THE ROLE OF ATTENTION IN BIOLOGICAL MOTION PERCEPTION: A BIASED
COMPETITION PERSPECTIVE

by

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DEDICATION

This dissertation is dedicated to my husband, Michael. Thank you for always being there to make me laugh or instill confidence when I needed it. This would not have been possible without your love and support.

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ABSTRACT

THE ROLE OF ATTENTION IN BIOLOGICAL MOTION PERCEPTION: A BIASED
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The ability to recognize and understand the movements and actions of others is
critical to everyday social interaction. Considering the ecological significance and
efficiency of biological motion perception, it has often been described as an automatic or
attention-free process. However, although perception of these complex stimuli may seem
effortless, evidence suggests that attention does play an important role, especially when
other stimuli are present. Even so, the nature of the relationship between biological
motion and attention has not been well defined. The four experiments of this dissertation
detail the relationship between attention and biological motion within the framework of
the biased competition model of attention. The biased competition model proposes that
attention acts by resolving the competition that arises when two or more objects occur
simultaneously, in favor of the attended stimulus. Behavioral and event-related
functional magnetic resonance imaging responses were measured while participants

viewed point-light animations of human and tool motion under different attentional conditions. Results illustrated that the neural mechanisms underlying biological motion perception are strongly modulated by selective attention: when attention was focused away from biological motion, responses were reduced compared to when biological motion was selected by attention. Additionally, consistent with the biased competition model, the spatial proximity between concurrently presented items influenced the neural response to biological motion. While separation between simultaneously presented objects resulted in increased responses when attention was focused on biological motion, directing attention away from biological motion led to decreased neural responses when stimuli were separated. These results indicated that there is involvement of both object-based and spatial attention. Finally, expectations regarding specific object categories did not influence visual processing by preactivating neural responses in brain regions involved in processing biological motion. Together, the findings presented here lend further evidence for a critical role of top-down influences on the neural mechanisms underlying biological motion perception and indicate that this role is partially consistent with the predictions of the biased competition model.

CHAPTER 1: INTRODUCTION

Human observers derive a significant amount of critical information through perceiving the actions of others and perception of this biological motion is important for social interaction. The experiments described in this dissertation aimed to characterize the role of selective attention in biological motion perception. This introduction will provide the literature and theoretical background on which these experiments were based. The first section will describe the motivation for studying this relationship.   The following sections will then address biological motion, attention, attentional modulation of biological motion processing, and functional magnetic resonance imaging (fMRI) each in turn.

The human body in action produces a complex pattern of motion, with multiple points of articulation and many degrees of freedom. Despite this complexity, healthy human observers show an impressive ability to recognize the movements and actions of others and derive, even from degraded stimuli, complex cues that are critical to everyday social interaction. Body movements can yield information including identity (Loula, Prasad, Harber, & Shiffrar, 2005; Troje, Westhoff, & Lavrov, 2005; Westhoff & Troje, 2007), gender (Jordan, Fallah, & Stoner, 2006), emotional state (Atkinson, Tunstall, & Dittrich, 2007), social status (Montepare & Zebrowitz-McArthur, 1988) and physical attractiveness (Johnson & Tassinary, 2007). Several accounts have described biological

motion perception as a bottom-up, attention-free process (Giese & Poggio, 2003; Johansson, 1973). Considering the ease of recognition (Mather, Radford, & West, 1992; Neri, Morrone, & Burr, 1998), apparent innate presence (Simion, Regolin, & Bulf, 2008) and ecological significance of biological motion, it would seem reasonable to expect that processing should be efficient and act in an automatic, preattentive manner. Automatic selection of biological motion would be predicted to occur even in the presence of other objects. A number of recent behavioral and neuroimaging studies have, however, indicated that attention might play an important role in the processing and perception of biological motion (Chandrasekaran, Turner, Bülthoff, & Thornton, 2010; Parasuraman et al., 2009; Pavlova, Birbaumer, & Sokolov, 2006; Safford, Hussey, Parasuraman, & Thompson, 2010; Thornton, Rensink, & Shiffrar, 2002). Given our busy and cluttered world in which many other objects are present simultaneously with biological motion stimuli, it is important to consider the role of top-down influences on the processing of biological motion to understand how these processes would operate in a more realistic environment.

Although healthy observers have robust abilities for perceiving biological motion stimuli, there are several neuropsychiatric disorders in which patients demonstrate deficits in this type of visual processing, for example; autism spectrum disorder (ASD) and schizophrenia. ASD is a neurodevelopmental disorder that involves social and communication deficits as well as repetitive and compulsive behaviors. A key finding in ASD is that individuals experience deficits in perceiving socially relevant stimuli, including faces (Langdell, 1978) and body movements (Koldewyn, Whitney, & Rivera,

2009). Similarly, there have also been deficits in visual perception, including biological

motion perception, observed among schizophrenic patients (Kim, Doop, Blake, & Park,

2005). These impairments have been linked with characteristic abnormal social

functioning. Additionaly, deficits in attention have been reported in individuals with

ASD (Belmonte & Yurgelun-Todd, 2003) and are characteristic of schizophrenia

(Elvevåg & Goldberg, 2000; Harris, Minassian, & Perry, 2007). Considering the co-

occurrence of these impairments in both ASD and schizophrenia, it would seem

reasonable that they are related in some manner. Alternatively, it is also possible that

while attention is impaired in these disorders, the social deficits are in addition to any

deficits due to attention problems. It is, therefore, critical to fully understand the nature

of the relationship between attention and processing of socially informative stimuli,

particularly human body movements. The goal of this project was to examine this

relationship in healthy individuals.

Background

Biological Motion

The following section will review some of the research conducted to develop a

better understanding of the psychological and neuronal processes involved in biological

motion perception. Here, point-light animations, the stimuli that are often employed to

study biological motion, will be described. This section will also include a description of

behavioral and neuroimaging evidence that supports an important concept in biological

motion research: that coherent perception involves integration of form and motion cues.

Finally, this section will conclude with an overview of the cortical network underlying action perception.

Perception of biological motion is often studied using point-light animations. These stimuli, originally described by Johansson (1973), are created when points of light are attached to the joints of a moving person who is otherwise invisible. When viewed in a stationary manner the display appears to be an unrecognizable jumble of lights, but when put into motion naïve observers can quickly and easily identify the presence of a moving human form from these impoverished stimuli. These point-light stimuli frequently portray a walking figure; however, they can also involve an actor performing a wide variety of complex actions, for example, dancing.

A classic finding with biological motion perception is its susceptibility to inversion of the point-light figure. As is the case with inverted faces (Valentine, 1988), performance at biological motion recognition is impaired when the figure is viewed upside down (Sumi, 1984). Importantly, this inversion effect seems to rely on the observer's global perception of the human figure as it operates in egocentric coordinates, rather than with respect to gravity (Troje, 2003), and prior knowledge that upside-down figures will be presented does not neutralize the effect (Pavlova & Sokolov, 2000).

Several descriptions of biological motion have emphasized the importance of local motion cues (Mather et al., 1992; Neri et al., 1998), while other researchers have supported the view that biological motion perception relies mainly, if not completely, on form cues (Beintema & Lappe, 2002; Chatterjee, Freyd, & Shiffrar, 1996).

Early researchers supported a form-from-motion perspective that biological motion is processed using mainly local motion cues. Mather and colleagues (1992) found that disturbing local motion detectors disrupts the ability to perceive biological motion. Similarly, Neri and colleagues (1998) found that both biological motion and simple transitory motion show a linear relationship between noise threshold and the number of stimulus dots necessary for detection. This mutual linear relationship indicated that the driving force for biological motion is the local-motion shared by the two stimulus types. Also, Garcia and Grossman (2008) used isoluminant point-light animations to demonstrate that motion cues are necessary for biological motion detection, although the motion cues alone may not always be sufficient.

An alternative line of research has suggested that configural cues, which convey information regarding the form of the moving figure, are critical to perception of biological motion. Neuropsychological data demonstrated that biological motion abilities can remain intact even when low-level motion perception is disrupted following brain damage (Vaina, Lemay, Bienfang, Choi, & Nakayama, 1990), suggesting that these perceptual processes occur through distinct mechanisms. Using an apparent motion paradigm, Chatterjee and colleagues (1996) illustrated that biological motion can be detected when no actual motion is present in the stimuli.

Additional support of the importance of form in biological motion perception involved a variation on the classical point-light animation separated information regarding the position of points on the body from information about the movement of those points over time (Beintema & Lappe, 2002). These sequential position stimuli,

created by placing point-lights at randomly changing positions along the limbs, rather than on the joints, showed a pattern of discriminability similar to traditional point-light biological motion stimuli. Even though frame-to-frame local motion was destroyed, observers viewing these displays were able to reliably detect the direction of a walker. Yet, as is the case with normal point-light animations, when the figure was inverted performance was degraded. Finally, Hiris and colleagues (2005) demonstrated that biological motion is processed in a global manner, using form information to organize the motion of the point-light display. Following training, observers were able to detect the presence of an "arbitrary" figure, created by relocating the dots from a point-light walker. However, the pattern of behavior was unlike that with an intact point-light walker; performing this task involved development of a strategy that involved looking for a characteristic cluster of dots and there was no effect of inversion.

There is also neuroimaging evidence that supports a critical role for form information in the neural mechanisms underlying processing of biological motion. Thompson and colleagues (2005) used fMRI to demonstrate that the superior temporal sulcus (STS) responds more strongly to an intact walker than to apart stimuli, suggesting that the STS uses form cues such as body configuration to analyze biological motion. When these form cues are not available because the spatial configuration has been modified, different brain regions including the superior parietal lobule (SPL) and middle temporal gyrus (MTG) are more involved.

Taken together, this evidence suggests that both form and motion cues are important for biological motion perception. Under certain conditions, form seems to play

a more important role whereas other times motion seems to be the critical factor. More recent research has focused on how these cues are integrated to form a coherent perception of human action. It has been hypothesized that since humans integrate stimulus information in a manner that is statistically optimal by designating weights to the incoming information based on the amount of noise present in the signal (Ernst and Banks, 2002), the contribution of each cue type to a whole biological motion percept, should be dependent on the reliability of that cue (J. C. Thompson & Baccus, 2012). It has also been suggested that the roles of the various brain regions involved in processing biological motion can be separated into form and motion processes. Consistent with the construct of a dorsal "where" and ventral "what" pathway, it has been shown that ventral regions are more involved in the shape of the biological form while dorsal regions respond more to the kinematics of the stimuli (Jastorff and Orban, 2009; Peuskens et al., 2005). Additionally, a theoretical model developed by Giese and Poggio (2003), involves integration of the hierarchically organized, parallel motion (dorsal) and form (ventral) streams for biological motion perception. Importantly, the integration of these signals may occur early in processing, an event related potential (ERP) study by Baccus and colleagues (2009) using an adaptation paradigm showed that there is a neural signal occurring as early as 200ms that is a reflection of both form and motion cues. Evidence from psychophysical, computational and neuroimaging studies has demonstrated that form and motion cues make independent contributions and successful biological motion perception involves a combination of the two types of information.

Action Perception Network

Neuroimaging, neurophysiological and neuropsychological studies have indicated the presence of neural mechanisms specialized for the processing of biological motion. This evidence has led to understanding a network of brain areas that work together to allow for perception and high-level comprehension of the actions of other people. This section aims to give an overview of this action perception network.

At a relatively basic level of processing, regions located in the posterior inferior temporal sulcus (ITS), including the extrastriate body area (EBA) and area MT+ are selectively responsive to intact biological motion compared to scrambled biological motion (Grossman & Blake, 2002; Jastorff & Orban, 2009; Peelen, Wiggett, & Downing, 2006). Consistent with the independent contributions from critical form and motion cues discussed in the previous section, the pattern of activity in these regions may constitute separate processing of these two features. While the EBA is defined by its preference for human bodies compared to other types of objects (Downing, Jiang, Shuman, & Kanwisher, 2001), motion sensitive area MT+ may be more involved in processing motion cues; although there is evidence that there may also be some extraction of body shape in MT+ (Peelen et al., 2006).

The next stop along the action perception network is the region most frequently implicated in biological motion, the STS, located in the lateral temporal cortex. The STS shows increased activation to viewing point-light biological motion stimuli as compared to scrambled motion stimuli (Grossman and Blake, 2001). Peuskens and colleagues (2005) further specified that while these biological motion stimuli activate a network involving several visual areas, including the EBA and area MT+, it is the STS that is

actually involved in processing the unique human action aspect of the stimuli. Additionally, when activity of the STS is disrupted using transcranial magnetic stimulation (TMS) biological motion processing impairments are observed (Grossman, Battelli, & Pascual-Leone, 2005). Importantly, the STS shows category selectivity with greater responses to human motion than to another category of object-motion, tool motion; on the other hand, inferior regions of the lateral temporal cortex such as MTG, particularly in the left hemisphere, prefer tool motion (Beauchamp, Lee, Haxby, & Martin, 2002, 2003; Safford et al., 2010). This body of evidence suggests that the role of the STS involves action representation, perhaps through integration of the form and motion cues that are processed earlier in the processing pathway.

Beyond the processes of detection and analysis of actions that seems to occur in the lateral temporal cortex, there are regions located in inferior parietal and inferior frontal cortices that are involved in understanding goals and intentions of actions. For example, Hamilton and Grafton (2006, 2008) used a repetition suppression paradigm to disentangle the representation of action outcomes from the kinematics involved in carrying out the action. Activity in the left anterior intraparietal sulcus (aIPS) was suppressed to repeated presentations of the same goal, indicating that this region represents the goal of an observed action (Hamilton & Grafton, 2006). Similarly, when the outcome of an action was repeated, suppression was observed in regions including the right inferior parietal lobule (IPL) and right inferior frontal gyrus (IFG) (Hamilton & Grafton, 2008). These frontoparietal regions appear to be critical for understanding the goals and intentions underlying the actions of other people.

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Another important issue to consider is the retinotopic organization of the high-level visual areas that are responsive to biological motion. It is well documented that receptive field (RF) size increases along the visual hierarchy (Kastner et al., 2001), such that areas later in the visual stream have large RFs that can potentially cover the entire visual field (Gattass et al., 2005). However, there is also evidence that higher-level object recognition regions such as TEO and IT may actually have smaller RFs (DiCarlo & Cox, 2007) or at least may be confined to a single quadrant of the contralateral hemifield (Kastner et al., 2001). Additionally, regions located in temporal, parietal and frontal cortex contain topographic representations (Hagler & Sereno, 2006; Kastner et al., 2007; Sereno, Pitzalis, & Martinez, 2001). Specifically, brain regions that respond to biological motion, including MT, EBA and STS, show contralateral preference (J. C. Thompson & Baccus, 2012) and retinotopic activity corresponding to the phase of a rotating display (Saygin & Sereno, 2008).

Attention

To develop an understanding of the relationship between biological motion and attention, it is necessary first to review a portion of the literature concentrating on attention. Such a review is the purpose of this section which will include a description of the principles of two influential models of attention, Feature Integration Theory and the Biased Competition model. The network of the cortical regions involved in controlling attentional modulations of sensory cortex will also be discussed.

Attention is a broad term used to describe a group of cognitive processes that involve the allocation of processing resources. There are multiple types of attention

including selection, vigilance, and executive control. Selective attention involves a filtering mechanism whereby relevant information is processed preferentially and there is little or no processing of irrelevant information. Vigilance, or sustained attention, refers to the maintenance of attention over prolonged periods of time. Finally, executive control enables goal-directed thought and action through planning the targets of attention. The primary focus here will be on selective attention, in particular visual attention.

Selective attention is a process through which the brain preferentially processes certain behaviorally relevant information to the exclusion of other information that has been labeled unimportant or irrelevant to the task at hand. A classic example of our abilities to filter out irrelevant information and selectively attend to relevant information is the cocktail party problem (Cherry, 1953). In a noisy room with music playing and multiple conversations going on at once, party goers are able to successfully isolate the auditory information from the conversation they are following and ignore all the others. Similarly, a typical visual scene is crowded and includes multiple objects each with several feature characteristics, such as shape, color, texture and motion; from this rich environment, observers can selectively pick out necessary information to identify targets and ignore the rest. This selection is necessary to limit the overwhelming computational demands to a level that can be managed by our limited processing resources.

The selective process is typically thought to be driven by spatial location (Posner, 1980; A. M. Treisman & Gelade, 1980) and indeed, typically we move our eyes and heads to attend to goal-relevant information at different locations. However, it is also known that selection can be based on featural (Motter, 1994; Saenz, Buracas, & Boynton,

2002) and categorical or object-related (O'Craven, Downing, & Kanwisher, 1999;

Peelen, Fei-Fei, & Kastner, 2009) cues as well. For example, Corbetta and colleagues

(Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1990) observed that when attention

is directed separately to visual features including shape, color and motion, neural activity

is increased in the extrastriate areas that are specialized for processing the selected

attribute. Object-based attention was first demonstrated by Duncan (1984) and

subsequently developed into a neural theory by Desimone and Duncan (1995). There is

considerable behavioral and neuroimaging evidence in support of both the spatial and the

object-based attention theories, including models that accommodate both theories within

a single unified architecture (Deco & Lee, 2002).

Feature Integration Theory

According to the feature integration theory of attention, accurate and meaningful

perception of complex visual scenes involves binding together of a limited set of

preattentive features into the correct combinations and, though perception often seems

effortless, spatially selective attention is required to prevent the binding of incorrect

combinations as illusory conjunctions (Treisman, 1998; Treisman and Gelade, 1980).

When targets of visual search differ from distracters by a single feature they tend to "pop-

out" and detection occurs rapidly regardless of the number of items in the array.

However, when a target is defined by the conjunction of two (or more) features, such as

the color and shape of an item, and some of these features are shared with the other items

in the display, attention is required to inspect each item in turn. In this case target

detection occurs more slowly and depends on the number of distracters that are inspected

prior to reaching the target. Similarly, when items are presented too briefly that focal

attention cannot address each object in a serial search, illusory conjunctions, or incorrect

combinations of the individual features, can occur (A. Treisman & Schmidt, 1982).

Biased Competition Model of Attention
Natural visual scenes typically contain many objects; yet, the visual system has

limited processing capacity and must selectively process only the behaviorally relevant

information. According to the biased competition model, simultaneously presented

stimuli compete for processing resources and attention is necessary to resolve this

competition by biasing the response in favor of the attended stimuli. The biased

competition theory of selective attention includes three general principles (Desimone &

Duncan, 1995). The first principle holds that simultaneously presented visual

information is processed in a competitive manner and additionally that competitive

interactions are strongest at the level of the RF. Second, this competition is controlled by

both bottom-up stimulus information and top-down mechanisms including task-demands

and attention. Finally, competition is integrated between systems so that as a system

becomes biased in favor of a particular stimulus, that stimulus gains dominance in other

systems as well. For example, when a particular object or spatial location gains

dominance in lower-level regions including visual cortex, that same object or location

will also become dominant in higher level regions including parietal and frontal cortices.

