). However, when the surfaces are segmented by dorsal stream features such as speed (**Figure 7C**) or spatial frequency (**Figure 7D**) the overlap is reduced due to tuning in multi-dimensional feature space and direction repulsion is decreased. Dorsal stream features are conjoined to produce

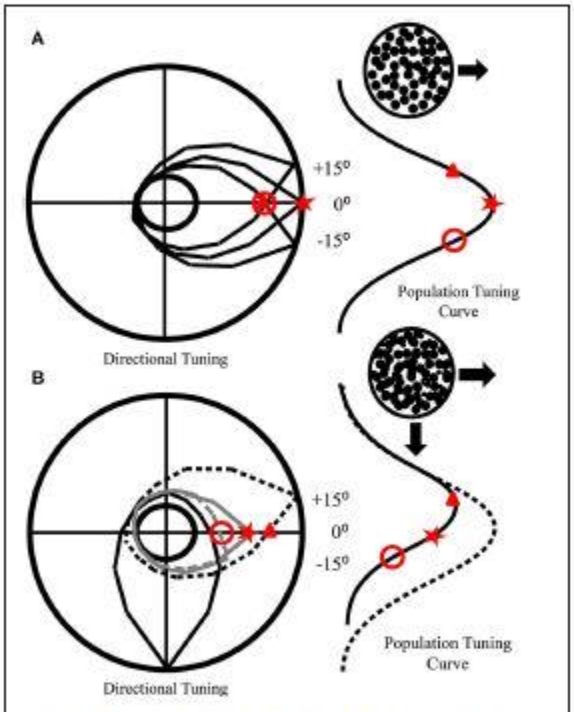

FIGURE 6 | How mutual inhibition produces direction repulsion. **(A)** Individual tuning curves of neurons preferring the direction of motion (0°) and nearby directions (±15°) are presented in the polar plot. The population tuning curve that arises from their responses to rightward motion is also depicted. **(B)** The addition of a second surface moving downwards produces inhibition of other directional neurons. This inhibition drops off as the difference in preferred directions increases. Hence, the −15° neuron is more strongly inhibited (gray dashes) than the 0° neuron (solid gray), while the +15° neuron (black dashes) is not inhibited. This produces a population tuning curve that is shifted away (solid black) from the real direction of motion (dotted line). As the inhibition is mutual, a similar shift would occur for neurons responding to downward motion.

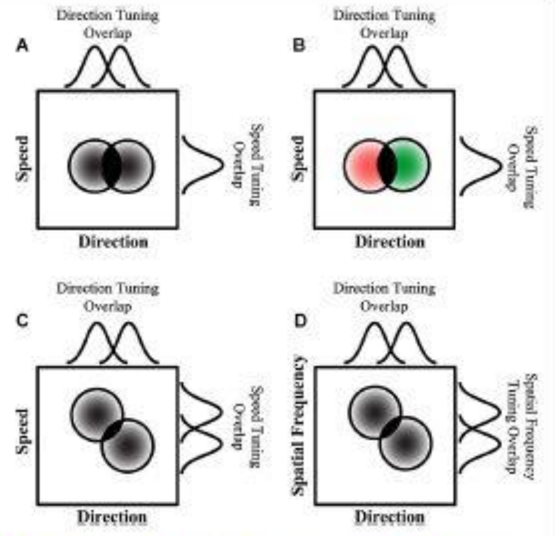

FIGURE 7 | How additional features affect mutual inhibition and direction repulsion. **(A)** Two surfaces that only differ in direction produce direction repulsion whose magnitude is dependent on the area of overlap between their tuning curves (directional tuning curves—top, and two dimensional tuning curves—circles, overlap depicted in solid black). **(B)** When the surfaces are different colors, there is no change in the direction tuning curve overlap which is consistent with color not affecting direction repulsion. However, when a second motion feature that is co-processed with direction, such as speed **(C)** or spatial frequency **(D)**, the population of neurons responding to each direction is segregated based on both features and as a result there is a reduction in the two-dimensional tuning curve overlap (solid black overlap in circles) which results in attenuated direction repulsion (overlaps in **(C)** and **(D)** are smaller than in **(A)** and **(B)**. **(A–D)** The circular plots represent multi-dimensional tuning, while the curves above and to the right of each plot represent the tuning in each dimension respectively (adapted from Perry et al., 2014).

multi-dimensional tuning and thus do not require integration into an object representation. This is supported by the fact that color, which is part of the object, does not affect this circuitry (**Figure 7B**). Overall, as direction repulsion is thought to arise from a local circuit in area MT governing global motion processing, the formation of an intermediate object representation that includes speed and color information likely occurs after that stage.

INTEGRATION OF FORM

Artists have long known how to depict motion in still images using features such as speed-lines (the "wake" of a moving object). These non-moving streaks have been shown to affect human perception of motion (Geisler, 1999; Burr and Ross, 2002) by providing a direction input along the orientation of the streak which can either enhance discrimination of a congruently moving stimulus or interfere with incongruent or orthogonal direction discrimination. This motion streak effect is thought to occur as early as V1, supported by computational (Geisler, 1999) and neurophysiological (Geisler et al., 2001) studies. Thus, speed-lines affect the perception of direction by, in effect, producing motion input for use along the dorsal stream. Similarly, glass patterns, paired dots that appear and disappear randomly on a display, give rise to the perception of bistable directions of motion along the contour of the pattern in the absence of underlying motion signals (Glass, 1969; Ross et al., 2000). These spatial patterns produce motion signals that are represented along with magnocellular motion signals in area MT and ST (Krekelberg et al., 2003), and integrate with real motion signals in perceiving direction (Burr and Ross, 2002).