The biased competition model predicts that competition between simultaneously

presented stimuli is greatest at the level of the RF. When stimuli are close together (or

spatially overlapping) competition between them is maximal because they fall within the

RF of the same population of neurons; separating the stimuli should reduce this competition, as they would no longer be competing for representation by the same neuron or group of neurons. This idea has been supported by fMRI experiments that show differences between sequentially and simultaneously presented stimuli reflecting the degree of competition (Beck & Kastner, 2005, 2007; Kastner et al., 2001; Kastner, De Weerd, Desimone, & Ungerleider, 1998). The strength of these competitive interactions increases with increasing RF sizes along the visual hierarchy. Areas with small RFs, such as V1 and V2, show lower levels of competition compared to regions with RFs large enough to cover more of the stimuli, including V4, TEO, V3A and MT, where competition is greatest. Additionally, varying the size and degree of spatial separation between the stimuli influenced the level of competition (Kastner et al., 2001). Again, these effects varied across the visual cortex, separating the stimuli reduced or abolished competitive suppression in V2 and V4, but did not have an effect in TEO when the stimuli remained within the same quadrant. There were, however, no significant sensory suppressive interactions between stimuli when they were located in separate quadrants in any of the regions including TEO.

Similar effects of spatial configuration on competitive interactions have been demonstrated behaviorally. For certain classes of stimuli, such as faces and natural scenes, varying the distance between individual stimuli influenced performance in dual-task, matching (VanRullen, Reddy, & Fei-Fei, 2005) and visual search tasks (Reddy & VanRullen, 2007), seemingly by reducing competitive interactions at greater distances. However, these effects did not occur for other stimuli, including bisected-colored discs.

Importantly, this distinction indicates that these spacing effects are dependent on the existence of neuronal populations selective for the stimuli. In these cases, attention is not required for recognition, but to resolve competition between target and distracters presented in the RF of the same neuron.

Another prediction of the biased competition model is that competition is biased according to top-down influences such as task demands in favor of the attended stimuli. A potential mechanism for this bias is through pre-activation of brain regions according to an internal 'template' (Desimone & Duncan, 1995). There is substantial evidence that effects of attention are present in the absence of any visual stimulation in addition to when the stimuli are actually present. Both single-cell physiology (Luck, Chelazzi, Hillyard, & Desimone, 1997) and human neuroimaging studies (Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; McMains, Fehd, Emmanouil, & Kastner, 2007; Sylvester, Jack, Corbetta, & Shulman, 2008; Sylvester, Shulman, Jack, & Corbetta, 2009) have demonstrated that directing attention toward a location increases neural baseline activity. Similar increases in baseline activity have also been shown that have some degree of feature specificity (Chawla, Rees, & Friston, 1999; Shulman et al., 1999). However, it has more recently been suggested that baseline increases reflect only information regarding the attended spatial location (Beck & Kastner, 2009; McMains et al., 2007), not stimulus properties such as features. Yet, there is also evidence from single-cell physiology (Chelazzi, Miller, Duncan, & Desimone, 1993) and fMRI studies (Esterman & Yantis, 2010) that expectations regarding particular object categories

selectively increase anticipatory activity in neurons and regions that are specifically responsive to these stimuli.

Attention Networks

As was discussed in the previous section, selective attention has been shown to facilitate the neural response to target stimuli and suppress activity corresponding to unattended and ignored stimuli. However, it is also important to appreciate how these modulations in sensory cortex are generated. Accordingly, research has identified complementary networks of brain regions that interact to combine top-down and bottom-up factors that control visual attention (Corbetta & Shulman, 2002). The dorsal frontoparietal attention network consists of core regions including the frontal eye field (FEF), located at the intersection of the superior frontal sulcus and the precentral sulcus, and the intraparietal sulcus (IPS). This network is primarily involved in top-down influences on processing of stimuli that are relevant to a specified task-goal. In contrast, the right hemisphere dominant ventral frontoparietal attention network, which includes the right temporoparietal junction (TPJ) and ventral frontal cortex (VFC), is involved in stimulus-driven reorienting to salient stimuli that are not involved in the task at hand but have some behavioral significance.

To better understand how attention is directed, experiments have taken advantage of cuing paradigms that separate preparatory control signals from top-down effects of an attentional set on the responses in neural populations that are selective for the target stimuli. Regions in the dorsal frontoparietal network become activated when advance information, such as an informative cue, is presented prior to a subsequent visual scene.

For example, Corbetta and colleagues (2000) presented an arrow cue instructing

participants to covertly attend to a peripheral location. In response to the cue, whereas

occipital regions showed transient activation reflecting sensory processing of the cue, the

IPS and FEF showed a sustained response that persisted throughout the period during

which participants were paying attention to the target location. These regions in the

dorsal frontoparietal network have been consistently reported as preparatory responses to

cues regarding locations (Corbetta et al., 2000) and features such as motion (Shulman et

al., 1999). Importantly, these control signals may generate the observed biases in visual

cortical areas reflecting selective sensory processing (Corbetta et al., 1990).

Additionally, switching attention between two objects activates similar regions in the

posterior parietal cortex (Serences, Schwarzbach, Courtney, Golay, & Yantis, 2004).

Taken together, this evidence suggests that the dorsal frontoparietal network, including

IPS and FEF, plays an important role in controlling attentional modulation through top-

down biases.

While the dorsal frontoparietal network is recruited for control of goal-directed

selective attention, a complementary network, including TPJ and VFC, appears to be

involved in re-orienting to unattended, yet behaviorally critical information (Corbetta &

Shulman, 2002). Unlike the dorsal frontoparietal network, the right ventral frontoparietal

network does not respond during cueing or expectation periods, but instead is activated

by target detection. For example, presentation of invalid cues necessitates subsequent

reorientation of attention to a targets appearing at uncued locations and this process

involves activation of TPJ and IFG (Arrington, Carr, Mayer, & Rao, 2000).   These

findings indicate that the function of the ventral frontoparietal network involves stimulus-driven orienting, rather than generation or maintenance of an attentional set.

Attentional Modulation of Biological Motion Processing

The previous sections focused separately on some of the research involving biological motion and attention. This section will review the experimental evidence that points toward a relationship between biological motion and attention.

Biological motion is easily perceived by human observers and perception has obvious evolutionary significance; for example we must be able to detect predators to ensure our survival as well as identify the intentions of others to determine whether they are friend or foe. Over the course of human history we have depended on others for our survival. Nevertheless, we also need to be able to identify threat so as to avoid getting too close to dangerous individuals. In our modern world, we rely on signals from sources such as body language to successfully participate as social creatures. For these reasons, it seems reasonable that biological motion would be processed in an automatic, preattentive manner. In accordance with this idea, when point-light walkers are presented as task-irrelevant flankers on either side of a central target walker, they are processed incidentally and incompatible flankers interfere with performance as response time is slowed (Thornton & Vuong, 2004). Biological motion has also been shown to reflexively draw spatial attention in the direction of a walker. Observers were asked to indicate the orientation of a peripherally presented Gabor patch following a non-predictive central point-light walker cue. When the probe was presented on the side that the figure was walking toward, performance was better than when the walker faced in the

opposite direction (Shi, Weng, He, & Jiang, 2010). These findings emphasize the inherent sensitivity of the visual system to these ecologically and socially critical signals.

While biological motion may have privileged access to visual processing resources and several accounts have described biological motion perception as a bottom-up, attention-free process (Giese & Poggio, 2003; Johansson, 1973), empirical evidence has indicated that under certain circumstances, attention is necessary for effective biological motion perception. For example, using a visual search paradigm with point-light walkers, Cavanagh and colleagues (2001) demonstrated that, even though it seems effortless, biological motion perception occurs as a serial process. Attention must be focused on each item (walker) one at a time causing the time to detect a target to increase as additional distracters are added to the display. Similarly, participants were asked to perform a point-light walker direction discrimination task while concurrently detecting orientation changes of four nearby rectangles. Importantly, interference from the dual task was more apparent when effective perception of the biological motion involved integration over space and time, such as by increasing the inter-frame interval and presenting the stimuli amongst noise dots created from scrambled biological motion (Thornton et al., 2002). These results indicate that top-down influences play a more critical role in biological motion when detection necessitates global integration and under these conditions perception places higher demands on attentional resources.

In agreement with the findings that biological motion is attentionally demanding when stimuli are degraded, attention is also needed to identify the intentions of an action presented in a noisy display. In a study where participants were asked to identify an

infrequent target intentional action, a vigilance decrement was observed as a decrease in detection rate as a function of time on task only when images were degraded making the stimuli difficult to discriminate. Critically, false alarms tended to be specifically to detecting the wrong intention. These findings imply that along with the perceptual demands involved, extracting high-level information from human actions, such as intention, is attentionally demanding and that as attention allocation fails over time these originally effortless processes fail as well (Parasuraman et al., 2009).

The relationship between biological motion perception and attention is further supported by research that compared individual differences in performance. Individuals' noise thresholds for direction discrimination of a point-light walker were correlated with attention measures that reflect executive control abilities, including stroop and flanker tasks. Results show that observers who are better able to selectively attend and ignore irrelevant competing information can perceive biological motion stimuli within greater levels of noise (Chandrasekaran et al., 2010) suggesting that these abilities may be somehow related.

Additional evidence that biological motion perception is influenced by attention comes from perceptual deficits exhibited by patients with specific patterns of brain damage. Following a bilateral lesion to motion sensitive area V5, patient LM showed specific deficits in low-level motion perception but was able to detect human actions in point-light animations (McLeod, 1996). This patient was unable to detect biological motion only when additional noise dots were added to the point-light animation, indicative that traditional motion regions are required for segregation by motion – as

opposed to the primarily object-centered coding possibly occurring in the other regions involved in biological motion processing. In contrast, patients with parietal lobe damage maintain intact performance on low-level motion tasks; however they have difficulty perceiving a moving figure from a point-light animation (Battelli, 2003). When multiple point-light animations are presented simultaneously during a visual search task they are unable to effectively identify a target. It is known that patients with similar parietal lobe lesions have attentional disabilities (J Duncan et al., 1999; Posner, Walker, Friedrich, & Rafal, 1984) and while this point-light walker visual search task is also performed serially by healthy controls (Cavanagh, 2001) it is even more challenging for these patients (Battelli, 2003). These results are consistent with evidence from healthy participants and suggest that biological motion perception is an active process that is dependent on attentional resources. Additionally, this evidence also points to critical involvement of the superior parietal lobe, particularly for complex perceptual tasks that require integration of different motion signals or segregation from competing moving objects.

Adding to the behavioral and neuropsychological evidence that biological motion perception is an attentionally demanding process, recent neuroimaging studies have suggested that the neural resources that are sensitive to biological motion are also modulated by attention. Using magnetoencephalography (MEG), Pavlova and colleagues (2006) demonstrated that while early responses to biological motion around 80ms following stimulus onset are similarly enhanced for both attended and ignored stimuli, later responses around 120ms for parietal and 155ms for temporal cortex, are unique to attended biological motion stimuli. The topographically and temporally distinct patterns

of evoked oscillatory gamma MEG activity elicited by attended and ignored walkers is evidence for a role of attention in the cortical processing of biological motion. Similarly, Chong and colleagues (2008) varied the attentional load of a central task while participants viewed task-irrelevant videos of hand actions. The left IFG was modulated by high attentional load but the STS and IPL were unaffected by the degree of attentional manipulation. Although these results seem to suggest that responses to biological motion in the STS are not influenced by the availability of attentional resources, since the action stimuli were irrelevant to the task in all conditions, it is unclear whether participants actually attended to them during the low load central task.

To directly test the influence of selective attention on the cortical response to biological motion, Safford and colleagues (2010) combined fMRI, high-density electroencephalography (EEG), and cortical source localization methods. In this experiment spatially overlapping point-light human and tool motion were presented simultaneously and attention was directed to one motion category or the other. The use of overlapping human and tool motion in this study made use of the previously demonstrated pattern of response to object motion in the lateral temporal cortex. The STS shows a greater response to biological motion than tool motion while the MTG/ITS is more sensitive to tool motion (Beauchamp et al., 2002, 2003). The results indicated that the response in regions that show a preference for biological motion, including the STS, was strongly attenuated when attention was directed away from the preferred motion category. Importantly, the response of the STS reflects the attentionally demanding processing and categorization of human actions, not simply the presence of

the stimuli. These findings support the suggestion that there is an important contribution of top-down, object-based influences on the neural processing of biological motion.

Importantly, the evidence presented here, that biological motion perception is modulated by attention suggests that this influence of attention is most relevant under conditions of high task difficulty; for example when the stimuli are ambiguous, degraded (Parasuraman et al., 2009) or presented along with other competing stimuli (Safford et al., 2010) or tasks (Thornton et al., 2002). This pattern of attentional modulation in some but not all circumstances is common among other types of natural stimuli such as faces and scenes (Li et al., 2002; Reddy et al., 2004; VanRullen et al., 2005) and gives an important clue as to the mechanism of attention. The experiments described in the following chapters aimed to better define this mechanism and tested the hypothesis that the role of attention in biological motion perception is to resolve competition between concurrently presented stimuli in favor of the attended stimulus.

Functional Magnetic Resonance Imaging

This introduction has provided a theoretical basis for the experiments which will be described in the remaining chapters of this dissertation focusing on the relationship between attention and biological motion. In this last section, the basis of fMRI, the primary technique utilized by these experiments, and the motivation for its use will be described. Magnetic Resonance Imaging (MRI) is a non-invasive neuroimaging technique that takes advantage of the magnetic properties of different tissue types in order to construct high resolution anatomical images of the brain. Functional MRI

(fMRI) allows for observation of changes in brain activity over time, often while participants perform some sort of cognitive task.

Relationship Between Neuronal Activity and the BOLD Response

The signal that is the basis for fMRI, the blood oxygen level dependent (BOLD) response, measures changes in blood flow and the relative concentrations of oxygenated and deoxygenated hemoglobin present as a reflection of the metabolic activity of the brain. Ogawa and colleagues demonstrated that deoxygenation decreases the T2* value of blood, indicating that the BOLD signal would be a useful, naturally occurring contrast mechanism for studying brain function (1990). When neurons are active (propagation of action potentials or postsynaptic potentials) during perceptual or cognitive tasks, ions move down their respective concentration gradients and, therefore, energy is required to operate ion pumps and restore the membrane potential to resting state.

Experiments involving the primate visual cortex have directly tested the relationship between fMRI and neuronal activity. Logothetis and colleagues collected simultaneous neural (intracortical) and hemodynamic (fMRI) recordings from the visual cortex of anesthetized monkeys (2001). Local field potentials (LFPs), and single- and multi-unit spiking activity were compared with the BOLD response. Multi-unit activity (MUA) reflects mainly the output of a neural population, while LFPs are generally representative of 'peri-synaptic' activity including excitatory and inhibitory postsynaptic potentials, dendritic afterhyperpolarizations and intrinsic membrane oscillations (Logothetis, 2003). Visual responses were elicited using a rotating checkerboard pattern and stimulus-induced increases were observed for both the hemodynamic and neural

measures. The BOLD time series for a given voxel was compared to the MUA and LFP signals that were recorded when the electrode tip was located within the region of interest. Results showed that only LFPs were significantly correlated with the BOLD response (Logothetis et al., 2001). While there was also a weaker correlation between BOLD and MUA, it is likely that this correlation stems mainly from the correlation between MUA and LFPs rather than from an actual relationship between MUA and BOLD (Ekstrom, 2010; Logothetis and Wandell, 2004). More recently, a study using awake behaving monkeys also showed significant correlations between the BOLD response and LFP recordings suggesting that LFPs are a more robust predictor of the BOLD signal (Goense and Logothetis, 2008). Taken together, these findings indicate that the neural mechanisms reflected by BOLD contrast involve input and intracortical processing of a given area as opposed to the spiking output of that region. Due to this relationship between the BOLD signal and cortical processing, fMRI is a useful tool for studying brain activity during cognitive processes. Unlike the intracortical recordings used to measure LFPs, which is a highly invasive technique, fMRI can be used to measure neuronal activity in the human brain. Thus, fMRI has become instrumental in relating the findings of primate neurophysiological research with the psychological constructs developed through behavioral experiments involving human participants. For this reason, fMRI was the method of choice to measure cortical activity in the experiments of this dissertation.

Experimental Designs

   A major advantage of fMRI is that it allows researchers to non-invasively observe

brain activity with high spatial resolution, on the order of approximately 1mm

(Logothetis, 2008). However, due to the sluggish nature of the hemodynamic response,

the temporal resolution of fMRI is in the range of 1-4 sec. Despite this limited temporal

resolution, recent advances in data collection and analysis procedures have enabled the

use of event-related fMRI designs to extract timing information following sensory or

cognitive events.

   Many fMRI studies have used blocked designs where multiple trials of a single

condition are presented in rapid succession. This type of paradigm has the advantage of

being extremely powerful for signal detection. However, the usefulness of these

procedures is limited in the ability to separate the processing stages of a given task and

these designs are not appropriate for answering certain experimental questions. Event-

related designs allow for different conditions to be presented in a random order which is a

major advantage for many cognitive tasks. Dale and Buckner (1997) demonstrated that

even with short inter-trial intervals (as fast as 2 seconds) robust activation could be

observed for randomly mixed trial types by using selective averaging techniques.

Additionally, Ollinger and colleagues (2000) described a technique to separate the BOLD

response to the components within a single trial, for example, stimulus presentation and

response selection. This technique involving presentation of partial trials has allowed

researchers to observe the neural mechanisms unique to each stage in a cognitive process.

These advances have benefited the field by increasing the range of questions that can be

addressed using fMRI methodology.

The experimental evidence presented in this introduction provided the basis for the experiments described in this dissertation. The next chapter will describe the rationale behind four experiments that were designed to develop an understanding for the role that attention plays in biological motion processing and perception. This will be followed by a detailed description of each experiment. The final chapter will then discuss general conclusions and implications for this research.

CHAPTER 2: RATIONALE AND PREDICTIONS

The novel experiments described in the following chapters seek to better define the relationship between selective attention and biological motion perception. This section describes the rationale behind each of these experiments and predictions regarding the possible outcomes and their implications.

Experiment One

The aim of the first experiment was to demonstrate that the brain's response to biological motion, as measured by event-related fMRI, shows category specific attentional modulation. Results from an earlier experiment (Safford et al., 2010) indicated that the responses in lateral temporal cortical regions that show a preference for biological motion, including a region in the STS, were strongly attenuated when attention was directed away from the preferred motion category. However, due to the use of a block design, these findings could be interpreted as changes in the overall attentional state, rather than responses to the individual stimuli. This project sought to replicate and expand on these results by showing that similar findings can be observed using an event-related fMRI paradigm. It is also critical to show that these effects of attention are robust using an event-related design in addition to a block design as the other experiments depended on use of an event-related paradigm. Additionally using this paradigm allowed

for examination of task related changes in effective connectivity of the network involved using a psychophysiological interaction (PPI) analysis.

Here, object-based attention was expected to show category-specific attentional modulation of the BOLD response. Biological motion preferring regions, including right STS, should show a reduced response to unattended biological motion compared to when attention is directed toward the biological motion stimuli. The responses in regions that prefer tool motion, such as the left ITG, were expected to be attenuated when attention is directed to biological motion compared to when attention was directed to tool motion.

Experiment Two

As discussed above, the biased competition model of attention predicts that there is competition between simultaneously presented visual stimuli and that this competition is greatest at the level of the RF. In experiment two, the effects of spacing between simultaneously presented stimuli on performance in biological motion recognition was measured. While previous experiments by other authors (i.e. Kastner and colleagues) used both sequential and simultaneously presented stimuli, in the experiments described in this dissertation, stimuli were only presented simultaneously to examine the effects on competition of separating the stimuli in the spatial domain rather than in the temporal domain. Additionally, spatial cues were used to reduce demands of spatial attention and assure that only object-based selective attention was manipulated. Here, peripherally presented biological and tool motion were presented either overlapping or spatially separated in three possible spatial configurations: overlapping, different quadrant/same hemifield, different quadrant/different hemifield.

If attentional demands are created by conflict between simultaneously presented stimuli falling within the same RF, separating the stimuli should reduce processing demands. Thus, performance would be best for the different hemisphere conditions, followed by the same hemisphere configuration and finally worst for the overlapping stimuli. An alternative possibility was that there could be no difference between the conditions; this could be explained by large RFs for processing this type of stimuli. If the RFs for these stimuli encompass a whole hemifield (but not the whole visual field), there would be no difference between the overlapping and same hemifield conditions, but improved performance for the different hemifield configuration. It was also possible that there would be no difference between the same and different hemifields, with both showing better performance compared to the overlapping configuration.

Experiment Three

In addition to the influence that spacing between stimuli was anticipated to have on performance, differences in the cortical response to biological motion were also expected. If the biased competition model can explain the attentional modulation of biological motion processing, separating stimuli into distinct RFs should reduce the attenuation of the response to unattended stimuli observed with an overlapping display. Alternatively, if the response in biological motion preferring regions remains the same regardless of spatial configurations, this could indicate that biased competition does not accurately describe the role of attention; perhaps attention as a spot-light or feature-integration process (A. M. Treisman & Gelade, 1980) may be more appropriate.

In addition to the effects that could be observed in high-level regions, lower-level visual regions might also demonstrate effects of spatial configuration. Although it was unlikely that these regions would show effects of category preference (biological motion vs tool motion), it was possible that the response to overlapping stimulus conditions would have been reduced compared to the separated conditions due to competitive interactions between the overlapping stimuli that were not present when the stimuli are presented in separate RFs. Additionally, the strength of such effects was likely to change along the visual hierarchy as a function of RF size.

Experiment Four

The biased competition model of attention maintains that competition between stimuli is resolved in favor of the attended stimulus and that a possible mechanism for this attentional influence is through "preactivation" of the brain regions involved in processing the attended stimuli. For this experiment, it was hypothesized that object-based attention would induce category specific increases in neural baseline activity. Biological motion preferring regions (such as the STS) should show an increase during the cue period when attention is directed toward human as compared to tool motion conditions. Alternatively, it was also possible that no category-specific baseline increases would be observed, suggesting that this pre-activation occurs only for spatially directed attention, while object-based attentional biases are manifest through some alternative mechanism.

CHAPTER 3: EXPERIMENT ONE

The purpose of the experiment described in this chapter was to establish that the cortical response to biological motion, as measured by event-related fMRI, is modulated by object-based attention. While previous research has suggested that the neural mechanisms underlying biological motion perception are modulated by attention (Safford et al., 2010), these results were limited by the use of a block design. Here, the focus of object-based attention was manipulated on a trial-by-trial basis while the event-related fMRI signal was measured. Additionally, to develop a better understanding of the cortical network involved in this process, an effective connectivity analysis was implemented. Results indicated that the response to biological motion was influenced by attention. When attention was directed toward tool motion, the response in biological motion preferring regions, including the STS, was reduced compared to when biological motion was the focus of attention. Additionally, a psychophysiological interaction analysis indicated that when conflicting visual information is present, regions in the frontoparietal attention control network interact to modulate the response to biological motion.

Background

Distinct regions of the lateral temporal cortex have shown differential selectivity for specific object-motion categories with superior areas (ie. STS) showing greater

responses to biological motion, especially in the right hemisphere, while inferior areas such as middle temporal gyrus (MTG), particularly in the left hemisphere, prefer tool motion (Beauchamp et al., 2002, 2003). Additionally, previous research has suggested that this preferential response to biological motion in lateral temporal regions including STS and MTG is modulated by selective attention such that there is a reduction when participants direct their attention to another motion category (tool motion) (Safford et al., 2010). However, this previous experiment was limited by the use of a block-design and the exact mechanism through which this attentional modulation occurs is unclear. With a block design, it is difficult to determine whether differences are actually due to the brain's response to the individual videos or based on changes in an attentional state. Accordingly, in this experiment, surface based event-related fMRI was used in combination with a psychophysiological interaction (PPI) analysis (Friston et al., 1997; Gitelman, Penny, Ashburner, & Friston, 2003) to look at task-related changes in effective connectivity between regions that show object-motion category-specific responses and attention control regions.

To develop a better understanding of the mechanism through which attention modulates the neural activity underlying biological motion perception, it is useful to observe how the brain regions involved work together as well as how these connections change as a function of task demands. PPI is a regression based method for testing context-dependent changes in coupling between active brain regions. This type of analysis, usefully, goes beyond the standard structure-function correlation of convolution models to examine network dynamics.

The present study provides additional support for attentional modulation of the cortical response to biological motion and extends these findings by showing that they are robust with event-related design and exploring the pattern of connectivity between the brain regions involved.

Methods

Participants

Eighteen healthy individuals (9 males; age range = 22-37 years; mean = 26.8; SD = 3.9) were recruited from the George Mason University community and participated in this event-related fMRI experiment. All participants were right handed with normal or corrected-to-normal vision. The experiment lasted approximately 2 hours. Participants were compensated $15 per hour and provided written informed consent in accordance with the Human Subjects Review Board at George Mason University (Fairfax, VA).

Stimuli and Task

Visual stimuli consisted of point-light animations of human and tool motion. The human motion stimuli were created by videotaping an actor who was dressed in black clothing with points of light affixed to the head and major joints (shoulders, elbows, wrists, hips, knees, ankles) in a dark room. Actions included jumping jacks, walking up stairs, sitting up, kicking right, kicking left, bending over to touch toes and walking in place. Point-light animations of tool motion were created by placing lights on several tools and moving them in an appropriate manner. The tools used included scissors, pitcher, broom, hammer, tongs, saw and pliers. Adobe Premiere Pro 2.0 (Adobe Systems) was used to edit the videos so that they were of uniform length, and the tools and humans were of relative size. Scrambled versions of the biological and tool motion

videos were created in Matlab (MathWorks). The motion of each light point was tracked on a frame-by-frame basis using a luminance-based clustering algorithm. The starting point, orientation, and temporal phase of each point were then scrambled, reapplied to the points, and converted into movie files. The tool and human videos were then overlaid with each other or the scrambled versions of the other type of motion, and a red central fixation cue was added.

Stimuli were presented during neuroimaging data acquisition using Presentation software (Neurobehavioral Systems). Prior to video presentation, participants' attention was directed toward either human or tool motion in the single and overlapping stimuli by a cue word ("Human" or "Tool") which was presented for 1.5 seconds. After an ISI of 1 second, the point-light video was presented for 2 seconds. Following the video, participants indicated by button press whether a probe word matched the video. The ITI was 2 seconds (Figure 1). With this task, participants were required to direct their attention to one motion category or the other at the level of object-based recognition on a trial-by-trial basis. The following four experimental conditions and a null trial condition were used: attend to biological motion (Biological$_{Intact}$ plus Tool$_{Scram}$ and Biological$_{Intact}$ plus Tool$_{Intact}$) and attend to tool (Tool$_{Intact}$ plus Biological$_{Scram}$ and Tool$_{Intact}$ plus Biological$_{Intact}$). Each subject completed eight runs of 40 trials each while fMRI data were collected using an event-related paradigm. In each run there were eight trials per condition, for a total of 64 trials per condition.
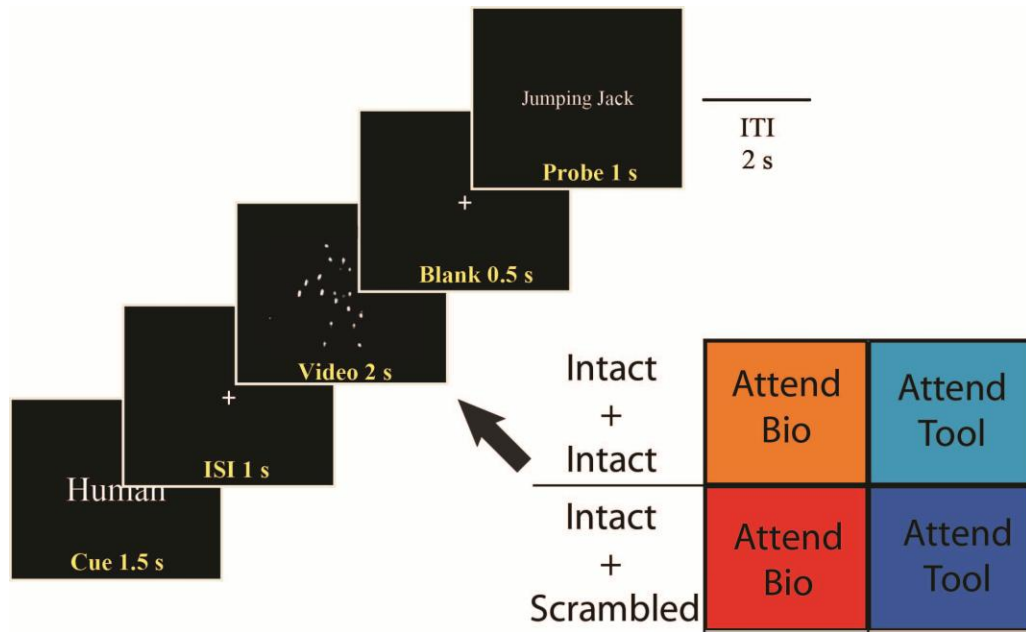
Figure 1: Experiment 1 – Task

Button presses were recorded for behavioral analysis and incorrect trials were removed from fMRI analysis. Additionally, there was apparent confusion over the "kicking-right" and "kicking-left" trials. These two videos were quite similar (basically a mirror image of one another) and some participants miss-assigned which was "kick-right" and which was "kick- left". This confusion made a significant contribution to the proportion of incorrect trials in the two biomotion conditions (with these trials performance is better for the tool conditions but without these trial performance is better for the biological motion conditions, see Results). Since it was unclear what this confusion represents cognitively in each participant, some understood the difference and some did not, these trials (whether they were correct or incorrect responses) were also removed from the fMRI analysis for all participants. Behavioral analysis included

examination of accuracy (% correct) and reaction times (RT); RTs were converted to log(RT) to reduce skewness.

fMRI Data Acquisition and Analysis

fMRI data were collected using a research-only Siemens Allegra 3T scanner at the Krasnow Institute for Advanced Study at George Mason University. Visual stimuli were displayed on a rear projection screen and viewed by participants on a head coil-mounted, angled mirror. The following parameters were used to acquire functional gradient-echo, echoplanar imaging scans: 33 slices (4 mm slice thickness; 1 mm gap), repetition time (TR)/echo time (TE) = 2000/30 ms, flip angle = 70°, 64 x 64 matrix with 3.75 x 3.75 mm in-plane resolution, field of view = 24 cm. In each run 174 volumes were collected. At the end of the fMRI scanning session, two T1 whole-head anatomical structural scans were collected using a three-dimensional, magnetization-prepared, rapid-acquisition gradient echo (MPRAGE) pulse sequence (160 1-mm-thick slices, 256 X 256 matrix, field of view = 260 mm, 0.94 mm voxels, TR/TE = 2300/3 ms).

Cortical surfaces were reconstructed from the two MPRAGE scans using FreeSurfer software (surfer.nmr.mgh.harvard.edu/). This automated processing involves motion correction, averaging of the two images, removal of nonbrain tissue, intensity normalization and segmentation to create a representation of the pial surface. The pial surface model was also inflated to support visualization of activation occurring within cortical sulci.

Preprocessing of fMRI data included removal of the first three volumes from each run to compensate for the time it took to reach equilibrium magnetization. The FEAT

(fMRI Expert Analysis Tool) software tool of the FSL (fMRI of the Brain Software Library) toolbox (www.fmrib.ox.ac.uk/fsl/) was used for fMRI analysis. The fMRI time series were high-pass filtered at 128 s and motion corrected. No spatial smoothing was applied at this stage of analysis. For each run, the onset and duration of each video was modeled, creating four regressors (one for each condition) that were convolved with a double gamma function (phase = 0) to estimate the response to the stimuli separately for each of the four conditions. Separate regressors of non-interest were also created for trials with incorrect trials and trials with the "kicking" videos (see above). Prewhitening was also used to remove temporal autocorrelation of the fMRI time series. Contrast-of-the-parameter estimate (COPE) images were calculated, and the estimates were averaged over the eight functional runs. The COPE images were then projected onto the FreeSurfer-generated surface of each individual, transformed into Talairach space, and smoothed with an 8 mm full width at half-maximum (FWHM) Gaussian kernel. A surface based mixed effects ANOVA with fixed factors of category (Biological vs Tool) and overlap (Intact plus Intact vs Intact plus Scram) and participants as a random effect was conducted. Results were viewed on the average inflated surface with a FDR of $p <$ 0.05. Plots were created by averaging COPEs across participants from within circular ROIs with radii of 4mm centered on the vertex of peak significance within each cluster, and within-subjects standard errors (SE) from the ANOVA effects were calculated using the method described by Loftus and Masson (1994).

Psychophysiological Interaction Analysis

In order to develop further insight into the network underlying attentional modulation of biological motion perception, a PPI analysis (Friston et al., 1997; Gitelman et al., 2003) was conducted using SPM8 software (Wellcome Department of Imaging Neuroscience, London, UK). Due to the interest in top-down modulation, a region of interest in the left SPL showing an effect of overlap (Intact plus Intact vs Intact plus Scram) was selected from the group surface-based results. Within this region the peak of significance was selected for each individual and a circular ROI with a 2mm radius was created. These surface-based regions were then transformed to volumes and the first eigenvariate of the timeseries from within these masks were extracted. A PPI-regressor was then generated for each of the four conditions by multiplying the deconvolved timeseries by a vector coding the onsets of videos for that condition. The four PPIs were then entered into a first-level general linear model (GLM) as regressors along with the psychological effects, the left SPL timeseries and regressors of no-interest (incorrect and "kicking" trials). For each PPI, subject-specific contrast images were generated by applying a t-contrast that was 1 for the PPI regressor and 0 elsewhere. A second-level 2X2 repeated-measures group ANOVA was then conducted to identify regions that showed changes in coupling with SPL in a task dependent manner. Group results were viewed in standard space with an uncorrected threshold of $p < 0.005$ and an extent threshold of 10 voxels.

Results

Behavioral and neuroimaging data were analyzed with a 2x2 repeated measures ANOVA with factors category (Bio vs Tool) and overlap (Intact plus Intact vs Intact plus

Scram). Trials with incorrect response and trials with "kicking" videos were discarded

from fMRI analyses.

Behavioral Results

       Behavioral task performance is summarized in Figure 2. Analysis of the log(RT)s

of correct responses for all trials showed no differences between conditions. Analysis of

accuracy showed a main effect of motion category, $F(1,17) = 25.50, p < 0.05$, which

indicated that participants' performance was better for the two tool conditions compared

to the two biological motion conditions. However, when the trials involving "kicking"

videos were removed, there was an RT main effect of attention (Intact plus Scram vs

Intact plus Intact), $F(1,17) = 7.455, p < 0.05$, which indicated that responses were faster

when both human and tool motion was overlapping with scrambled motion compared to

when the videos were overlapping with intact versions of the other motion type. There

was also a main effect of motion category for accuracy, $F(1,17) = 5.03, p < 0.05$,

however, here this effect was reversed indicating that performance was better for the

biological motion conditions compared to the tool motion conditions.
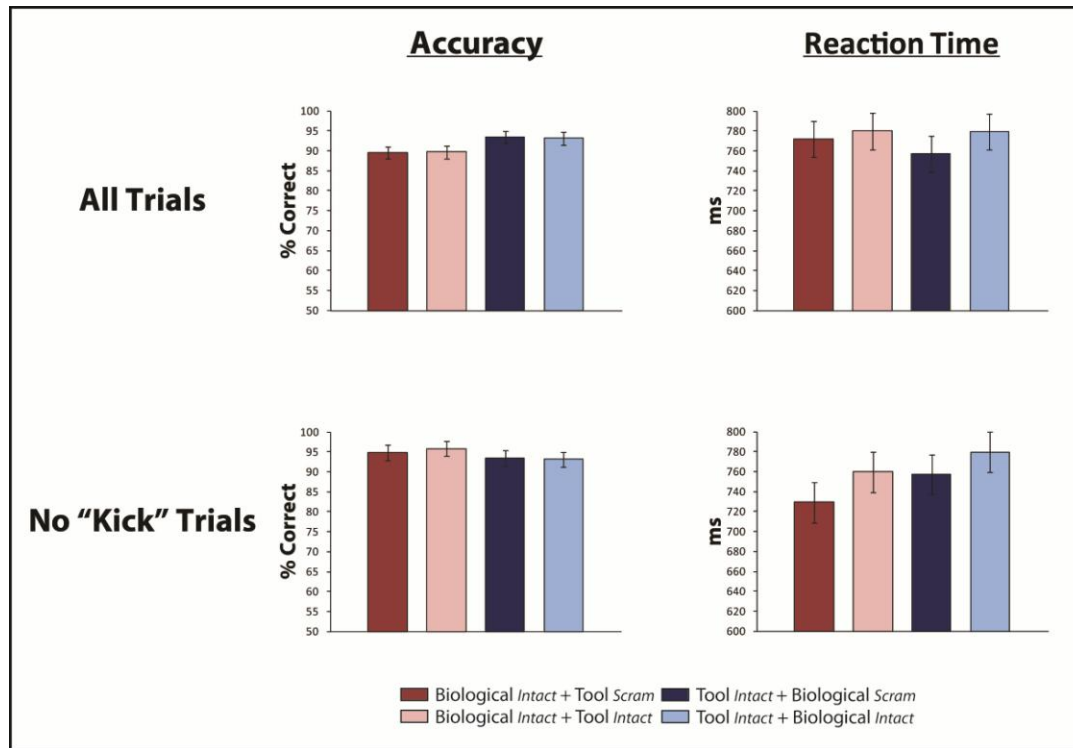
Figure 2: Experiment 1 – Behavioral performance data – Accuracy and RT for each of four conditions with and without "Kicking" trials

Cortical Surface-Based Analysis of fMRI Data

The fMRI responses of each participant were mapped onto their cortical surface

and then transformed into standard space for group analysis. Group-based fMRI

responses were then analyzed on an average surface using a mixed-effects ANOVA.