In essence, these form inputs to the dorsal stream provide the equivalent of motion input to mid-level areas in the dorsal stream starting in area MT (Krekelberg et al., 2003). It is likely that the motion produced by these form inputs is then integrated into the object file as motion features (speed, direction) instead of form features. These effects differ from color which is integrated as its own feature into an intermediate object representation later in the dorsal stream hierarchy. That still leaves an open question as to whether other ventral stream features that do not give rise to the perception of motion could also be integrated into dorsal stream object files. Other features could be tested with the same direction repulsion paradigm as described earlier. For example, direction repulsion and processing time could be determined for surfaces distinguished by different contrast levels. As the dorsal stream saturates at much lower contrast than the ventral stream (Heuer and Britten, 2002), if decision-making processing time is affected by contrast differences that are above the saturation point for the dorsal stream, then the dorsal stream object file integrates ventral stream contrast information. Additionally, would a size difference between the dots of the two surfaces result in speeded perceptual decision-making similar to the effects of color? The effects of shape (varying the form of the RDK elements, i.e., dots vs. squares vs. triangles) also needs to be tested.

INTERMEDIATE OBJECT REPRESENTATIONS IN THE DORSAL STREAM

Thus far, the evidence presented suggests two main concepts. First, global direction computations are based on the co-processing of dorsal stream motion information. Surfaces segmented by speed or spatial frequency (but not color) result in an improvement in direction computations and thus an attenuation of direction repulsion. Secondly, both speed and color are integrated into a dorsal stream intermediate object representation (or object file) which in turn is used by decision making processes to speed processing times. Speed and direction would need to be independent features in a dorsal stream object file, because this allows for awareness of changes in one dimension independent of the other velocity feature. For example, a moving ball provides velocity information (conjoined speed and direction). If it changes speed but continues to move in the same direction, the population of MT cells that would respond to the conjoined speed/direction selectivity changes. Without independence of these motion features in the object representation, switching underlying MT populations would mark a change in all of the conjoined features. Instead, with independence observers are aware of the speed changing while the direction does not. Thus a dorsal stream object file can denote changes in speed or changes in direction independently. We propose that the dorsal stream object file would also include ventral stream information such as color. Decision-making then works on object files instead of direction information alone, and therefore distinguishing features in the object files can be used to selectively focus decision-making on the relevant direction information.

The features that are placed in the object file are dependent upon which features are important to completing the specified task (Harel et al., 2014). Theoretically then, using the direction repulsion paradigm as an example, task relevant would mean that any feature that distinguished the two superimposed surfaces from each other would be a feature added to the object file. This is what occurred with both speed and color, and therefore it would be logical to extrapolate that other task relevant features would also be included in an object file. We have previously suggested (Section Integration of form) how other form features, such as size, shape and contrast, could be tested for integration into a dorsal stream object file.

We propose that global motion processing occurs on conjoined motion features such as speed and direction, whereas the accumulation of perceptual information to reach a decision is performed on intermediate object representations. While these hypotheses are yet to be directly tested at the neurophysiological level (e.g., in animal models), in the next section we propose the likely neural substrates and dorsal stream areas subserving each of these processes, based on known properties of these areas.

POSSIBLE LOCATION OF OBJECT REPRESENTATIONS IN THE DORSAL STREAM

Figure 8 provides an overview of processing along both the ventral and dorsal pathways with known object representations in the ventral stream and hypothesized object representations in the dorsal stream. Given that object files are considered to be mid-level representations, and are found at intermediate stages of ventral stream processing, they should similarly be found in and around area MT in the dorsal stream. Perceived color is processed in area V4, and thus color processing would need to reach this stage before being incorporated into an object representation in either the ventral or dorsal stream. Color is not integrated with direction prior to direction computation circuits in MT as the addition of color did not reduce direction repulsion. However, color and speed *did* reduce the time needed to fully process both directions of motion. Therefore while global motion direction computations which are computed in area MT are not performed on object files, color and speed are integrated into an object file after direction computation in MT.

Evidence of motion computations relying on object representations comes from smooth pursuit. Color is known to affect smooth pursuit eye movements to moving surfaces (Tchernikov and Fallah, 2010) which are dependent upon the processing of velocity signals for both the surface and the background in area MST (Dürsteler and Wurtz, 1988; Komatsu and Wurtz, 1988, 1989; Thier and Erickson, 1992; Ilg, 2008). Intuitively, eye movements should be color blind. Instead color biases selection of one superimposed surface over the other based on a color hierarchy, and the competition between the two colored surfaces modulates the speed of pursuit (Tchernikov and Fallah, 2010). This suggests that it is not only the reaching and grasping systems later in the dorsal stream that work on object features, but as part of the vision for action pathway, smooth pursuit computations are based on object files. Thus the integration of color into the dorsal stream object file may occur as early as area MST, or at least before the frontal eye fields (FEF) generate the motor plan.

After MST in the dorsal stream, area LIP in the parietal lobe has been shown to be involved in the accumulation of motion information for perceptual decision-making (Shadlen and Newsome, 1996; Huk and Shadlen, 2005; Palmer et al., 2005). This stage of processing works on object files as color and speed differences reduce the time needed to reach the decision threshold. Beyond this stage, a number of areas in the posterior parietal cortex are selective for objects, a function necessary for visuomotor guidance of grasping. Such object selectivity has been found in areas anterior intraparietal (AIP) and 7a (Taira et al., 1990; Murata et al., 2000; Phinney and Siegel, 2000).

This hypothetical framework for object representations in the dorsal stream (**Figure 8**) can be tested in future neurophysiological studies. Specifically, global motion processing in area MT neurons and the concomitant direction repulsion of the population tuning should not be affected by the addition of color differences. Whereas responses of neurons in area MST that give rise to pursuit motion should be modulated by the color differences in superimposed surfaces (Tchernikov and Fallah, 2010). Finally, decision-making neurons in area LIP should show steeper slopes and reach decision thresholds faster when a second distinguishing feature such as color or speed is present.