Cortical regions that showed a significant ($p < 0.05$ FDR-corrected) main effect of

motion category (Biological vs Tool) are listed in Table 1 and visualized on an inflated

average cortical surface in Figure 3. Additionally, Figure 4 shows plots of COPE values

for each of the four conditions. As expected, the BOLD response of regions in the lateral

temporal cortex showed a preference for motion category, and, as has been previously

reported, these responses showed a degree of hemispheric lateralization (Beauchamp et al., 2002, 2003). There were large bilateral regions showing significantly greater activation to the biological motion relative to tool motion conditions in lateral occipital temporal cortex including STS and MTG for both the Intact plus Scram and Intact plus Intact conditions ($p < 0.05$ FDR-corrected). Additional regions that showed this preference for biological motion included bilateral precuneus, fusiform gyrus,   In left inferior temporal gyrus (ITG) a significantly greater response was observed to the Intact plus Scram and Intact plus Intact tool motion conditions compared with the Intact plus Scram and Intact plus Intact biological motion conditions ($p < 0.05$ FDR-corrected).
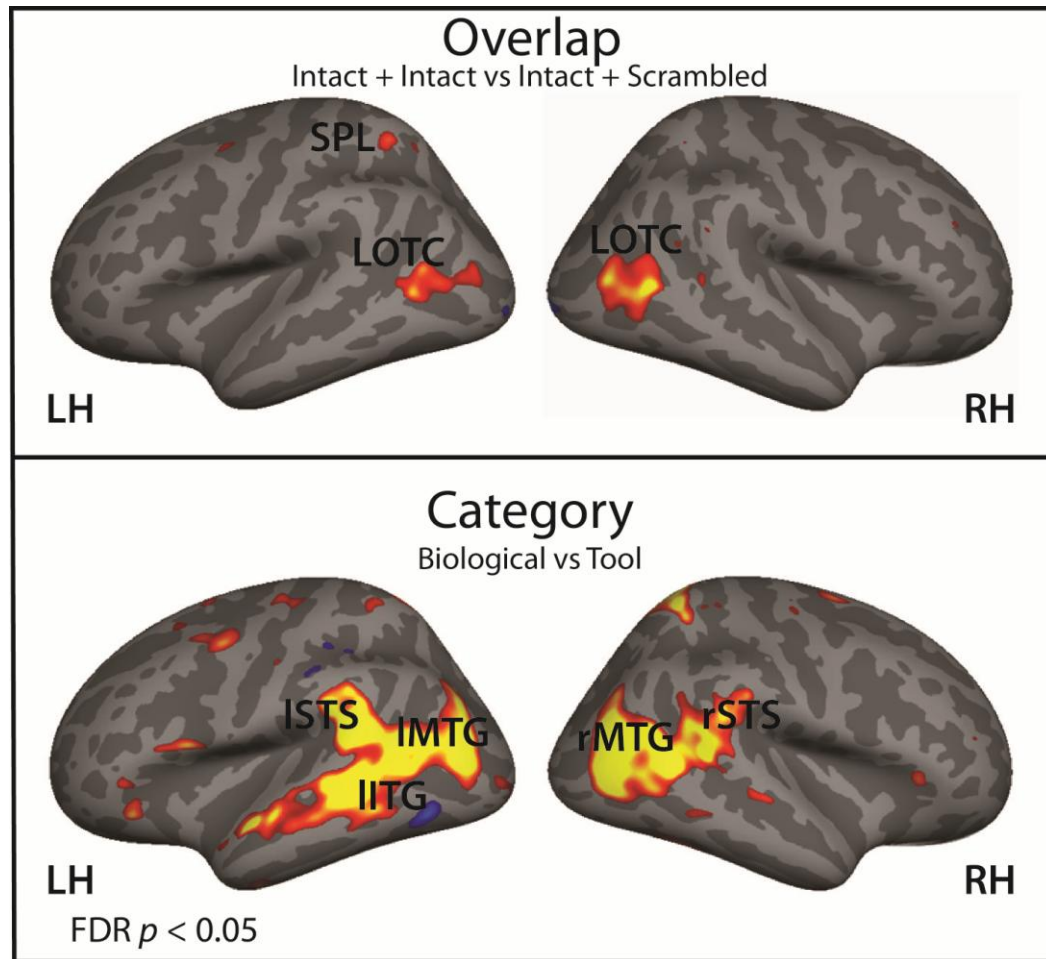
Figure 3: Experiment 1 – Cortical surface-based fMRI results displayed on inflated surface of the FreeSurfer fsaverage brain.
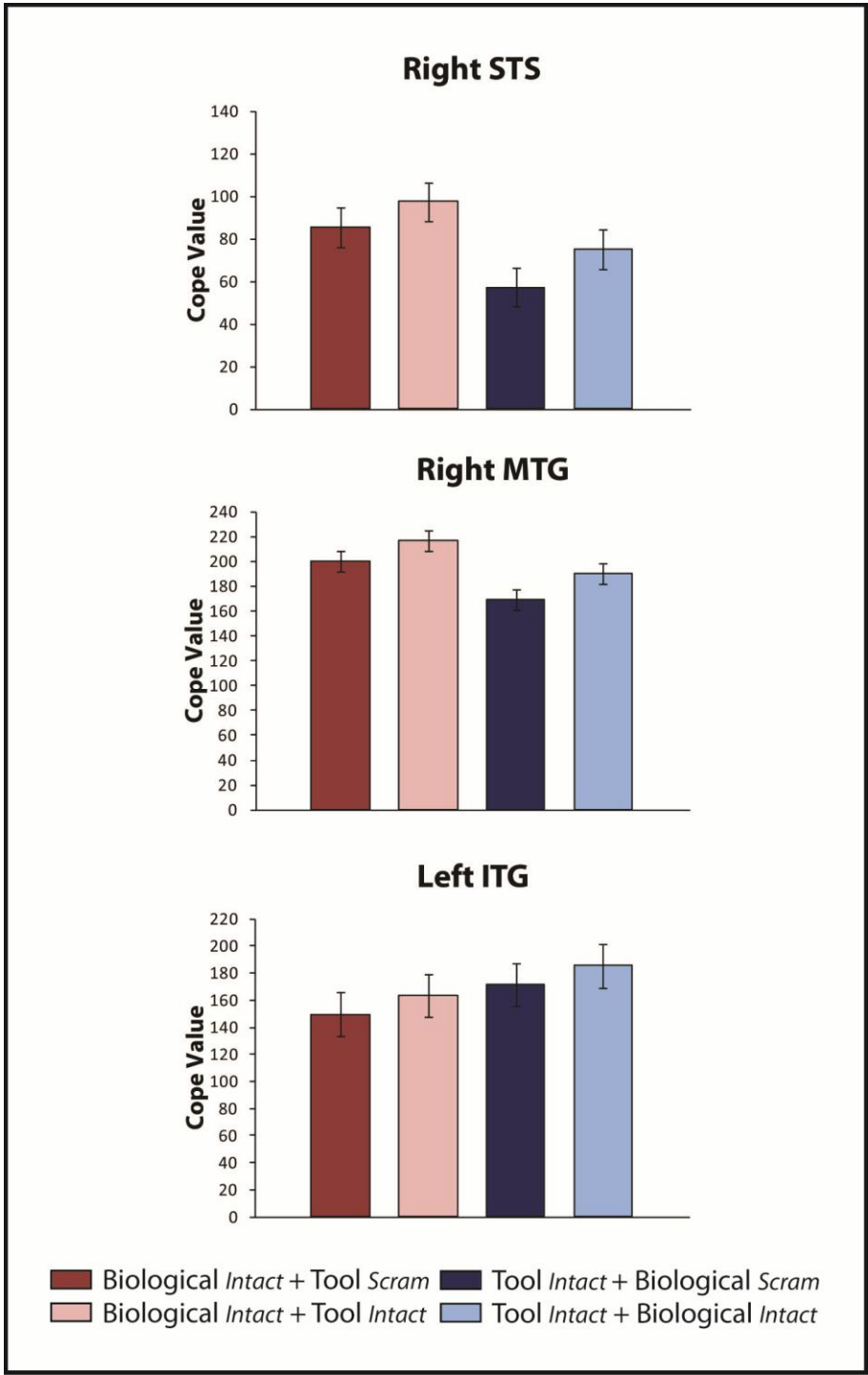
Figure 4: Experiment 1 – Cortical surface-based fMRI results - Plots of COPE values for each of the four experimental conditions within a 4mm radius circular ROI surrounding the local maxima for significant regions. Error bars represent the within-subjects confidence interval.

Importantly, consistent with previous findings (Safford et al., 2010), these responses were dependent on selectively attending to the preferred motion category; when biological motion was present but attention was directed to the tool motion (Tool Intact plus Biological Intact condition), the responses in the biological motion preferring regions (e.g., bilateral STS and MTG) were significantly reduced compared to when attention was directed toward biological motion (Biological Intact plus Tool Scram and Biological Intact plus Tool Intact conditions) ($p < 0.05$ FDR-corrected). Likewise, when tool motion was present but attention was directed to the biological motion (Biological Intact plus Tool Intact condition), the responses in tool motion-preferring regions were significantly lower compared with when attention was directed toward tool motion (Tool Intact plus Biological Scram and Tool Intact plus Biological Intact conditions) ($p < 0.05$ FDR-corrected).

Table 1: Experiment 1 – Cortical surface-based fMRI results: Talairach position of regions showing main effects of motion category and overlap condition.
Values in the Max column correspond to the maximal value of –log10(p) significance. Bio, Biological; I, Intact; S, Scrambled; LH, left hemisphere; RH, right hemisphere; LOTC, lateral occipital temporal cortex; MTG, middle temporal gyrus; ITG, inferior temporal gyrus; STS, superior temporal sulcus; SPL, superior parietal lobule.

Region	Coordinates			Cluster size (mm2)	Max	Hemi
	x	y	z			
Bio > Tool						
LOTC	48.8	-72.4	10.9	4110.49	8.328	RH
MTG	48.8	-72.4	10.9		8.328	RH
STS	49.7	-37.9	12.9		7.803	RH
Precuneus	12.6	-48.1	58.7	3446.36	6.230	RH
Superior Parietal	12.6	-48.1	58.7		6.230	RH
Precuneus	14.2	-43.5	37.1		5.252	RH
Lateral Fusiform	40.4	-52.6	-10.8	320.11	5.043	RH

Medial Fusiform	31.9	-33.8	-10.6	276.41	4.723	RH
Precentral	22.1	1.5	57.0	116.11	3.826	RH
LOTC	-60.3	-42.5	17.0	6235.30	9.740	LH
Supramarginal	-60.3	-42.5	17.0		9.740	LH
Anterior STS	-53.7	-42.0	-0.5		8.579	LH
MTG	-47.2	-73.6	13.3		8.179	LH
Posterior STS	-43.0	-52.2	11.5		7.827	LH
Precuneus	-10.3	-56.7	52.9	2857.42	6.912	LH
Medial Fuisform	-36.2	-38.5	-11.2	309.87	6.778	LH
Lateral Fusiform	-44.3	-18.9	-23.4	542.24	5.791	LH
Precentral	-43.1	3.4	43.2	360.73	3.880	LH
Tool > Bio						
ITG	-43.4	-61.0	-1.5	149.94	-3.525	LH
I+I > I+S						
MTG	46.7	-58.8	8.5	928.96	6.159	RH
Precuneus	8.1	-48.1	51.4	96.29	3.962	RH
MTG	-49.5	-59.0	7.2	640.17	5.239	LH
SPL	-33.7	-49.7	56.1		4.546	LH

In addition to regions showing main effects of category there were also regions
that showed a main effect of overlap (Intact plus Intact vs Intact plus Scram); these are
listed in Table 1 and visualized on an inflated average cortical surface in Figure 3. This
effect was observed in bilateral MTG/LOTC as well as left superior parietal lobule (SPL)
($p < 0.05$ FDR-corrected).

PPI Analysis

PPI analyses revealed that presentation of two intact objects produced significant
changes in the coupling between the left SPL and a network of brain regions including
attention control regions and biological motion processing regions, shown in Figure 5 and
listed in Table 2. The left SPL region showed increased overlap-dependent interactions

with bilateral regions in the inferior frontal gyrus (IFG) as well as the left STS ($p < 0.005$,

uncorrected, extent threshold = 10 voxels).

Table 2: Experiment 1 – PPI results. Talairach position of regions showing significant PPI with the left SPL during Overlap.
Values in the Max column correspond to the maximal value of Z statistic. LH, left hemisphere; RH, right hemisphere; IFG, inferior frontal gyrus; STS, superior temporal sulcus.

Region	Coordinates			Cluster size (voxels)	Max	Hemi
	x	y	z			
IFG	44	32	2	98	3.35	RH
IFG	54	18	8	18	3.01	RH
IFG	-56	22	22	17	3.03	LH
STS	-50	-42	10	17	2.78	LH
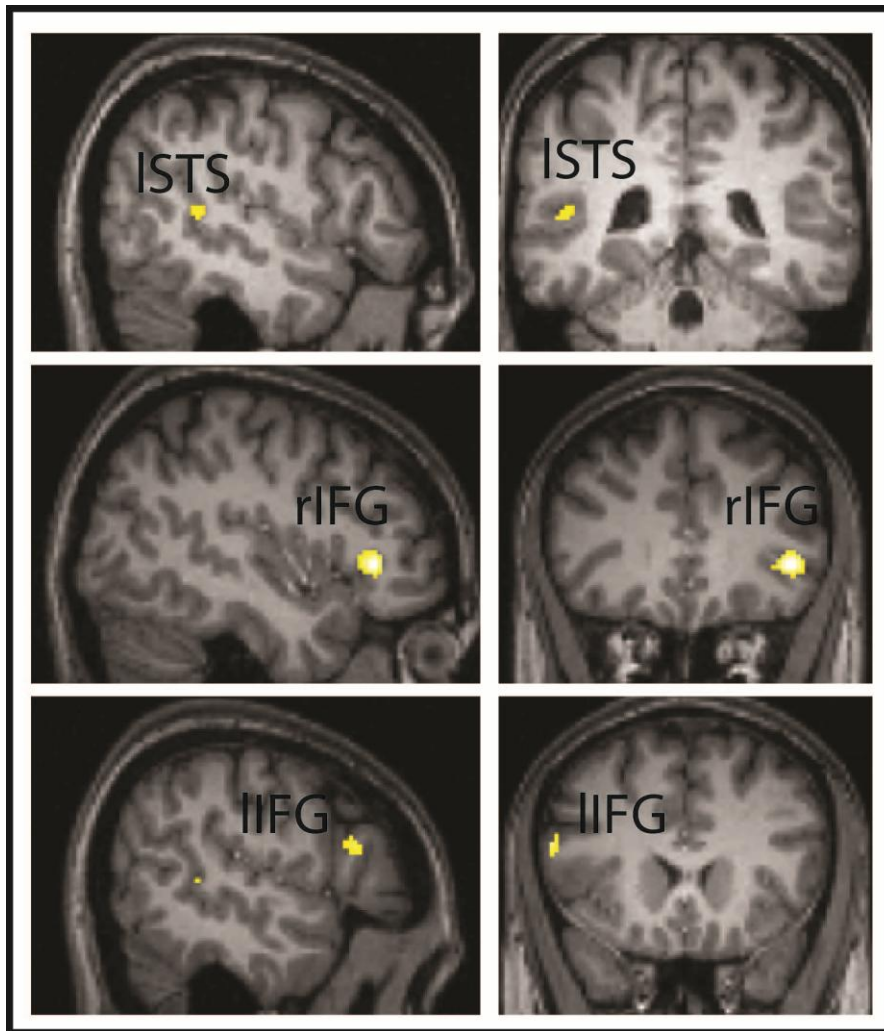
Figure 5: Experiment 1 – PPI with the left SPL during Overlap; p < 0.005, uncorrected, extent thresh = 10 voxels.

Discussion

The experiment described in this chapter aimed to demonstrate that event-related

fMRI could reveal attentional modulation of the cortical response to biological motion.

Here, spatially overlapping point-light animations of human and tool motion were

presented simultaneously and the level of brain activity was compared when selective

attention was directed toward one category or the other at the level of object-based

recognition on a trial-by-trial basis. If the response to biological motion is influenced by

attention and task-demands, the BOLD signal should be reduced when the biological

motion stimuli are unattended and irrelevant to the task at hand.

Taken together with previous findings (Safford et al., 2010), these results support

this hypothesis and emphasize the critical role that attention plays in processing

biological motion stimuli. When object-based attention was directed toward competing

visual information – in this case tool motion – the neural response to biological motion

was reduced compared to when participants attended to the biological motion stimuli.

Likewise, when tool motion was present but attention was directed toward overlapping

biological motion, the fMRI response of left ITG was reduced. Importantly, here the use

of an event-related fMRI design allows these conclusions to be related to the visually

presented stimuli, rather than limited to the attentional state of an entire block that was a

possible explanation with the earlier design.

In addition to this effect of attentional modulation of object-motion category

selective responses, regions in bilateral LOTC and left SPL showed increases in the two

conditions in which participants had to segregate the attended motion category from the

unattended category relative to when participants had to segregate the attended motion

category from a scrambled version. Using high-density EEG and cortical source

localization methods, earlier work has demonstrated that this effect occurs earlier in

processing, around 200 ms (Safford et al., 2010), and reflects the attentionally modulated

N1 component (Luck, Fan, & Hillyard, 1993; Mangun & Hillyard, 1991; Parasuraman,

1980). As the N1 component has been shown to reflect discriminative processing (Hopf, Vogel, Woodman, Heinze, & Luck, 2002; Vogel & Luck, 2000), the fMRI response observed in this experiment understandably represents the greater need to discriminate between two objects in the overlapping stimulus conditions. One possibility is that this discrimination-related activity in the SPL is a source (or relay) of top-down influences that are required under the more demanding discriminative conditions created with the overlapping stimuli.

To test this hypothesis, a PPI analysis was used to measure the influence that SPL has on biological motion processing regions under different task conditions. Stronger connectivity between SPL and STS was observed during the conditions involving greater competition between moving objects and where biological motion must be extracted from a background that includes other object motion. Additionally, SPL was also shown to have similar task-related interactions with the IFG, a well known component of the fronto-parietal attention control network (Corbetta & Shulman, 2002). These results support the suggestion that the attentional modulation observed in STS may be, at least in part, driven by top-down influences received via SPL. When conflicting stimuli are presented, SPL interacts with other regions in the attention control network, including IFG, to modulate the response to biological motion in STS. Importantly, these findings also emphasize the utility for effective connectivity techniques, such as PPI, for elaborating on the cortical mechanisms underlying cognitive processes including biological motion perception and attention.

These results support the idea that biological motion perception, while efficient and robust, is not attention free, and show that these effects are resilient enough to be observed using an event-related fMRI paradigm. PPI analyses showed that this attentional modulation comes at least in part from top-down influences from the frontoparietal attention network, particularly the SPL. However, the exact mechanism of this modulation remains uncertain. One possibility is that, consistent with the biased competition model (Beck & Kastner, 2009; Desimone & Duncan, 1995), the role of attention is to resolve competition between simultaneously presented visual stimuli. This competition is thought to be maximal for objects occurring within the RF of the same neural population. Thus, the experiment described in the next section aimed to explore this option by measuring the influence of spacing between concurrently presented stimuli on biological motion perception performance.

CHAPTER 4: EXPERIMENT TWO

The previous chapter described an experiment that demonstrated that the cortical response to biological motion is strongly modulated by selective attention. These results, combined with earlier findings, have indicated that selective attention plays an important role in processing of biological motion (Safford et al, 2010); however, it is unclear exactly what that role is. The experiment described below was designed to test the hypothesis that, in accordance with the biased-competition model of selective attention (Desimone and Duncan, 1995), the role of attention is to resolve competition between simultaneously presented stimuli in favor of the attended stimulus. This mutually suppressive competition is thought to be greatest when objects fall within the RF of the same neural population and is reduced when objects occur in separate RFs. For this reason, performance was measured while the spatial proximity of simultaneously presented point-light animations of human and tool motion was varied. Results showed improvements in performance when objects were separated, compared to when they were overlapping, and support the idea that the role of attention in processing biological motion stimuli is to resolve competition when stimuli are overlapping.

Background

There are multiple possible roles for attention, including integration of multiple features for recognition and resolution of competition that occurs between simultaneously

presented items. The specific mechanism that is involved in a given situation depends on the task at hand and the stimuli involved. Behavioral evidence that biological motion perception is modulated by attention (Thornton et al., 2004; Parasuraman et al., 2009) has suggested that this influence of attention is most relevant under conditions of high task difficulty; for example when the stimuli are ambiguous, degraded or presented along with other competing stimuli or tasks (Thompson and Parasuraman, 2012). This pattern of attentional modulation in some but not all circumstances is common among other types of natural stimuli such as faces and scenes (Li et al., 2002; Reddy et al., 2004; VanRullen et al., 2005) and gives an important clue as to the mechanism of attention.