OTHER EVIDENCE FOR DORSAL STREAM OBJECT REPRESENTATIONS

Other studies have shown selection of objects in the dorsal stream that upon reflection would support intermediate object representations. For example, judging the direction of a brief translation of one of two counter-rotating superimposed surfaces is improved when that surface is selected by color (Valdes-Sosa et al., 2000), an effect the authors attributed to the use of object files by the dorsal stream. The different motions between the two surfaces provides noise in accumulating direction information, but reducing noise through selection of that object file would speed processing such that the decision threshold could be reached during the brief translation period. Similarly, if the object file is selected by a transient motion feature capturing attention, selection of that object file is maintained and again improves the discrimination of a subsequent brief translation (Reynolds et al., 2003) along with modulating the visually evoked N1 component, a marker of selective attention (Pinilla et al., 2001; Khoe et al., 2005). In fact, when one of two superimposed surfaces is selected by a color segmentation cue, the selective advantage for processing brief translations of that surface survives the removal of color differences (Mitchell et al., 2003), once again showing that selection is maintained via an object file. In fact, concurrent judgments of simple form (square or circle) and motion are impaired when made across two superimposed surfaces compared to when they are made for the same surface (Rodríguez et al., 2002). This is similar to Duncan (1984), which showed that attending to an object representation allows judgments of multiple ventral stream form features "for free" but that there was a cost associated with having to make judgments across two superimposed objects. Together, these studies suggest that there are also object representations in the later stages of the dorsal stream. Furthermore, competitive selection processes work not only on objects in the ventral stream (Desimone, 1998; Reynolds et al., 2003; Fallah et al., 2007), but also on objects in the dorsal stream.

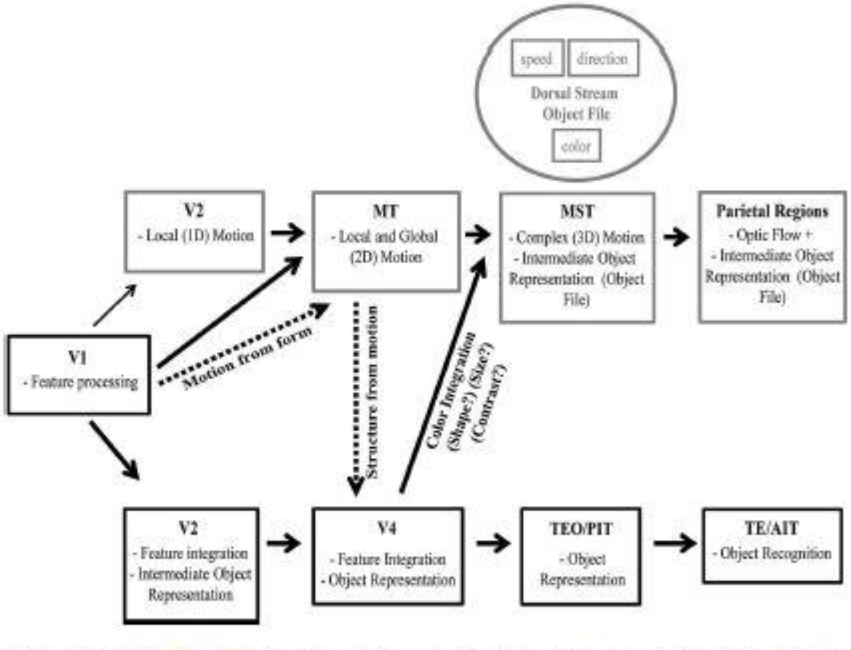

FIGURE 8 | Intermediate object representation model. Visual processing along the ventral stream is depicted along with known object representations starting in area V2. We also depict visual processing along the dorsal stream with the hypothetical stages which process dorsal stream object files. As visual processing progresses along the dorsal pathway stimulus parameters are calculated and this information is provided to area MT. In MT, information regarding speed, direction and spatial frequency are co-processed forming multidimensional selectivity. After local and global motion processing circuits in MT, an intermediate object representation is formed that incorporates independent motion features (such as speed and direction) and ventral stream features (such as color, with other features such as shape and size to be determined). This intermediate object representation is in place prior to decision making circuitry that represents motion or guides action.

VISION FOR ACTION

The dorsal stream object representation would not need to progress to the level of object recognition however. As already discussed, the vision for action theory states that the dorsal pathway's reaching and grasping system uses object features as a means of guiding action in real time. With damage to the ventral stream, patients can still orient their hand and scale their grip according to the orientation and shape of the item to be grasped. This does not require that the object is fully processed through to recognition, just that a list of features associated with a specific object be available for selection (Freiwald, 2007). An object file would provide such a list from which different features could be used to select the correct object among multiple, even superimposed, objects (Valdes-Sosa et al., 1998, 2000; Pinilla et al., 2001; Wannig et al., 2007; Perry and Fallah, 2012; Perry et al., 2014).

DORSAL TO VENTRAL INTEGRATION

Our proposal is that the dorsal stream integrates features, from both the dorsal and ventral pathways, into an object representation that can be used by decision making circuitry (contained within the dorsal stream) for selection purposes. A similar process occurs in the ventral stream, and it is not only features processed within the ventral stream that are integrated to form object representations used in object recognition and decision making. As early as V4, motion information from the dorsal pathway is used to define stationary edges that occur between moving stimuli (kinetic boundaries—Mysore et al., 2006). However, MT also plays a role in segmentation mechanisms (Born and Bradley, 2005) as a necessary component of surface reconstruction (Andersen and Bradley, 1998). This is what allows MT to separate the motion of multiple moving stimuli from each other (Snowden et al., 1991; Stoner and Albright, 1996), even under conditions of occlusion (Nowlan and Sejnowski, 1995), and to separate moving objects from background (Bradley and Andersen, 1998; Born and Bradley, 2005). Similarly, superimposed dots patterns, moving in opposite directions and moving at variable speeds can be integrated to create a percept of a rotating cylinder. This indicates that processing along the dorsal pathway also allows for perception of 3D structures (Bradley et al., 1998; Dodd et al., 2001). Moving dots are also known to give rise to human shape percepts. Moreover, this perception of biological motion goes beyond shape and form processing. Higher order features, such as gender, are also derived from biological motion (Barclay et al., 1978; Mather and Murdoch, 1994; Jordan et al., 2006). As gender is derived from the global, not local motion, and gender adapts with prolonged exposure to biological motion (Jordan et al., 2006), this occurs at a stage beyond area MT. Biological motion is represented in the superior temporal polysensory area (STP: Perrett et al., 1989) and as such is an object representation later along the dorsal stream, which gives rise to gender representation.

ALTERNATIVE LOCATION FOR THE OBJECT REPRESENTATION

While evidence supports the dorsal stream decision-making processes working on object representations, the site for these representations are unknown. We have suggested that intermediate object representations are built up at later stages in the dorsal stream (**Figure 8**). However, these decision making circuits in the dorsal stream could instead be modulated by object representations contained in the ventral pathway.

For this to occur, motion information would have to be a tag (e.g., Finger of INSTantiation (FINST): Pylyshyn, 1989, 1994) associated with object processing in the ventral stream, which would then have to be passed back to the dorsal stream in time for direction decisions to be made. While this is possible, Occam's razor suggests the more parsimonious explanation of dorsal stream object files is likely the correct one. There is a means of testing whether intermediate object representations occur in the dorsal stream. As visual agnosiacs have damage to the ventral stream but retain certain form information used to guide grasps, they could be tested to see whether motion decision-making could be sped up without ventral stream object representations. If so, then there must be dorsal stream intermediate object representations separate from those in the ventral stream. Such intermediate object representations would not give rise to recognition but would incorporate the form features maintained in the dorsal stream to provide real-time visual guidance for actions such as hand orientation, grip scaling, and pincer grip locations (Goodale et al., 1991, 1994; Milner et al., 2012). Note that even if the intermediate object representation was to be created in the ventral stream, it would still be used by decision-making areas in the dorsal stream. The areas that give rise to the object representation would change, but the later stages of dorsal stream processing would still be dependent on object representations, not just motion information.

CONCLUSIONS

We have provided a framework for not only how the dorsal stream extracts motion information but also builds up an object representation that is used in decision making processes. The hierarchical nature of visual processing, in both the ventral and dorsal pathways, provides the basis for where an object representation in the dorsal pathway would exist. Both color and speed information, as independent object features, are integrated into motion processing circuits beyond direction computations (such as in area MT) and prior to decision making and attentional selection (such as in area LIP). In fact, color-dependent smooth pursuit may indicate an intermediate object representation occurs as early as area MST. It is also likely that later parietal areas that guide grasping, such as AIP, may also contain the requisite circuitry for intermediate object representations in the dorsal stream. We have suggested that this object representation would not give rise to object recognition as in the ventral stream but instead would contain a list of object features upon which decisions could be made and actions performed. Object files are a possible mechanism through which information necessary for dorsal stream decision making and selection could be collected and updated as needed. The use of dorsal stream information for the creation of objects in the ventral pathway supports our proposal of parallel mechanisms existing in the dorsal stream. Testing visual agnosiacs on dorsal stream decision making, requiring the use of object representations, would be a way to determine if the dorsal pathway alone can support these intermediate object representations.

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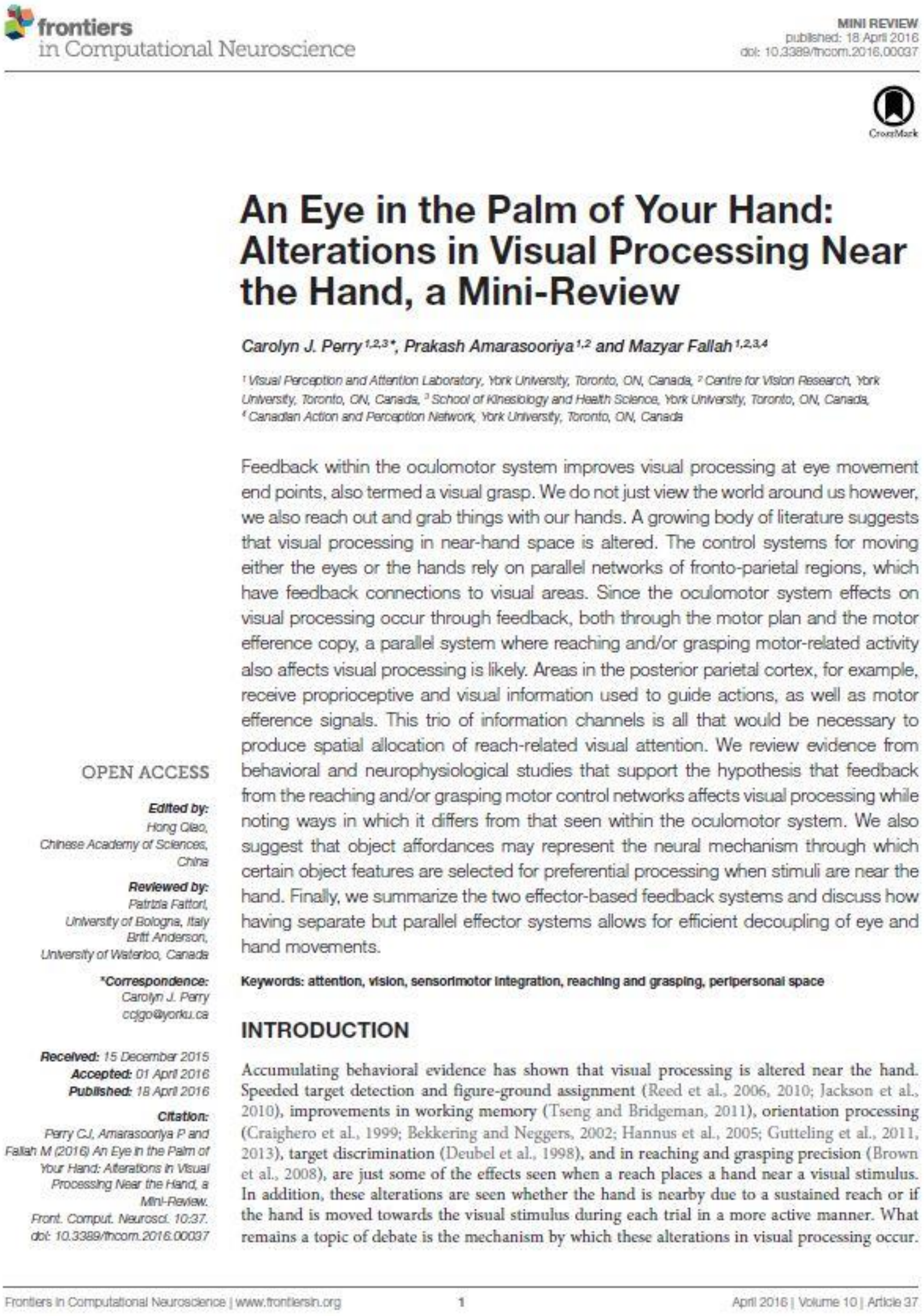