While the feature integration theory of attention, argues that perception involves binding together preattentive features and that this is always an attentionally demanding process, (Treisman, 1998; Treisman and Gelade, 1980), there are certain classes of stimuli that have been shown in some situations to be processed to the level of categorization independent of attention (Li et al., 2002; Peelen et al., 2009; VanRullen et al., 2005). These include certain types of ecologically significant stimuli that we have considerable amounts of experience with, for example, faces, bodies and natural scenes. Importantly, specialized neural populations have been identified that respond preferentially to these "special" stimuli (Downing et al., 2001; Kanwisher and Yovel, 2006). For these stimuli, while attention is not always required for recognition, it is still needed to resolve competition when stimuli are presented simultaneously (Reddy and VanRullen, 2007), which is often the case in the visual scenes of our busy and cluttered

world – this is the concept proposed by the biased competition model of attention (Desimone and Duncan, 1995).

The biased competition model argues that when multiple stimuli are present simultaneously they compete for representation. Importantly, this competition is thought to occur at the level of the RF. When stimuli are presented close together, competition between them is greatest because they fall within the RF of the same population of neurons. By increasing the spatial separation between simultaneously presented stimuli, competition (along with attentional requirements) should be reduced and performance should improve.

Effects of spatial configuration on the competitive interactions between simultaneously presented stimuli have been demonstrated behaviorally. Reddy & VanRullen (2007) varied the interstimulus spacing of items in separate visual search tasks involving faces and bisected colored discs. Participants were asked to identify the presence of a target in an array of between 2 and 6 items and possible spacing between adjacent items included 0.8°, 1.5°, 2.1°, 2.6°, 2.9° and 3°. Results from this experiment showed that when items were close together, search occurred serially for both tasks; however, increased spacing led to improved performance for face discrimination but not for the bisected disc task. The effect of spacing on the face discrimination task was explained as a reduction of competitive interactions between the stimuli at greater distances, which led to reduced attentional demands and improved performance. The bisected disc task showed no such improvement and this difference was explained by the existence of a neuronal population selective for faces but not for specific combinations of

colors in the bisected discs. Since there is no neural population selective for the bisected discs, attention was required for recognition, regardless of competitive interference from other items. For the faces, on the other hand, since there is a selective neural population, attention was needed to resolve competition only when items were presented close together. When the items were separated such that they fell into RFs, neuronal competition was reduced along with the need for attention.

Consistent with the findings that attention seems to be required for biological motion perception only in certain circumstances but not others (Parasuraman et al., 2009; Thornton et al., 2002; Thornton & Vuong, 2004) and given that there are brain regions that respond selectively to biological motion (Puce & Perrett, 2003; Vaina & Gross, 2004), it was hypothesized that when biological motion is presented with competing stimuli, attention is not required for recognition, but to resolve competition between target and distracters when they are presented in the RF of the same set of neurons. The behavioral data presented here tested this hypothesis by comparing performance on a biological motion identification task when point-light stimuli are spatially overlapping with another type of object motion (tool motion) and when the two objects were separated.

Pilot Experiment

To ensure that performance levels on the main task would not be at ceiling levels, a pilot experiment was conducted to determine the presentation conditions necessary for approximately 85% accuracy on the point-light biological/tool motion action/tool identification task. This level of accuracy was desired because it was approximately two

standard deviations away from 100% accuracy, but also well above chance performance (50%). As a result there would be sufficient room to see differences in performance between conditions. To increase the difficulty of the task, noise masks were added both before and after the point-light animations and additional noise dots were superimposed over the biological and tool motions. Then five possible stimulus durations were tested: 100ms, 200ms, 400ms, 800ms and 1600ms.

Methods

Participants

Two groups of healthy individuals (Group 1: N = 19; 7 males; 17 right handed; age range = 18-24 years; mean = 19.05; SD = 1.35; Group 2: N = 12; 3 males; 11 right handed; age range = 18-53 years; mean = 22.92; SD = 9.83), were recruited from the undergraduate participant pool through the SONA system at George Mason University to participate in the pilot portion of this experiment. The experiment lasted approximately 1 hour and participants received one credit toward course requirements. Prior to the experiment, participants gave written informed consent in accordance with the Human Subjects Review Board at George Mason University.

Stimuli and Task

Visual stimuli consisted of point-light animations of human and tool motion that were overlapping with scrambled versions of the other motion type. The task was similar to that used in Experiment One and involved identification of biological and tool motion on a trial-by-trial basis. Stimuli were presented using Presentation software (Neurobehavioral Systems). Prior to video presentation a category cue, either "Human" or "Tool" was presented for 1.5 sec. The category cue was 100% valid. Then, following

a 1 sec ISI, point-light videos of human or tool motion were presented. To increase task difficulty, additional noise dots, created from the trajectories of the human and tool motion with spatially scrambled start points, were superimposed on the intact human and tool motion. Two levels of noise were tested, group 1 had 44 noise dots and group 2 had 22 noise dots. Additionally, a mask was added to the beginning and end of the videos so that the intact stimuli began 500ms following the onset of the mask. The mask and videos were created such that the total number of moving dots remained consistent across the entire video. Five durations of the intact portion of the video were tested: 100ms, 200ms, 400ms, 800ms and 1600ms. Following the video, participants indicated by button press whether or not a probe word matched the video. The ITI was 2 seconds.

Each participant completed five runs of 60 trials each. In each run there were six trials per each of the ten conditions, for a total of 30 trials per condition. Button presses were recorded for behavioral analysis, which included examination of accuracy (% correct).

Results

Task performance is displayed in . These results indicate that accuracy for biological motion identification was closest to 85% when the intact point-light actions were presented with 22 additional noise dots at stimulus duration of 1600 ms. Accuracy for identification of tool motion was close to 85% for 400 ms, 800 ms and 1600 ms with 22 noise dots. A 2 X 2 X 5 (Group X category X duration) ANOVA shows that overall, performance was significantly worse when there were 44 noise dots compared to when there were 22 noise dots, $F(1, 32) = 24.691$, $p < 0.05$. Mauchly's test indicated that the

assumption of sphericity had been violated for the main effect of duration and the interaction between category and duration. Therefore, degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity ($\varepsilon = .697$ for the main effect of duration and .703 for the interaction). When collapsing across groups, there was a significant interaction between category and duration $F(2.81, 89.99) = 4.47$, $p < 0.05$. There was also a significant main effect of duration which showed that performance improved with longer presentation durations, $F(2.79, 89.21) = 73.26$, $p < 0.05$. Finally, a significant main effect of category showed that performance was better for tool motion compared to biological motion, $F(1, 32) = 47.19$, $p < 0.05$.
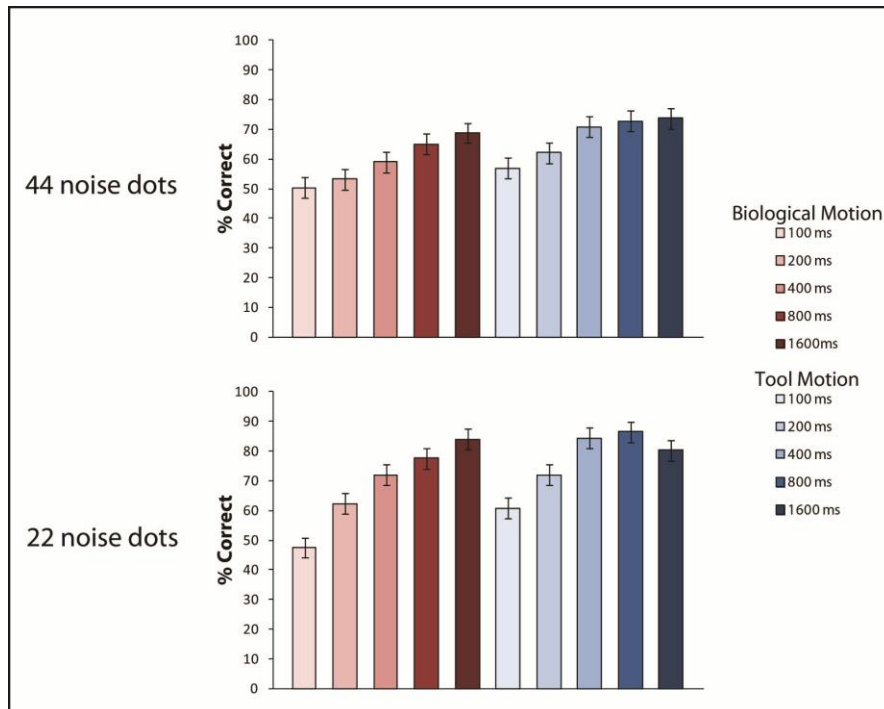
Figure 6: Experiment 2 – Pilot experiment results

Main Experiment

The goal of this experiment was to test the effect of spatial configuration on performance (accuracy and reaction time (RT)) by presenting point-light animations of human and tool motion simultaneously. Based on the findings of the pilot experiment, a presentation time of 1600ms with 22 noise dots was used in the main experiment.

Methods

Participants

Forty healthy individuals (15 males; 37 right handed; age range = 18 - 52 years; mean = 22.1; SD = 5.96), were recruited from the undergraduate participant pool through the SONA system at George Mason University to participate in this psychophysiological experiment. The experiment lasted approximately 1 hour and participants received one credit toward course requirements. Prior to the experiment, participants gave written informed consent in accordance with the Human Subjects Review Board at George Mason University.

Stimuli and Task

Visual stimuli consisted of point-light animations of human and tool motion made up of white dots on a black background. In this experiment, rather than being presented centrally, videos were presented in four quadrants (upper right, upper left, lower right and lower left) simultaneously at 5.8° eccentricity from fixation. The two motion categories were presented either overlapping or spatially separated resulting in three possible spatial configurations: overlapping, different quadrant/same hemifield (ie. upper and lower right or left), and different quadrant/different hemifield (ie. right and left upper or lower). In all conditions, there was the same amount of moving dots (either noise or point-light

animation) in each of the four quadrants. The centers of the videos were separated by

8.2°. As before, prior to video presentation a category cue ("Human" or "Tool") was

presented for 1800ms. A spatial cue was used in all conditions to eliminate the

possibility that RT could be slower for the two separated conditions, relative to the

overlapping, simply because these two conditions might require greater visual search.

For the separated conditions, the locations where the biological and tool motion

subsequently appeared were cued. For the overlapping trials, cues were presented in the

location where the overlapping biological and tool motion appeared plus one other

quadrant so that there were an equal number of cued same and different hemifield

combinations. The 100% valid spatial cues were presented for 300ms during the category

(Human or Tool) cue. Following the video, participants indicated by button press

whether a probe word matched the video. The ITI was 2 seconds (Figure 7).
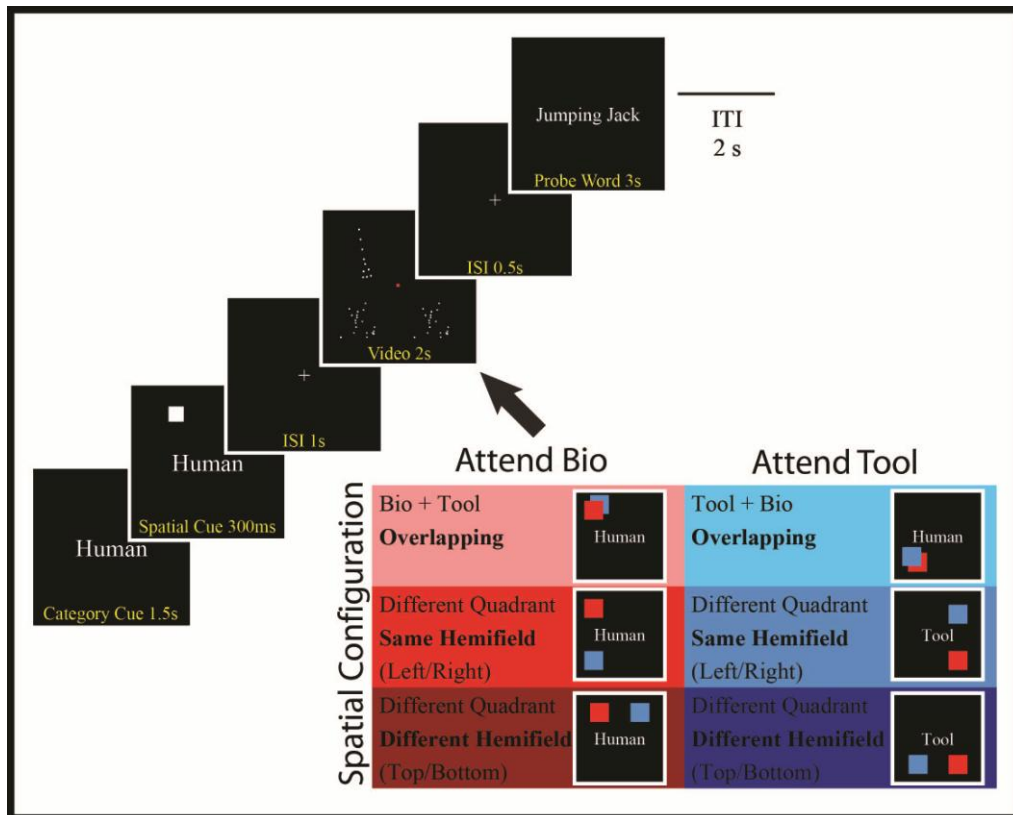
Figure 7: Experiment 2 – Main task

Prior to completing the main task, participants were trained using a progressive practice during which they were shown each of the point-light biological and tool motion videos with the word that would subsequently be used to describe the action or tool. Participants were also given the chance to perform the task under less difficult (ie. no added noise) conditions to ensure that they fully understood the task. During the main experiment, participants were instructed to respond as quickly and accurately as possible while maintaining central fixation.

Each participant completed 5 runs of 48 trials each. In each run there were 8 trials per each of the six conditions, for a total of 40 trials per condition. Button presses were recorded for behavioral analysis. Behavioral analysis included examination of accuracy (% correct) and RT; RTs were converted to log(RT) to reduce skewness.

Results

Behavioral task performance is displayed in Figure 8. Analysis of the RTs of correct responses showed main effects of both motion category, $F(1, 39) = 12.81$, $p < 0.05$, and spatial configuration, $F(1, 39) = 4.82$, $p < 0.05$. These effects indicated that log(RT)s were significantly faster for tool motion compared to biological motion and that responses were slower when the intact point-light stimuli were overlapping compared to the two separated conditions. Additionally, analysis of accuracy showed a main effect of spatial configuration, $F(1, 39) = 13.72$, $p < 0.05$, which indicated better performance on the separated conditions (both same and different hemifield) compared to the overlapping conditions. However, unlike with RTs, there was no significant difference in accuracy between the biological and tool motion conditions, $F(1, 39) = 1.43$, $p > 0.05$.
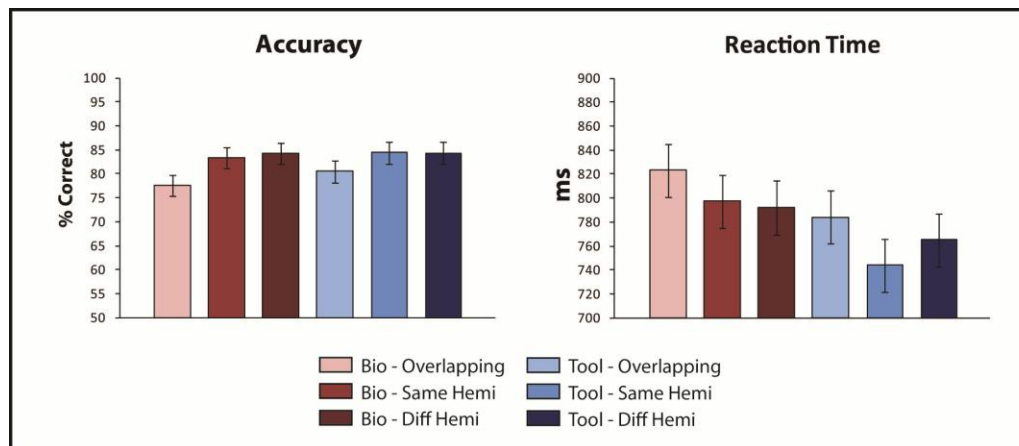
Figure 8: Experiment 2 – Main experiment results

Discussion

The present experiment sought to develop a better understanding of the role of attention in biological motion perception by determining the influence of spacing between simultaneously presented stimuli. It was hypothesized that as intact object motion stimuli were moved from overlapping to separate quadrants, competition between the stimuli would be reduced and performance would improve.

Previous psychophysiological experiments have demonstrated that increasing spacing between simultaneously presented items can influence performance on tasks involving natural stimuli (VanRullen et al., 2004; VanRullen et al., 2005; Reddy and VanRullen, 2007). Specifically, VanRullen and colleagues (2007) found that face discrimination improved in a visual search task as the stimuli were separated. Given these earlier findings, the results of the current experiment were anticipated – showing an improvement in performance (as measured by both accuracy and speed of response)

when biological motion stimuli were separated from competing tool motion stimuli compared to when the two stimuli were overlapping. These findings provide evidence for the idea that the role of attention in processing biological motion is to resolve competition when stimuli fall within the same RF. This interpretation is consistent with the evidence that attention seems to be particularly important when task conditions are more difficult, for example when actions are degraded or ambiguous or when competing visual information is present (Parasuraman et al., 2009; Safford et al., 2010., Thompson and Parasuraman, 2012; Thornton et al., 2002).

One unexpected result of this experiment was that there were no differences found between separating the "same" and "different" hemifields conditions. It is well established that RF sizes increase along the visual hierarchy (Kastner et al., 2001) and areas late in the visual stream have large RFs that can potentially cover the entire visual field (Gattass et al., 2005) or at least an entire hemifield. Given the expected size of the RF of the neurons involved in processing biological motion stimuli, the improvement in performance should be even greater when stimuli are moved into different hemifields compared to when they are in separate quadrants within the same hemifield. That these did not show this pattern of results indicates that the RF for biological motion stimuli may be at least as small as one quadrant. Additionally, these results are compatible with face discrimination experiments that have found 50% improvement in performance on a visual search task with stimulus spacings as small as 1° (Reddy and VanRullen, 2007).

The behavioral results presented in this chapter indicated that performance on a biological motion identification task improved as stimuli were separated from

overlapping, task irrelevant tool motion. These findings indicate that attention is involved in biological motion perception in order to resolve competition that occurs when stimuli are close together. The next experiment, described in Chapter 5, used an identical paradigm with an event-related fMRI design to examine changes in attentional modulation of the cortical response to biological motion stimuli as a function of stimulus spacing.

CHAPTER 5: EXPERIMENT THREE

The experiment described in the previous chapter tested the hypothesis that the role of attention in biological motion perception is to bias competition between simultaneously presented stimuli in favor of the attended object. It was hypothesized that competition would be greatest when objects occurred within the RF of the same neural population such that competitive interactions would decrease as a function of the degree of spatial separation between the objects. The behavioral evidence supported this hypothesis, demonstrating that performance on a biological motion identification task improved when point-light animations of human actions were spatially separated compared to when they were overlapping with another category of object motion (tool motion). The experiment described in this chapter sought to further explore this hypothesis by examining the influence of spacing between simultaneously presented object motion on the cortical response to biological motion as measured by event-related fMRI. Results were consistent with the behavioral data and indicated that responses in biological motion preferring regions increased when objects were separated, compared to when they were overlapping. There was also an influence of spatial attention; directing attention away from biological motion resulted in decreased responses when the objects were separated.