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An Eye in the Palm of Your Hand: Alterations in Visual Processing Near the Hand, a Mini-Review

Carolyn J. Perry[1,2,3]*, *Prakash Amarasooriya*[1,2] *and Mazyar Fallah*[1,2,3,4]

[1] *Visual Perception and Attention Laboratory, York University, Toronto, ON, Canada,* [2] *Centre for Vision Research, York University, Toronto, ON, Canada,* [3] *School of Kinesiology and Health Science, York University, Toronto, ON, Canada,* [4] *Canadian Action and Perception Network, York University, Toronto, ON, Canada*

Feedback within the oculomotor system improves visual processing at eye movement end points, also termed a visual grasp. We do not just view the world around us however, we also reach out and grab things with our hands. A growing body of literature suggests that visual processing in near-hand space is altered. The control systems for moving either the eyes or the hands rely on parallel networks of fronto-parietal regions, which have feedback connections to visual areas. Since the oculomotor system effects on visual processing occur through feedback, both through the motor plan and the motor efference copy, a parallel system where reaching and/or grasping motor-related activity also affects visual processing is likely. Areas in the posterior parietal cortex, for example, receive proprioceptive and visual information used to guide actions, as well as motor efference signals. This trio of information channels is all that would be necessary to produce spatial allocation of reach-related visual attention. We review evidence from behavioral and neurophysiological studies that support the hypothesis that feedback from the reaching and/or grasping motor control networks affects visual processing while noting ways in which it differs from that seen within the oculomotor system. We also suggest that object affordances may represent the neural mechanism through which certain object features are selected for preferential processing when stimuli are near the hand. Finally, we summarize the two effector-based feedback systems and discuss how having separate but parallel effector systems allows for efficient decoupling of eye and hand movements.

Keywords: attention, vision, sensorimotor integration, reaching and grasping, peripersonal space

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Hong Qiao,
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China

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University of Bologna, Italy
Britt Anderson,
University of Waterloo, Canada

***Correspondence:**
Carolyn J. Perry
ccjgo@yorku.ca

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INTRODUCTION

Accumulating behavioral evidence has shown that visual processing is altered near the hand. Speeded target detection and figure-ground assignment (Reed et al., 2006, 2010; Jackson et al., 2010), improvements in working memory (Tseng and Bridgeman, 2011), orientation processing (Craighero et al., 1999; Bekkering and Neggers, 2002; Hannus et al., 2005; Gutteling et al., 2011, 2013), target discrimination (Deubel et al., 1998), and in reaching and grasping precision (Brown et al., 2008), are just some of the effects seen when a reach places a hand near a visual stimulus. In addition, these alterations are seen whether the hand is nearby due to a sustained reach or if the hand is moved towards the visual stimulus during each trial in a more active manner. What remains a topic of debate is the mechanism by which these alterations in visual processing occur.

A number of studies suggest that visual processing near the hand is altered through spatial attention selection mechanisms (di Pellegrino and Frassinetti, 2000; Schendel and Robertson, 2004; Reed et al., 2006, 2010; Abrams et al., 2008). These studies have hypothesized that populations of fronto-parietal bimodal neurons underlie enhanced visual selection in near-hand space; however, these neurons are also thought to influence near-hand processing in the absence of spatial attention influences (Brown et al., 2008). More recently, enhanced magnocellular processing has been postulated as an alternative explanation for the near-hand effect (Gozli et al., 2012). For this review, we investigate the hypothesis that these effects are driven by a novel, effector specific, attentional selection mechanism that is different from either oculomotor-driven visual spatial or feature-based attention, and is mediated by feedback from fronto-parietal regions involved in reaching and grasping networks. We will first review the anatomical similarities between the oculomotor and the reaching/grasping networks, and provide evidence of feedback influences within the oculomotor system. We will then compare the neurophysiological alterations in visual processing near the hand to alterations in visual processing due to the oculomotor system and provide supporting evidence of feedback influences in the reaching and grasping system. We suggest that links between the visual system and the motor systems could drive enhanced processing of action-relevant object features, but that de-coupled eye and hand movements indicate the need for separate, effector-based selection mechanisms.

NEURAL CIRCUITRY

The reaching, grasping, and oculomotor systems all involve parallel networks of fronto-parietal areas (**Figure 1**). A dorsomedial stream, projecting from visual area V6 (Rizzolatti and Matelli, 2003; Passarelli et al., 2011), consisting of the medial intraparietal (MIP) area and area V6A in the superior parietal lobule (SPL), along with the dorsal premotor cortex (PMd) in the frontal lobe, which forms what is thought to be the neural network for reaching in the non-human primate (Caminiti et al., 1996; Culham et al., 2006; Filimon, 2010), with homologs in humans (Culham et al., 2006; Filimon, 2010). As with reaching, it has been suggested that there is a parallel dorsolateral circuit specialized for grasping (Fagg and Arbib, 1998; Luppino et al., 2001; Filimon, 2010) that projects from visual area MT/V5 (Rizzolatti and Matelli, 2003), and that this circuit is mainly dependent upon connections between the anterior intraparietal (AIP) region in the inferior parietal lobule (IPL) and the ventral premotor cortex (PMv), with homologous areas in humans (Fagg and Arbib, 1998; Culham et al., 2003, 2006; Frey et al., 2005). The reaching and grasping circuits however, appear to not be as completely functionally distinct as once thought as recent work has also found grasping related activity in the dorsomedial stream in non-human primate (Raos et al., 2003, 2004; Fattori et al., 2009, 2010, 2012) and human populations (Gallivan et al., 2011; Monaco et al., 2011). In fact, it has been suggested that the visual, somatosensory, and motor properties of V6A indicate a role for this area in the online error control for all of prehension, including reaching and grasping (Fattori et al., 2015). For movements of the eyes, the cortical oculomotor system in non-human primates and humans is comprised of the lateral intrapariental area (LIP)/parietal eye fields (PEF) and the frontal eye fields (FEF; Goldberg and Segraves, 1989; Bisley and Goldberg, 2003; Culham and Valyear, 2006; Culham et al., 2006). Due to the similarity between the anatomical components of these systems, we suggest that it is possible that oculomotor feedback mechanisms enhancing visual processing, could be replicated by the reaching and grasping networks to alter visual processing near the hand.

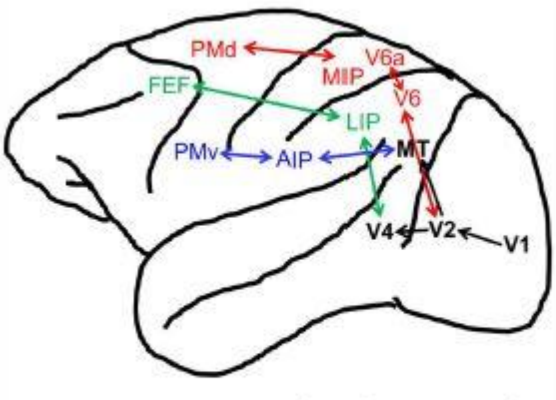

FIGURE 1 | Reach, grasp, and oculomotor control brain regions in the macaque. Shown are the cortical brain regions associated with the reach (in red), grasp (in blue), oculomotor (in green), and visual (in black) systems. Not pictured are anatomical cross-talk connections between the reaching and grasping networks (i.e., between V6A and anterior intraparietal (AIP)/Ventral premotor cortex (PMv), see Fattori et al., 2015).

FEEDBACK IN THE OCULOMOTOR SYSTEM

The influence of feedback, from fronto-parietal motor related areas, on visual processing is already well-supported for the oculomotor system. Early psychophysical work established an indirect link between alterations in visual processing due to shifts in attention and saccade motor planning (Rizzolatti et al., 1987; Kowler et al., 1995; Sheliga et al., 1994; Deubel and Schneider, 1996; Kustov and Robinson, 1996; Nobre et al., 2000; Castet and Montagnini, 2006; van der Stigchel and Theeuwes, 2006; Baldauf and Deubel, 2008). In general, visual processing was improved when a visual target coincided with the endpoint of a planned saccade suggesting a close relationship between the oculomotor system and attention related changes in visual processing. These studies led to investigations that more causally associated activations of eye-movement related brain regions to shifts in spatial attention and consequently alterations in visual processing at the end points of planned saccades (Moore and Fallah, 2001, 2004; Moore and Armstrong, 2003; Müller et al., 2005; Neggers et al., 2007; Van Ettinger-Veenstra et al., 2009; Gutteling et al., 2010; Bosch et al., 2013). For example, subthreshold microstimulation of the FEF resulted in increased visual sensitivity at the end-point of the unactivated motor plan behaviorally (Moore and Fallah, 2001, 2004) and within area V4 (Moore and Armstrong, 2003). This would suggest that recurrent connections between FEF and V4 allow for signals from FEF to feed back into the occipital lobe to influence subsequent visual processing (Armstrong et al., 2006; Armstrong and Moore, 2007; Ekstrom et al., 2008, 2009; Squire et al., 2012). Further evidence in primates comes from a study by Supèr et al. (2004) who found that in primary visual cortex neural activity corresponding to the location of the saccade target was enhanced approximately 100 ms before the onset of memory and visually-guided saccades. Studies in humans using transcranial magnetic stimulation (TMS) provide additional support for oculomotor feedback modulating visual processing. A single TMS pulse activates neurons in the targeted area. As such single pulse TMS over FEF enhances visual processing (Grosbras and Paus, 2003; Ruff et al., 2008; Van Ettinger-Veenstra et al., 2009) presumably by activating the feedback connections to visual processing areas. In contrast, a triple pulse disrupts the normal processing in an area. Triple pulse TMS used to disrupt the FEF results in impaired discrimination of a subsequently presented target (Neggers et al., 2007) suggesting that oculomotor feedback is necessary for spatial attention. Both the primate microstimulation studies and the human TMS studies support oculomotor feedback producing spatial attention effects behaviorally and within visual neurons. This would require attention signals to occur in the frontal lobe and propagate back to the occipital lobe. This is indeed what Van Ettinger-Veenstra et al. (2009) showed with EEG neuroimaging. They found that frontal activity associated with a saccade-go signal preceded activity in the occipital cortex associated with the appearance of a visual target. Thus, feedback projections from oculomotor-related frontal areas alter processing in posteriorly located visual areas.