Background

  The biased competition model predicts that simultaneously presented visual stimuli compete for processing resources and that this competition is greatest at the level of the RF. When stimuli are close together (or spatially overlapping) competition between them is maximal because they fall within the RF of the same neuron; separating the stimuli should reduce this competition, as they would no longer be competing for representation by the same neuron or group of neurons. This idea has been supported by fMRI experiments that show differences between sequentially and simultaneously presented stimuli reflecting the degree of competition (Beck and Kastner, 2005,2007; Kastner et al., 1998; Kastner et al., 2001). The strength of these competitive interactions increases with increasing RF sizes along the visual hierarchy. Areas with small RFs, such as V1 and V2, show lower levels of competition compared to regions with RFs large enough to cover more of the stimuli, including V4, TEO, V3A and MT, where competition is greatest. Additionally, varying the size and degree of spatial separation between the stimuli influenced the level of competition (Kastner et al., 2001). Again, these effects varied across visual cortex, separating the stimuli reduced or abolished competitive suppression in V2 and V4, but did not have an effect in TEO when the stimuli remained within the same quadrant. There were, however, no significant sensory suppressive interactions between stimuli when they were located in separate quadrants in any of the regions including TEO.

  While these experiments by Kastner and colleagues compared sequential and simultaneously presented stimuli, this experiment compared the BOLD responses to stimuli that were presented simultaneously and the degree of spatial separation between

intact object motion was varied. Here the influence of spatial proximity of simultaneously presented information was examined in the brain areas that respond selectively to biological motion (STS), tool motion (ITG) and general motion (MT+). Additionally, such effects in retinotopic visual areas, including V1, V2, V3, V3a and V4 were investigated.

Methods

Participants

Twelve healthy individuals (6 males; age range = 19-30 years; mean = 23.2; SD = 3.77), were recruited from the George Mason University community to participate in this event-related fMRI experiment. All participants were right handed with normal or corrected-to-normal vision. The experiment consisted of two separate scanning sessions each lasting approximately 2 hours. Prior to the first scanning session, participants completed a 30 minute training session during which they were instructed on how to perform the task correctly. Participants were compensated $15 per hour and provided written informed consent in accordance with the Human Subjects Review Board at George Mason University.

Stimuli and Task

The task used in this experiment was identical to the main task described in Experiment Two. Briefly, point-light videos of human and tool motion were presented in four quadrants (upper right, upper left, lower right and lower left) simultaneously at 5.8 degrees eccentricity. The two motion categories were presented either overlapping or spatially separated resulting in three possible spatial configurations: overlapping, different quadrant/same hemifield (ie. upper and lower right or left), and different

quadrant/different hemifield (ie. right and left upper or lower). In all configurations each of the four quadrants contained motion stimuli, either noise or object (biological or tool) motion.
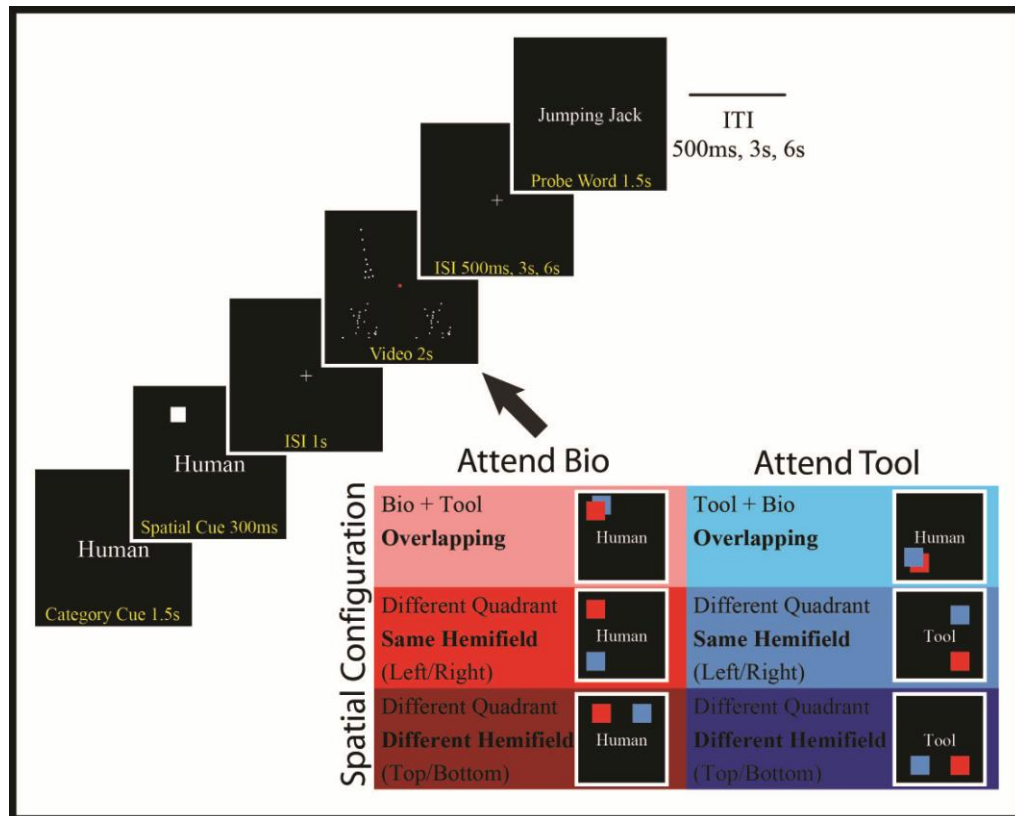
Figure 9: Experiment 3 – Task

As in the previous experiment, prior to video presentation attention was directed toward biological or tool motion by presenting a category cue ("Human" or "Tool") for 1800ms with 100% valid spatial cues presented for the last 300ms of the category cue. For this fMRI experiment, to better separate the response to the videos from the response

to the preceding cues, partial trials consisting of the category and spatial cues followed by a 1 second ISI were presented on 25% of trials. Following the video, a probe word was presented for 1500ms and participants indicated by button press whether this word matched the video. To separate the response to the videos from the response to the probe word and subsequent response, the ISI between the video and word was jittered such that it was 500ms for 60% of trials, 3000ms for 30% of trials and 6000 for 10% of trials. The ITI duration was jittered with the same distribution (Figure 9).

Across two separate scanning sessions, each subject completed a total of 10 (five in each session) runs of 48 trials each while fMRI data were collected using an event-related paradigm. In each run there were six trials per condition, for a total of 60 trials per condition. Button presses were recorded for behavioral analysis and incorrect trials were removed from fMRI analysis. Behavioral analysis included examination of accuracy (% correct) and RT; RTs were converted to log(RT) to reduce skewness.

fMRI Data Acquisition and Analysis

fMRI data were collected over two scanning sessions using a research-only Siemens Allegra 3T scanner at the Krasnow Institute for Advanced Study at George Mason University. Visual stimuli were displayed on a rear projection screen and viewed by participants on a head coil-mounted, angled mirror. The following parameters were used to acquire functional gradient-echo, echoplanar imaging scans: 33 slices (4 mm slice thickness; 1 mm gap), TR/TE = 2000/30 ms, flip angle = 70°, 64 x 64 matrix with 3.75 x 3.75 mm in-plane resolution, field of view = 24 cm. In each run 215 volumes were collected. At the end of each fMRI scanning session, one T1 whole-head anatomical

structural scans was collected using a three-dimensional, magnetization-prepared, rapid-acquisition gradient echo (MPRAGE) pulse sequence (160 1-mm-thick slices, 256 X 256 matrix, field of view = 260 mm, 0.94 mm voxels, TR/TE = 2300/3 ms).

Cortical surfaces were reconstructed from the two MPRAGE scans using FreeSurfer software (surfer.nmr.mgh.harvard.edu/). This automated processing involves motion correction, averaging of the two images, removal of nonbrain tissue, intensity normalization and segmentation to create a representation of the pial surface. The pial surface model was also inflated to support visualization of activation occurring within cortical sulci.

Preprocessing of fMRI data included removal of the first three volumes from each run to compensate for the time it took to reach equilibrium magnetization. The FEAT (fMRI Expert Analysis Tool) software tool of the FSL (fMRI of the Brain Software Library) toolbox (www.fmrib.ox.ac.uk/fsl/) was used for fMRI analysis. The fMRI time series were high-pass filtered at 128 s, slice timing corrected and motion corrected. No spatial smoothing was applied at this stage of analysis. For each run, the onset and duration of each video was modeled with each of the six conditions separated into four possible target locations (upper right, lower right, upper left and lower left), creating 24 regressors that were convolved with a double gamma function (phase = 0) to estimate the response to the stimuli separately for each condition. In addition, incorrect trials were modeled as regressors of non-interest. Prewhitening was also used to remove temporal autocorrelation of the fMRI time series. Contrast-of-the-parameter estimate (COPE) images were calculated collapsing across the upper and lower visual field separately for

the right and left hemifeilds for each of the six main conditions. The estimates were then

averaged over the ten functional runs. The average COPE values from within

functionally-defined regions of interest (ROIs) (see Functional Localizers described

below) were then extracted for each participant and entered into a 2 (category) x 3

(spatial configuration) ANOVA. Plots were created by averaging COPEs from these

ROIs across participants, and within-subjects SEs from the ANOVA effects were

calculated using the method described by Loftus and Masson (1994).

Identification of Regions of Interest

In addition to the main experiment, three independent functional localizer tasks

were used to identify several regions of interest. Regions that respond selectively to

biological motion (i.e. STS), tool motion (i.e. ITG) and scrambled motion (i.e. hMT+)

were identified based on a combination of functional and anatomical criteria.

Additionally, retinotopic cortical visual regions, including V1, V2, V3, V3a and V4 were

identified with retinotopic mapping.

Category and Motion Selective Regions

Regions that respond selectively to biological motion, tool motion and scrambled

motion were identified using point-light animations of human and tool motion similar to

the videos used in the main experiment. For this localizer task, the videos presented were

the same size and in the same location as the main experiment, however, here, the videos

did not contain any extra noise dots and the same video was presented in all four

quadrants simultaneously. In addition to the point-light biological and tool motion, there

were also blocks of videos of scrambled dot motion as well as static frames of the same

scrambled array of white dots on a black background. Accordingly, there were four

conditions: biological motion, tool motion, scrambled motion and static dots.

Participants were asked to attend to the stimuli and respond via button press when they

detected a consecutive repeat (1-back task) while maintaining central fixation. Stimuli

were presented in blocks of 12 seconds with 12 second long blank periods between each

block. Each participant completed 3 runs of 16 blocks each, which lasted approximately

6.5 minutes. In each run there were 4 blocks per each of the four conditions, for a total of

12 blocks per condition.

fMRI data acquisition parameters were identical to those used in the main task

and here, 210 volumes were collected in each of three runs. Data processing and

analyses were conducted using the Freesurfer functional analysis stream (FSFAST).

Preprocessing involved removal of the first three volumes from each run to compensate

for the time it took to reach equilibrium magnetization. The data were high-pass filtered

at 128 s, slice timing corrected, motion corrected, projected onto the FreeSurfer-

generated surface of each individual, and smoothed with a 6 mm FWHM Gaussian

kernel. For each run, the onset and duration of each block were modeled, creating four

regressors (one for each condition) that were convolved with a canonical SPM HRF with

0 deriviatives to estimate the response to the stimuli separately for each of the four

conditions. The following contrasts were made: biological motion vs. scrambled motion,

tool motion vs. scrambled motion and scrambled motion vs. static dots.
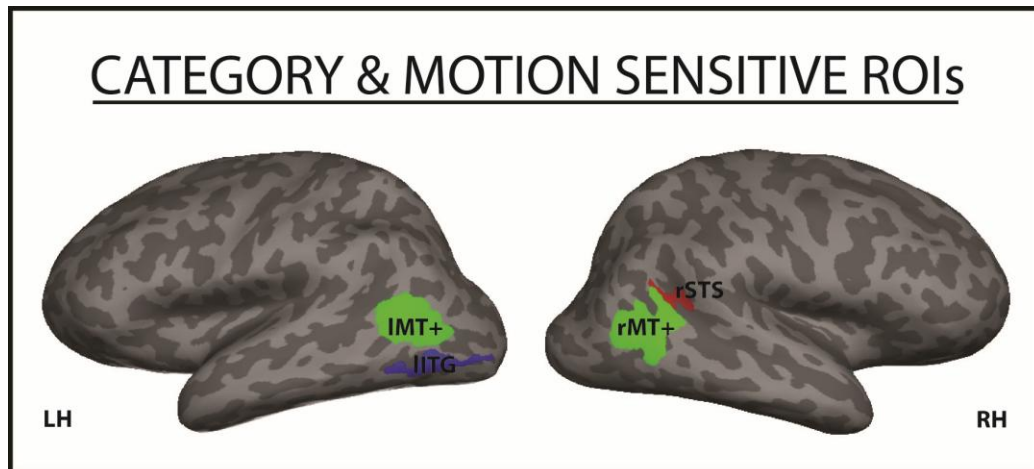
Figure 10: Experiment 3 – Category and Motion sensitive ROIs, displayed on the cortical surface of a representative participant.

Based on the data from this task, regions that respond selectively to biological motion (i.e. STS), tool motion (i.e. ITG) and scrambled motion (i.e. hMT+) were identified on the cortical surface of each individual participant. The STS was defined as the cluster showing a greater response to intact biological motion versus scrambled motion that was located in the posterior portion of the STS. Similarly, the ITG was defined as the cluster showing greater response to intact tool motion versus scrambled motion that was located on the ITG. Finally, the motion sensitive region hMT+ was specified as the cluster that responded more to scrambled motion versus static dots. These individually defined surface based ROIs were then converted into volumes in the space of the participant's functional data and used to extract and perform statistical analyses on data from the main experiment. These category and motion selective ROIs are shown on the inflated surface of a representative subject in Figure 10.

Retinotopic Cortical Visual Regions

Retinotopic cortical visual regions, including V1, V2, V3, V3a and V4, were identified with a retinotopic mapping technique, similar to that used previously by Scalf & Beck (2010). Here, a black and white checkerboard wedge flickering at a rate of 4 Hz extended 6° from the midpoint of the screen into the upper and lower visual fields (vertical meridian) and left and right visual fields (horizontal meridian). Blocks, 12 seconds in duration, alternated between the vertical and horizontal wedge. Participants were instructed to passively view the stimuli while maintaining central fixation and were asked to respond with a button press when they saw the fixation point change color. Each participant completed 2 runs of 12 blocks each. In each run there were 6 blocks per each of the two conditions, for a total of 12 blocks per condition.

Additionally, the response to complex visual stimuli presented in the location of the stimuli in the main experiment was recorded by presenting complex fractal images in each of the four quadrants separately. Colorful fractal stimuli were obtained from the website: http://www.cnspace.net/html/fractals_gallery01_03.html. Again, participants were asked to passively view the stimuli while maintaining central fixation and press a button when they saw the fixation point change color. During blocks of 16 seconds, fractal stimuli covering 6.45° vertical by 8.5° horizontal visual angle, were presented in one of four locations: upper right, upper left, lower right, lower left, with 12 second rest periods between each block. Each participant completed 3 runs of 12 blocks each. In each run there were 3 blocks per each of the four conditions, for a total of 9 blocks per condition.

Again, fMRI data acquisition parameters were identical to those used in the main task. For the wedge task 141 volumes were collected in each of two runs and 190 volumes were collected in each of the three fractal task runs. Processing and analyses were conducted using the FEAT software tool of the FSL toolbox. Preprocessing included removal of the first three volumes from each run to compensate for the time it took to reach equilibrium magnetization. The fMRI time series were high-pass filtered at 128 s, slice timing corrected and motion corrected. No spatial smoothing was applied for this analysis. For both tasks in each run, the onset and duration of each block was modeled creating regressors that were convolved with a double gamma function (phase = 0) to estimate the response to the stimuli separately for each condition. In addition, the temporal derivative was added to the model. Prewhitening was also used to remove temporal autocorrelation of the fMRI time series. COPE images were calculated and the estimates were averaged over all functional runs.

ROIs were identified on the cortical surface of each individual based on specific patterns of activation during these localizer tasks. Using the contrast between responses to the horizontal and vertical wedge blocks, lines were drawn along the alternating representations of the horizontal and vertical meridians (see Figure 11), which were then used as borders to identify the retinotopically organized visual regions.
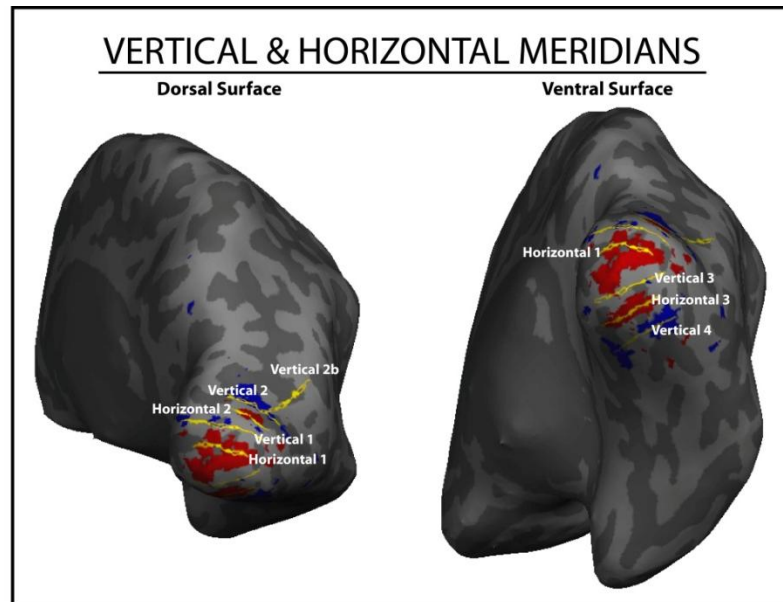
Figure 11: Experiment 3 – Vertical and horizontal meridians, displayed on the cortical surface of the right hemisphere from a representative participant. These borders were used to identify retinotopically organized visual regions.

Area V1 was defined as the region falling across the calcarine sulcus (Horizontal 1) between the first vertical meridians in both the dorsal and ventral surfaces (Vertical 1 and Vertical 3 in Figure 11) that responded to the fractal stimuli in all locations. Proceeding along the dorsal surface, the dorsal area V2 was identified as the region between Vertical 1 and Horizontal 2, dorsal area V3 was the region between Horizontal 2 and Vertical 2, and area V3a was the area falling within the "V" of Vertical 2 and Vertical 3b. On the ventral surface, ventral area V2 was located between Vertical3 and Horizontal 3, ventral area V3 was located between Horizontal 3 and Vertical 4. Finally, area V4 was located in the posterior portion of the fusiform gyrus that showed a differential response to visual stimuli in the upper and lower visual fields with greater

response to the upper visual field medially and greater response to the lower visual field more laterally. The right hemisphere ROIs for a representative participant are shown on the cortical surface in Figure 12, similar ROIs were also identified in the left hemisphere.
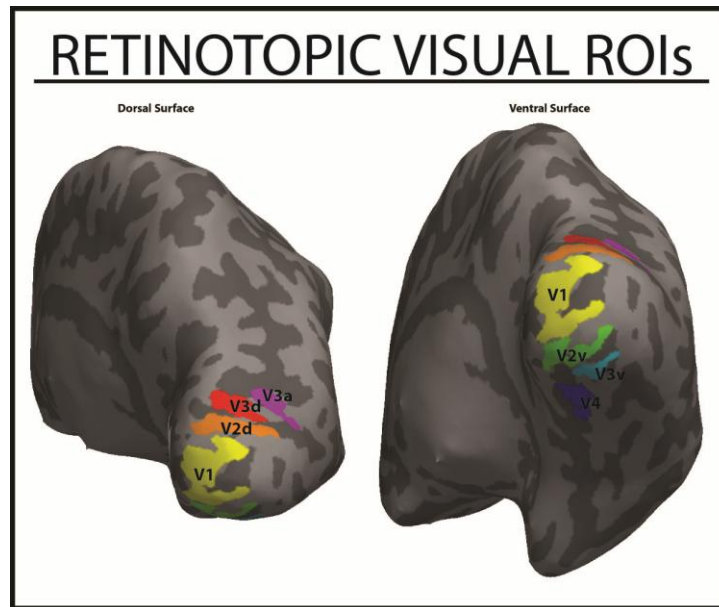
Figure 12: Experiment 3 – Retinotopically organized visual ROIs, displayed on the cortical surface of a representative participant.