VISUAL PROCESSING NEAR THE HAND

As mentioned previously, behavioral studies have provided indirect evidence suggesting that the space near the hand is prioritized. One prevailing theory suggests that alterations in visual processing occur as a result of attentional selection of near-hand space (di Pellegrino and Frassinetti, 2000; Schendel and Robertson, 2004; Reed et al., 2006, 2010; Abrams et al., 2008; Brown et al., 2008). Much like visual processing at the end point of a saccade is altered, the parallel within the reaching and grasping system would be a change in visual processing that occurs at the end point of a reach or grasp, i.e., in the workspace near the hand. One can imagine the benefit of this type of mechanism. This is especially true when reaching for an object while simultaneously viewing something in a different location that draws oculomotor driven spatial attention away from the object to be picked up. The underlying neural mechanisms that would drive altered visual processing near the hand have, as yet, not been well studied. A very recent neurophysiological study however, has shed light on the neural underpinnings of near-hand visual processing (Perry et al., 2015). Neuronal activity was recorded from area V2 which is an area that is known to be selective for orientation (Motter, 1993), a feature important for reaching and grasping (Murata et al., 2000; Raos et al., 2004; Fattori et al., 2009), modulated by attention (Motter, 1993; Luck et al., 1997), and directly linked to fronto-parietal reaching and grasping areas (Gattass et al., 1997; Passarelli et al., 2011; Fattori et al., 2015). Instead of allocating classic visual spatial attention with a cue (Moran and Desimone, 1985; Motter, 1993; McAdams and Maunsell, 1999; Treue and Martinez-Trujillo, 1999), Perry et al. (2015) used the presence or absence of a nearby hand to determine the effects of near-hand attention on neuronal responses in area V2. Under these conditions, there was a significant increase in response at the preferred orientation when the hand was nearby. This is consistent with classic visual spatial studies which produce a "gain-modulation" of neuronal responses: responses are multipled by the same factor regardless of selectivity (McAdams and Maunsell, 1999; Seidemann and Newsome, 1999; Treue and Martinez-Trujillo, 1999; McAdams and Reid, 2005). This results in a scaling of the tuning curve. However in contrast to gain modulation, there was no corresponding increase at the orthogonal orientation when the hand was near. Consequently, this produced a sharpening, instead of a scaling, of the orientation tuning curves when the hand was near, suggesting a different underlying mechanism than for oculomotor driven spatial attention. Sharpening of orientation tuning curves would result in greater orientation selectivity.

In addition to spatial attention, neuronal enhancement is also found with feature-based attention, where attending to a feature (such as a vertical bar) enhances processing of that specific feature (vertical), which aids greatly in visual search. Feature-based attention is described by the feature-similarity gain model of attention which predicts that enhancement of neuronal responses are strongest when the orientation of the grasp target (attended feature) and the orientation of the visual stimulus are matched, falling off as the difference in their orientations increased (Treue and Martinez-Trujillo, 1999). No such relationship was found. These results (Perry et al., 2015) suggest then that the attentional prioritization of near-hand space does not conform to known spatial or feature-based attentional mechanisms and that a novel, effector based, mechanism exists. This mechanism would preferentially process features (such as orientation) necessary for grasping, which would then improve the accuracy of an upcoming grasp.

EVIDENCE FOR FEEDBACK IN THE REACHING AND GRASPING SYSTEMS

While the effects of near-hand attention are seen in early visual areas, behaviorally these effects cannot be driven by the oculomotor system. The control system for near-hand attention, albeit separate from the oculomotor system, would likely be driven through the parallel feedback from fronto-parietal motor planning areas. It has been shown that neuronal response variability is reduced in premotor cortex during reaching (Churchland et al., 2010) and in the FEF during oculomotor preparation (Purcell et al., 2012). Notably, neurons in V4 undergo a reduction in neuronal response variability prior to the onset of a saccade (Steinmetz and Moore, 2010). This suggests that reductions in oculomotor response variability propagate back to posteriorly located visual processing regions. If feedback from fronto-parietal reaching and grasping networks is the method through which neurons in V2 undergo alterations in their response properties (such as sharpened tuning—Perry et al., 2015), it would be expected that response variability would also be reduced. This is, in fact, what was found (Perry et al., 2015). Thus, both oculomotor and near-hand spatial attention rely on feedback projections which concomitantly reduce response variability.

In human populations, this premise of feedback connections mediating changes in visual response properties was tested by Gutteling et al. (2013). They investigated whether activation of the anterior portion of the intraparietal sulcus (aIPS) prior to a grasping or pointing movement improved orientation perception. aIPS has been shown to be part of a network of fronto-parietal areas that are involved in the control of grasping movements (Taira et al., 1990; Gallese et al., 1994; Sakata et al., 1995). Furthermore, aIPS has been shown to be selective for the orientation of the object to be grasped (Murata et al., 2000) and connected to occipital visual areas (Nakamura et al., 2001; Ruff et al., 2008; Blankenburg et al., 2010), including ventral stream regions (Borra et al., 2008) that would be sensitive to changes in orientation. Activation of aIPS during action preparation (Gutteling et al., 2013) improved orientation sensitivity, suggesting that aIPS is involved in modulating visual information during action planning. In addition, compared to pointing, grasping a 3-dimensional oriented bar, has been shown with electroencephalography to strengthen the N1 component and associated selection negativity in lateral occipital regions suggesting that the plan to grasp influences early ventral stream visual processing (orientation) of action-relevant features (Van Elk et al., 2010). Improved sensitivity and strengthened selection negativity is consistent with improved orientation tuning found in non-human primate V2 neurons when a hand is nearby (Perry et al., 2015).

Area V6A is another candidate area whose feedback could sharpen orientation tuning, as it has been found to be sensitive to the orientation of the wrist (Fattori et al., 2009), selective for grip type (Fattori et al., 2010), contains cells selective for orientation (Gamberini et al., 2011), and has direct connections to early visual processing areas (Passarelli et al., 2011). In addition, activity in V6A has been shown to be modulated by shifts in covert, oculomotor driven, spatial attention (Galletti et al., 2010), suggesting that it may play a similar role in hand driven attention.

Recurrent feedback loops between fronto-parietal and early visual processing areas (e.g., V2) would provide relevant corollary motor discharge information to enhance visual information relevant to reaching and grasping objects (i.e., sharpened orientation tuning) that would then update ongoing motor plans. As a movement progresses, sharpened orientation tuning information could be used to improve or correct hand shaping and wrist orientation resulting in improved reach and grasp accuracy. Given that V6A is thought to be involved in online error control of both reaching and grasping (Fattori et al., 2015), recurrent feedback loops between V2 and V6A are the likely candidate mechanism to underlie this process.

AFFORDANCES

Orientation is considered to be part of the processing that occurs in the ventral stream that results in object recognition. It is not thought to be necessary for processes in the dorsal stream that culminate in knowing where something is, for computations of complex motion of an object, or for execution of movement. Why then would orientation processing in V2 be improved simply because the hand is near? Close links between the visual and motor systems have been at the core of the *affordance* literature for years. Gibson (1979) suggested that one of the key functions of the visual system was to provide information to the motor system about the possible actions that could be implemented, or alternatively, the possible actions that the visual information *affords*. Since then, Tucker and Ellis (1998, 2001) and Ellis and Tucker (2001) have argued that the motor system itself could extract visually pertinent information that would produce affordances. In fact, they have used the term micro-affordances to refer to object properties that are action-relevant and could be used to inform subsequent movements to interact with the object of interest (Tucker and Ellis, 2001). Orientation is an object feature that informs the "graspability" of an object. For example, object orientation can either facilitate or impede response times depending on whether the object orientation produces a motor affordance (Tucker and Ellis, 1998). In other words, the orientation of an object informs the grasp that needs to be planned. Regions within the parietal lobe, integral to reaching and grasping movements, show selectivity for the size, shape and orientation of an object both during fixation and grasping movements (Taira et al., 1990; Gallese et al., 1994; Murata et al., 2000; Fattori et al., 2009, 2010, 2012; Breveglieri et al., 2015), suggesting these areas play a key role in the integration of visual and motor information and object affordances. Therefore, orientation is a feature necessary to grasp objects accurately and is processed within the fronto-parietal grasping network, especially within area AIP.

Even if there is not a representation of the object as a whole in the dorsal stream, the vision for action theory (Goodale and Milner, 1992; Goodale, 2008, 2013) would also suggest that there are features of an object that are action relevant and therefore worthy of preferential processing, or attentional selection, by the dorsal stream action system. Patients with visual agnosia, who can still scale and orient their hand to an object to be grasped in spite of being unable to recognize the object they are grasping, speak to this point (Goodale et al., 1991, 1994; Milner et al., 2012). Given that object features such as orientation have been shown to affect subsequent motor affordances, and that object properties are extracted to inform the scale and orientation of the hand in patients who cannot recognize objects, it logically follows that orientation be an object feature preferentially processed within the dorsal stream in parallel to its processing within the ventral stream for object recognition.

ADVANTAGES OF SEPARATE EFFECTOR MECHANISMS

Being able to separate the deployment of attention between effectors allows for the decoupling of actions. Many examples exist of instances where we reach for one thing while looking elsewhere. In fact, optic ataxia, in which there is an inability to reach to peripheral targets, results from damage to the posterior parietal cortex (Milner and Goodale, 1995; Carey et al., 1997; Jackson et al., 2005). It has been shown that reaching to centrally located targets activates the MIP sulcus and PMd, while reaching to peripherally located targets additionally activates the parietal occipital junction and more rostral parts of PMd. These differentiated networks support dissociation between where gaze and grasp are deployed (Prado et al., 2005). Furthermore, recent work has shown that when a sequence of reaching movements are planned, visual discrimination is significantly enhanced not just at the first movement goal but also at the second (Baldauf et al., 2006; Baldauf and Deubel, 2008, 2009). So while an eye movement would be planned and then executed to the first target, the second is already enhanced suggesting that reach execution is separate from oculomotor planning and in turn, that movement planning and execution in the posterior parietal cortex already accommodates separate representations of gaze and reach targets (Jackson et al., 2009). These decoupled eye and hand movements are supported by the presence of neuronal populations in parietal areas that produce multiple types of reference frame transformations to encode targets in eye-centered or hand-/body-centered frames of reference (Lacquaniti et al., 1995; Batista et al., 1999, 2007; Buneo et al., 2002, 2008; Cohen and Andersen, 2002; Marzocchi et al., 2008; Chang et al., 2009; Chang and Snyder, 2010; McGuire and Sabes, 2011). As populations encoding targets in either eye- or hand-centered reference frames support decoupled movements, it follows then that there should exist separate effector-based attentional mechanisms.

CONCLUSION

We have reviewed literature in support of the hypothesis that there exist parallel, but separate, effector-based attentional systems. Whereas the oculomotor system enhances visual responses through gain modulation, near-hand attention sharpens orientation tuning and, potentially, other features relevant to reaching and grasping. Thus, these effector-based systems may be specialized for the actions those effectors can perform. We suggest that improved orientation processing is a feature important for accurate reaching and grasping, and that separate effector-based attentional mechanisms allow for the decoupling of visual enhancements associated with eye and hand movements. Future investigations are needed to further support this hypothesis for example, by systematically testing grasp-relevant and irrelevant features. In addition, testing whether both the reaching and grasping or grasping alone is involved in near-hand attention which will provide details regarding which fronto-parietal networks may be involved and what other object features may be preferentially processed.

AUTHOR CONTRIBUTIONS

CJP, PA, and MF all contributed to the writing and revision of this article.

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