The dorsal and ventral portion of V2 and V3 were combined for statistical analysis. As with the category and motion sensitive ROIs, these retinotopic visual ROIs were converted into volumes in the space of the participant's functional data and used to extract data from the main experiment for further statistical analyses.

Results

Behavioral Results

Behavioral task performance during the fMRI scanning session is summarized in Figure 13. Analysis of the RTs of correct responses showed a significant main effect of spatial configuration, $F(2, 22) = 8.54$, $p < 0.05$. Simple contrasts revealed that log(RT)s were significantly faster for the separated conditions (both same, $F(1,11) = 12.97$, $p < 0.05$, and different hemifield, $F(1,11) = 14.09$, $p < 0.05$) compared to the overlapping conditions. This result is similar to that found when the same task was performed outside of the scanner (see Chapter 3: Main Experiment Results); however, here there was no significant RT difference between biological and tool motion $F(1, 11) = 2.73$, $p > 0.05$.

Additionally, analysis of accuracy showed a significant interaction between category and spatial configuration, $F(2, 22) = 3.47$, $p < 0.05$, as well as both main effects of spatial configuration, $F(2, 22) = 10.24$, $p < 0.05$, and category, $F(1, 11) = 6.30$, $p < 0.05$. When collapsing across category, the main effect of spatial configuration in accuracy shows effects to RT. Again, simple contrasts revealed that participants were less accurate when intact object motion was overlapping compared to when the point-light objects were presented in separate quadrants in either the same, $F(1,11) = 5.82$, $p < 0.05$, or different hemifields, $F(1,11) = 26.18$, $p < 0.05$. The interaction indicates that spatial configuration had different effects on performance for biological motion and tool motion. Although both categories showed the same relationship between overlapping and separated conditions – better performance for the two separated conditions – simple contrasts showed that there was more of a difference between overlapping and different hemifield conditions for biological motion than tool motion $F(1,11) = 7.43$, , $p < 0.05$.

However, the difference between overlapping and same hemifield conditions was the same for biological and tool motion, $F(1, 11) = 1.40$, $p > 0.05$. Additionally, the category main effect demonstrates that performance was overall better for tool motion compared to biological motion.
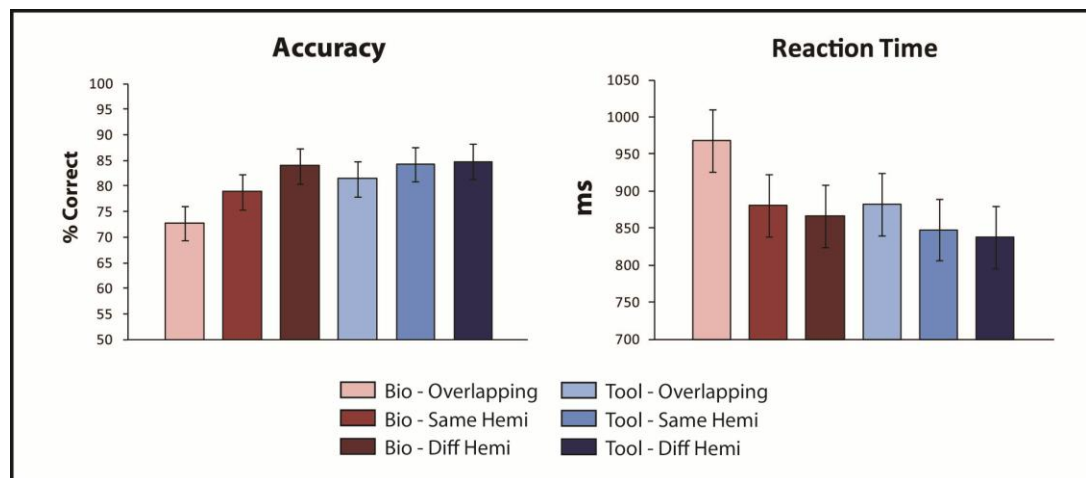
Figure 13: Experiment 3 – Behavioral performance results

ROI Analysis Results

Category and Motion Selective ROIs

Biological motion sensitive cortical regions located in the STS were identified using an independent functional localizer that contrasted the BOLD response to videos of biological motion to scrambled motion videos. Using this method, STS was identified for nine out of twelve participants in the right hemisphere and seven out of twelve participants in the left hemisphere. To increase the number of participants included in the analyses, data from the right and left hemisphere were averaged together such that

responses to targets in the ipsilateral and contralateral field remained separated. For example, participants who had STS ROIs in both the right and left hemispheres the contralateral STS consisted of an average between the right STS response when targets were in the left visual field and the left STS response when targets were located in the right visual field. For participants who had only one STS ROI (either right or left hemisphere) the data from just that ROI was included. As a result, analyses included data from all expect one participant for whom an STS ROI could not be identified in either the right or left hemisphere. Plots from the STS ROIs are shown in the upper portion of Figure 14.
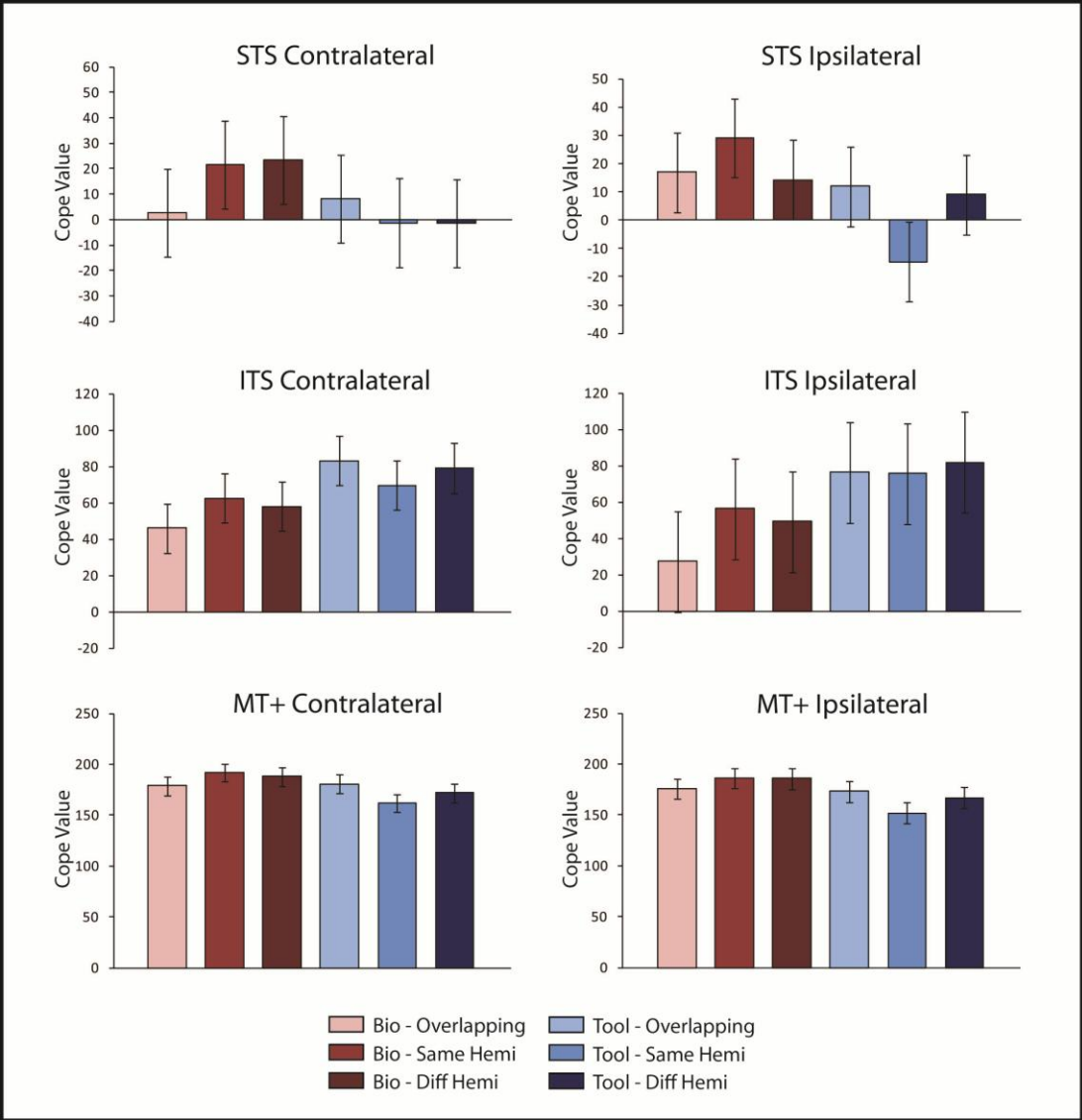
Figure 14: Experiment 3 – Motion and Category selective ROI results

As expected fMRI responses from the contralateral STS showed a main effect of motion category, $F(1, 10) = 7.45$, $p < 0.05$, with greater responses to conditions when attention was directed toward biological motion compared to when attention was directed toward tool motion. Responses in the ipsilateral STS showed a similar trend of motion

category, $F(1, 10) = 4.01$, $p = 0.07$, however, for the ipsilateral STS this effect was not significant.

In addition to the main effect of motion category, there was also an interaction between motion category and spatial configuration, that approached significance in the contralateral STS $F(2, 20) = 2.10$, $p = 0.15$, and was significant for the ipsilateral STS, $F(2,20) = 5.48$, $p < 0.05$. For the contralateral STS, planned-contrasts show that the interaction between category and configuration was significant when comparing the overlapping and same hemifield configurations, $F(1, 10) = 6.93$, $p < 0.05$. This finding demonstrates that the pattern of response in STS to overlapping and separated stimuli was different for biological compared to tool motion. When attending to biological motion, as objects were separated, responses increased. However, when attention was directed toward tool motion, separation of the stimuli led to a reduction in BOLD response. In the contralateral STS, there were no differences observed between the same and different hemifield configurations, $F(1, 10) = 0.01$, $p > 0.05$.

In the ipsilateral STS, similar to the contralateral STS, planned-contrasts show that the interaction between category and configuration is significant when comparing the overlapping and same hemifield configurations, $F(1, 10) = 10.30$, $p < 0.05$. Attending to biological motion yielded an increased response when objects are separated, while attention to tool motion led to a reduction in response with separation of the stimuli. Additionally, for the ipsilateral STS, unlike the contralateral STS, there was also a significant interaction when the same and different hemifield configurations were compared, $F(1, 10) = 6.68$, $p < 0.05$. Here, there was a reduction in response to the

different hemifield configuration compared to the same hemifield condition when attending to biological motion, but the opposite occurred when attending to tool motion.

Tool motion sensitive cortical regions were identified in the ITS by contrasting the BOLD response to videos of tool motion to scrambled motion videos. These, tool motion selective, ROIs were identified in only the left hemisphere of 9 out of 12 participants. Plots from the ITS ROIs are shown in the middle portion of Figure 14. The left ITS showed a main effect of motion category to both contralateral, $F(1, 8) = 20.39$, $p < 0.05$ and ipsilateral, $F(1, 8) = 11.91$, $p < 0.05$, targets. These effects are consistent with previous findings (Beauchamp et al., 2002, 2003; Safford et al., 2010), and demonstrate that this region responded more strongly when attention was directed toward tool motion compared to when biological motion was the focus of object-based attention. However, unlike with the STS, there were no effects of spatial configuration or an interaction between motion category and spatial configuration observed for the ITG to either contralteral (spatial configuration: $F(2, 16) = 0.065$, $p > 0.05$; interaction: $F(2, 16) = 1.84$, $p > 0.05$) or ipsilateral targets (spatial configuration: $F(2, 16) = 1.73$, $p > 0.05$; interaction: $F(2, 16) = 0.982$, $p > 0.05$).

The motion sensitive MT+ complex was defined by the contrast between scrambled motion and static dots. MT+ was identified for all 12 participants and data from the right and left hemispheres was combined into contralateral and ipsilateral responses. Plots of results from the MT+ ROIs are shown in the bottom portion of Figure 14. The pattern of responses in MT+ was similar to that of STS and showed a main effect of motion category as well as an interaction between motion category and spatial

configuration. The main effect of motion category to both contralateral, $F(1, 11) = 12.89$, $p < 0.05$, and ipsilateral, $F(1, 11) = 25.32$, $p < 0.05$, targets indicated that MT+ responded more strongly when attention was directed to biological motion rather than tool motion.

Similar to the biological motion sensitive STS, area MT+ also showed an interaction between motion category and spatial configuration that was significant for both contralateral MT+, $F(2, 22) = 6.65$, $p < 0.05$, and ipsilateral MT+, $F(2, 22) = 5.24$, $p < 0.05$. For contralateral MT+, there were significant differences between the overlapping and same hemifield configurations, $F(1, 11) = 10.15$, $p < 0.05$, and the overlapping and different hemifield configurations, $F(1, 11) = 5.42$, $p < 0.05$, that varied as a function of motion category. However, there was no difference between the same and different hemifield configurations, $F(1, 11) = 2.74$, $p > 0.05$. These effects demonstrate that in the conditions where attention is focused on biological motion, separation of intact objects led to increase in the response, whereas when attention is directed toward tool motion, separation of the stimuli led to a reduction in BOLD response.

This relationship between motion category and spatial configuration was similar, but not identical for the ipsilateral MT+. For ipsilateral MT+, planned-contrasts showed the same pattern of category dependent differences between overlapping and same hemifield configurations, $F(1, 11) = 7.18$, $p < 0.05$. Again, this finding indicates that BOLD responses increased with separation for attended biological motion and decreased when tool motion was attended. Also, similar to the ipsilateral STS, ipsilateral MT+ showed an interaction between category and the difference between same and different

hemifield configurations that approached significance, F(1,11) = 3.71, $p > 0.05$. This effect indicates there when attending to tool motion, there was an increase in response to the different hemifield configuration compared to the same hemifield condition; however, when attending to biological motion, responses to the two separated configurations was similar.

Retinotopic Cortical Visual ROIs

Retinotopic cortical visual regions were identified in individual participants using a meridian mapping technique. As with the category and motion sensitive ROIs, responses in the left and right hemifield were averaged together, but here only contralateral responses were examined. Plots of the results from these retinotopic ROIs are shown in Figure 15.

Responses in area V1 showed a significant interaction between motion category and spatial configuration, F(2, 22) = 4.31, $p < 0.05$, as well as a main effect of spatial configuration F(2, 22) = 18.37, $p < 0.05$. The interaction effect showed that, while when attending to tool motion the response to separated, same hemifield, objects was reduced compared to overlapping objects, there was no difference between these configurations for biological motion F(1, 11) = 7.74, $p < 0.05$. The main effect of spatial configuration shows that when collapsing across motion categories, compared to the overlapping conditions, responses are reduced for the same hemifield configuration, F(1, 11) = 11.23, $p < 0.05$, but that for the different hemifield configuration responses are greater compared to both the overlapping, F(1, 11) = 15.02, $p < 0.05$ and same hemifield configurations, F(1, 11) = 22.81, $p < 0.05$.

Areas V2 and V3 showed similar patterns of responses. There were significant main effects of spatial configuration in both area V2, $F(2, 22) = 8.45$, $p < 0.05$, and area V3, $F(2, 22) = 3.67$, $p < 0.05$. As in area V1, this effect of spatial configuration indicates that, for both biological and tool motion, responses increased in the different hemifield configuration, compared to overlapping and same hemifield configurations. In area V3a, however, there were no significant differences between conditions for either main effects of motion category, $F(1, 10) = 2.10$, $p > 0.05$, spatial configuration, $F(2, 20) = 0.11$, $p > 0.05$, or an interaction between category and configuration, $F(2, 20) = 2.06$, $p > 0.05$.

Area V4 showed a pattern of responses similar to STS and area MT+ with a motion category by spatial configuration interaction that was approaching significance, $F(2, 22) = 3.04$, $p > 0.05$. This interaction suggests that when attention is directed to biological motion, separating object motion results in increased responses, but when tool motion is the focus of attention, separation is associated with a reduction in responses.
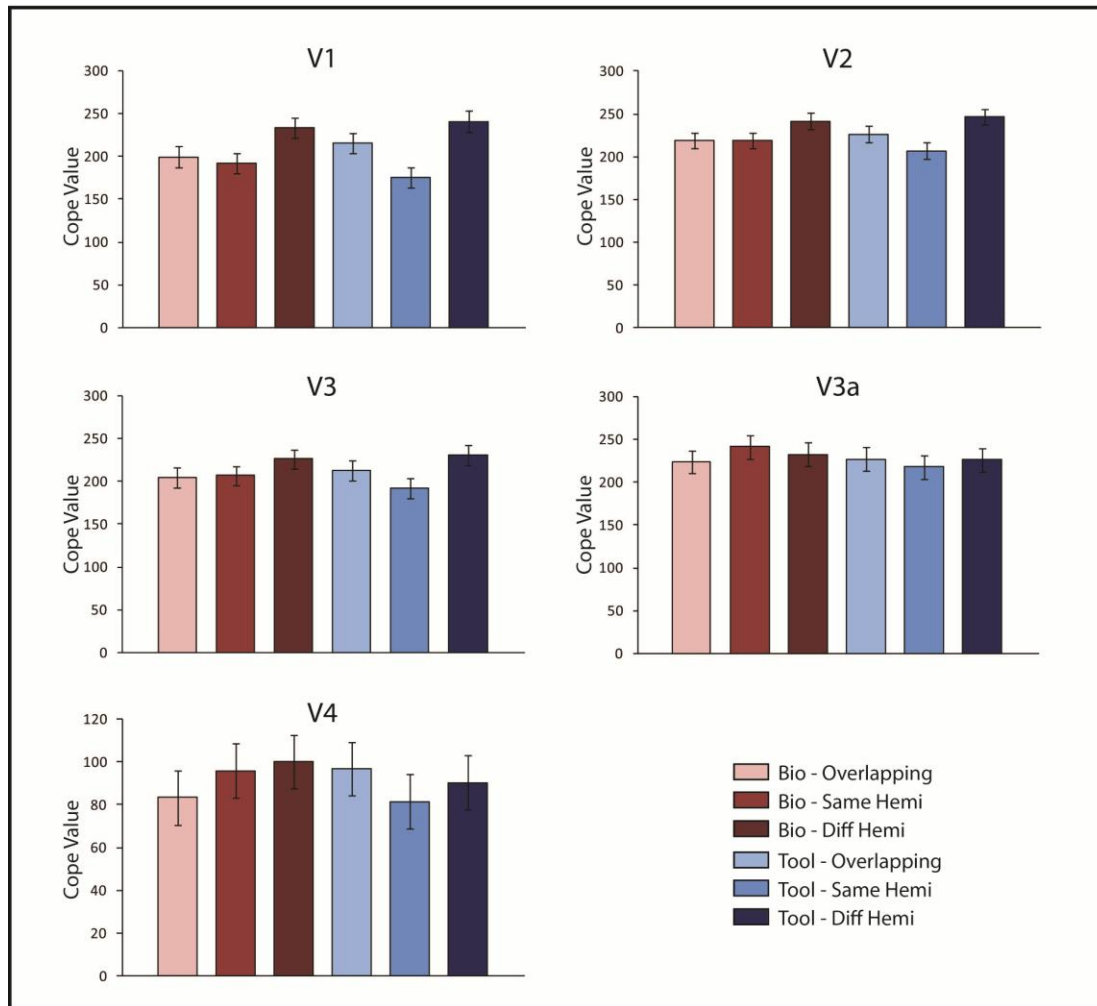
Figure 15: Experiment 3 – Retinotopic visual ROI results

Discussion

The aim of the third experiment was to test the hypothesis that the role of attention in biological motion processing is to bias competition between simultaneously presented objects and that this function is influenced by the degree of spatial separation between stimuli using event-related fMRI. Here, videos of point-light biological motion were presented simultaneously with point-light tool motion in one of three spatial

configurations, overlapping, separated and in the same hemifield, and separated into different hemifields. In all configurations, attention was directed to either the biological or tool motion on a trial-by-trial basis. It was expected that spatially separating objects would reduce the amount of competition between them because they would no longer fall within the same RF. This reduction in competition would be apparent as an increased response to the separated conditions. The experimental results partially support this hypothesis, while some caveats provide further insight to biological motion perception and the involvement of selective attention.

Results from the biological motion sensitive regions located in the STS showed that when attention was directed toward biological motion, there was an increase in BOLD response in the separated configurations compared to the overlapping condition. This finding is consistent with the prediction that there is competition between simultaneously presented and spatially overlapping visual information and that separating such stimuli would reduce these mutually suppressive interactions, resulting in an increased BOLD response. Using more basic colorful patterned visual stimuli, similar findings of suppressive interactions among multiple stimuli have previously been reported in brain regions across visual cortex (Beck & Kastner, 2009; Kastner et al., 2001, 1998). Importantly, lending support to the hypothesis that competitive interactions occur most strongly with a single RF, the strength of these interactions is influenced by the size of the display and the spacing between competing objects (Kastner et al., 2001). The findings of the current fMRI experiment are also consistent with the observed pattern of behavioral results, which showed improvements in performance when objects are

separated, and extend such concepts to support understanding of the neural mechanisms involved in biological motion perception, particularly in visually cluttered natural environments.

Interestingly, the same pattern of increased responses with separation did not occur when biological motion was not the focus of attentional selection. When attention was focused on tool motion, responses in the STS were reduced with spatial separation. Since in the separated conditions, unattended biological motion appeared outside the attended location, this result likely indicates involvement of a spatial attention component in addition to object-based attention which was emphasized by the task. Although, the degree of spatial visual search was limited by the use of valid spatial cues, the component of spatial attention could not be completely eliminated as it was in the previous experiments with centrally presented stimuli. In the separated conditions, spatial attention serves to facilitate processing of the attended object by filtering out information appearing in an unattended location. Recent findings have suggested that spatial and object-based attention do not have to be mutually exclusive, but that interactions occur between the separate forms of attention to facilitate coherent perception (Kravitz & Behrmann, 2011). This suggestion is consistent with a distributed attention mechanism that involves competition at different levels of perceptual representation. The findings discussed here further support this concept. When unattended biological motion is presented outside the spatial locus of attention (ie. where the attended tool motion is presented), spatial attention interacts with object-based attention to bias the limited pool of processing resources to favor the task relevant tool motion. Since, in these conditions,

both types of attention select against biological motion, the cortical regions that normally respond to this type of stimuli are inhibited.

There is considerable evidence that the RFs of biological motion responsive neurons in STS are as large as a hemifield (Grossman et al., 2000; J. C. Thompson & Baccus, 2012). However, the results of this experiment indicate that there were differences in the responses to stimuli in the overlapping and same hemifield configurations, the assumption being that these effects of spatial configuration would be observed because separation resulted in the two objects then falling within separate RFs, thereby reducing the competitive suppressive interactions between them. This finding could indicate that the RFs of STS neurons are in fact as small as a quadrant. However, since there are similar effects occurring in response to targets located in the ipsilateral and contralateral visual fields, it is unlikely that this is the complete explanation and some additional mechanism is probably occurring as well. For example, the overlapping configuration could be a special case where a somewhat different, and more challenging, process of segregation from the background is required compared to the two separated conditions.

One unexpected result of this experiment was that there were no differences in STS between attention to biological and tool motion in the overlapping configuration. This result conflicts with previous findings (Safford et al., 2010) that when biological and tool motion are spatially overlapping, the response in biological motion preferring regions is reduced when attention is directed toward tool motion. This inconsistency might reflect the differences between the specific tasks used. The task used in the current

experiment was intentionally made more difficult by presenting the stimuli for a shorter duration and increasing the amount of background noise dots. Additionally, in this experiment videos were presented in the periphery, which also increases task difficulty (B. Thompson, Hansen, Hess, & Troje, 2007), and adds a spatial component to the task.

Interestingly, effects similar to those observed in STS were also shown in the motion sensitive area MT+. While this area was not defined by its biological motion selectivity but rather its response to motion in general, responses in this area during the primary experimental task mirrored the pattern of activation in STS and did show a preference for biological motion as well as effects of spatial configuration. Area MT+ is known to be at least partially overlapping with the extrastriate body area (EBA), a region that has been shown to respond more to the form of the human body compared to other objects. Therefore, it would seem reasonable that the biological motion selective pattern of responses observed in this region could originate from EBA or MT+ separately or some combination of both.

The responses observed in retinotopically organized visual ROIs including V1, V2, and V3 showed increases when object motion was separated into distinct visual hemifields compared to when they were overlapping or appearing in the same hemifield. A possible explanation for this pattern of activation is based on an involvement of spatial attention. When the stimuli were separated in different visual hemifields, enhancement of activity in the portion of retinotopically organized visual cortical regions that represent the spatial locus of attention, facilitated processing of the target stimulus.

The experiment described here sought to test whether the degree of spatial overlap between concurrently presented objects would influence the attentional modulation of the cortical response to biological motion. Taken together, the results of experiment three indicate that the regions that respond to biological motion are modulated by the spatial proximity of competing visual stimuli such that responses are enhanced when competing objects are farther away, or at least not overlapping. Additionally, when biological motion is not selected by object-based attention, separation between objects leads to a further reduction in responses as spatial attention interacts with object-based attention.

CHAPTER 6: EXPERIMENT FOUR

The experiments discussed thus far have indicated that biological motion perception is modulated by selective attention. Additionally, the role of attention might be to resolve competition among conflicting stimuli and bias neural resources in favor of biological motion when it is the focus of attention. The biased competition model proposes that this attentionally driven bias could be implemented through preactivation according to an internal 'template'. The experiment described in this chapter further elaborated on the mechanism through which attention acts during biological motion processing by examining the pattern of pre-stimulus neural activity during an expectation period prior to video presentation. In this fMRI experiment participants' attention was again directed toward biological or tool motion on each trial and the pattern of activation in regions that responded to visual stimulation was observed prior to video onset. Results indicated that object-category expectations did not lead to changes in pre-stimulus activation of these brain regions.

Background

The biased competition model of selective attention predicts that the competition that occurs among stimuli that are simultaneously present in a visual scene is biased according to top-down influences, such as task demands, in favor of the attended stimuli. A potential mechanism for this bias is through pre-activation of brain regions according

to an internal 'template' (Desimone and Duncan, 1995). There is substantial evidence that effects of attention are present in the absence of any visual stimulation in addition to when the stimuli are actually present. Both single-cell physiology (Luck et al., 1997) and human neuroimaging studies (Kastner et al., 1999; McMains et al., 2007; Sylvester et al., 2008, 2009) have demonstrated that directing attention toward a location increases neural baseline activity. Similar increases in baseline activity have also been shown that have some degree of feature specificity (Chawla et al., 1999; Shulman et al., 1999). However, there has been some debate as to whether baseline increases reflect only information regarding the attended spatial location (Beck & Kastner, 2009; McMains et al., 2007), not other stimulus properties such as features. There is some evidence from single-cell physiology (Chelazzi et al., 1993) and human fMRI studies (Esterman & Yantis, 2010) that expectations regarding particular object categories selectively increase anticipatory activity in neurons and regions that are specifically responsive to these stimuli. For example, Easterman and Yantis (2010) cued observers to anticipate the emergence of a particular object category (either a face or a house), which would appear from within phase-scrambled noise that cohered gradually into an intact image. These researchers found baseline increases that showed category-specificity during a noise period prior to reaching the degree of coherence necessary for reliable object categorization (35%). Importantly, these anticipatory increases occurred in visual cortical regions that subsequently showed category-selective responses to visual stimulation. For example, activity in face-selective regions located in the fusiform gyrus and STS increased during expectation of faces compared to expectation of the appearance of an image of a house.

The experiment described in this chapter aimed to test the degree to which object-based attention to biological (or tool) motion would elicit increases in pre-stimulus baseline activity in regions that were subsequently responsive to the presence of such object motion. In this event-related fMRI experiment, similar to experiment one, centrally presented videos of point-light biological and tool motion were spatially overlapping with intact or scrambled versions of the other motion type and participants were instructed to attend to one motion category or the other. Here, color-coded category specific attentional cues were given several seconds prior to video onset and the cortical activation was examined while this information was maintained through an expectation period.

Methods

Participants

Fifteen healthy individuals (6 males; age range = 18-33 years; mean = 21.5; SD = 3.66) were recruited from the George Mason University community and participated in this event-related fMRI experiment. All participants were right handed with normal or corrected-to-normal vision. The experiment lasted approximately 2.5 hours. Participants were compensated $15 per hour and provided written informed consent in accordance with the Human Subjects Review Board at George Mason University (Fairfax, VA).

Stimuli and Task

Visual stimuli consisted of point-light animations of human and tool motion. In this experiment actions included jumping jacks, walking up stairs, sitting up, kicking left, bending over to touch toes and walking in place. Point-light animations of tool motion, created by placing lights on several tools and moving them in an appropriate manner,

included scissors, pitcher, broom, hammer, saw and pliers. The task in this experiment was similar to the task used in Experiment 1. However, here, a cue consisting of a colored square (blue or yellow), representing which motion category to attend, replaced the written category cue, see Figure 16. To ensure that participants' anticipation of video onset persisted throughout the expectation period the duration of the ISI between the cue and the video was varied with 17% 500ms, 17% 2000ms and 66% 6000ms. Color-object mapping was held consistent for each subject, but was counterbalanced between subjects. As in experiment 1, four experimental conditions and a null trial condition were used: attend to biological motion (Biological$_{Intact}$ plus Tool$_{Scram}$ and Biological$_{Intact}$ plus Tool$_{Intact}$) and attend to tool (Tool$_{Intact}$ plus Biological$_{Scram}$ and Tool$_{Intact}$ plus Biological$_{Intact}$). In addition, to better separate the BOLD response to the videos from that to the category cues, catch trials consisting of a neutral cue (an orange square) were used on 20% of the trials.
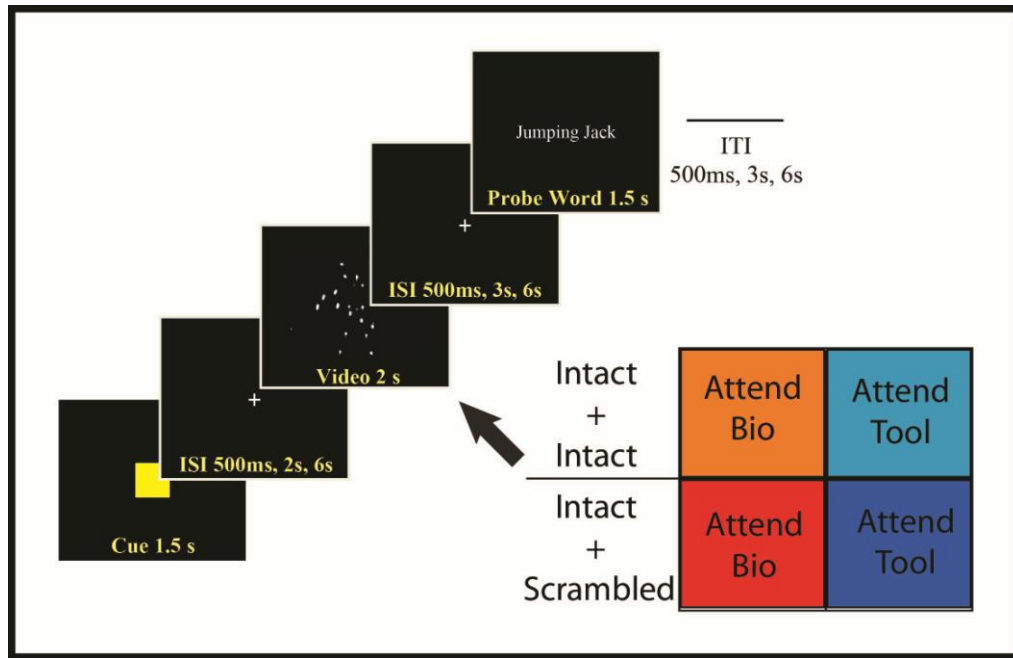
Figure 16: Experiment 4 – Task

Button presses were recorded for behavioral analysis and incorrect trials were removed from fMRI analysis. Behavioral analysis included examination of accuracy (% correct) and RT; RTs were converted to log(RT) to reduce skewness.

fMRI Data Acquisition and Analysis

fMRI data were collected using a research-only Siemens Allegra 3T scanner at the Krasnow Institute for Advanced Study at George Mason University. Visual stimuli were displayed on a rear projection screen and viewed by participants on a head coil-mounted, angled mirror. The following parameters were used to acquire functional gradient-echo, echoplanar imaging scans: 33 slices (4 mm slice thickness; 1 mm gap), TR/TE = 2000/30 ms, flip angle = 70, 64 x 64 matrix with 3.75 x 3.75 mm in-plane resolution, field of view = 24 cm. In each run 175 volumes were collected. At the end of the fMRI scanning

session, two T1 whole-head anatomical structural scans were collected using a three-dimensional, magnetization-prepared, rapid-acquisition gradient echo (MPRAGE) pulse sequence (160 1-mm-thick slices, 256 X 256 matrix, field of view = 260 mm, 0.94 mm voxels, TR/TE = 2300/3 ms).

Cortical surfaces were reconstructed from the two MPRAGE scans using FreeSurfer software (surfer.nmr.mgh.harvard.edu/). This automated processing involves motion correction, averaging of the two images, removal of nonbrain tissue, intensity normalization and segmentation to create a representation of the pial surface. The pial surface model was also inflated to support visualization of activation occurring within cortical sulci.

Whole-Brain Cortical Surface-Based Analysis

To identify the regions that were activated by the videos and showed attentionally modulated, category specific responses to the stimuli, a whole-brain surface-based analysis was conducted. The prestimulus activity in areas was then examined in a subsequent time-course analysis. Preprocessing of fMRI data included removal of the first three volumes from each run to compensate for the time it took to reach equilibrium magnetization. The FEAT (fMRI Expert Analysis Tool) software tool of the FSL (fMRI of the Brain Software Library) toolbox (www.fmrib.ox.ac.uk/fsl/) was used for fMRI analysis. The fMRI time series were high-pass filtered at 128 s and motion corrected. No spatial smoothing was applied at this stage of analysis. For each run, the onset and duration of each video was modeled, creating four regressors (one for each condition) that were convolved with a double gamma function (phase = 0) to estimate the response

to the video presentation separately for each of the four conditions. Separate regressors

of non-interest were also created for trials with incorrect trials as well as the onset of the

cue periods. Prewhitening was also used to remove temporal autocorrelation of the fMRI

time series. Contrast-of-the-parameter estimate (COPE) images were calculated, and the

estimates were averaged over the seven functional runs. The COPE images were then

projected onto the FreeSurfer-generated surface of each individual, transformed into

Talairach space, and smoothed with an 8 mm full width at half-maximum (FWHM)

Gaussian kernel. A surface based mixed effects ANOVA with fixed factors of category

(Biological vs Tool) and overlap (Intact plus Intact vs Intact plus Scram) and participants

as a random effect was conducted. Results were viewed on the average inflated surface

with at $p < 0.005$, uncorrected. Based on this group analysis regions were that showed

attentionally dependent category preference to video presentation were identified to use

as ROIs for further analysis of the fMRI response during the expectation period prior to

video onset.

Cortical Surface-Based Time-Course Analysis

To examine the influence of category specific expectations prior to video onset,

the timeseries of BOLD responses over the course of a trial were estimated with Finite

Impulse Response (FIR) basis functions (n = 13, window = 26s) using FSFAST. As

before, preprocessing involved removal of the first three volumes from each run to

compensate for the time it took to reach equilibrium magnetization. The data were high-

pass filtered at 128 s, slice timing corrected, motion corrected, projected onto the

FreeSurfer-generated surface of each individual, and smoothed with a 6 mm FWHM

Gaussian kernel. For each of the critical trials (the 66% with 6 second ISI between cue

and video), 13 basis functions were modeled beginning 0.5s prior to cue onset and

continuing until 16s following video onset separately for each of the four conditions.

These regressors were estimated with an FIR which made no assumptions about the

shape of the hemodynamic response and generated an estimate of the response to the

stimuli separately for each of the four conditions at separate timepoints throughout the

trial. Contrasts for each condition were calculated and the estimates were averaged over

the seven functional runs. ROIs from the group surface based analysis described above

were transformed into the cortical surface space of each individual and the mean

timeseries for each ROI was calculated by averaging the percent signal change for

vertices above the median for that ROI.

Results

Behavioral and neuroimaging data were analyzed with a 2x2 repeated measures

ANOVA with factors category (Bio vs Tool) and overlap (Intact plus Intact vs Intact plus

Scram). Trials with incorrect responses were discarded from fMRI analyses.

Behavioral Results

Behavioral task performance during the fMRI scanning session is summarized in

Figure 17. Analysis of the RTs of correct responses showed a significant interaction

between motion category and overlap, $F(1, 14) = 9.23$, $p < 0.05$. These effects indicated

that for biological motion log(RT)s were significantly faster for the Biological$_{Intact}$ +

Tool$_{Scram}$ condition compared to the Biological$_{Intact}$ + Tool$_{Intact}$ condition. Tool motion on

the other hand, showed faster log(RT)s for Tool$_{Intact}$ + Biological$_{Intact}$ compared to

Tool$_{Intact}$ + Biological$_{Scram}$. Additionally, analysis of accuracy showed a main effect of

motion category, F(1, 14) = 24.48, $p < 0.05$, which indicated significantly better

performance on the biological motion conditions compared to the tool motion conditions.

However, unlike with RTs, for accuracy, there was no interaction between category and

overlap, F(1, 14) = 1.43, $p > 0.05$. Overall, performance results show that accuracy

levels were quite high and participants performed well on the task.
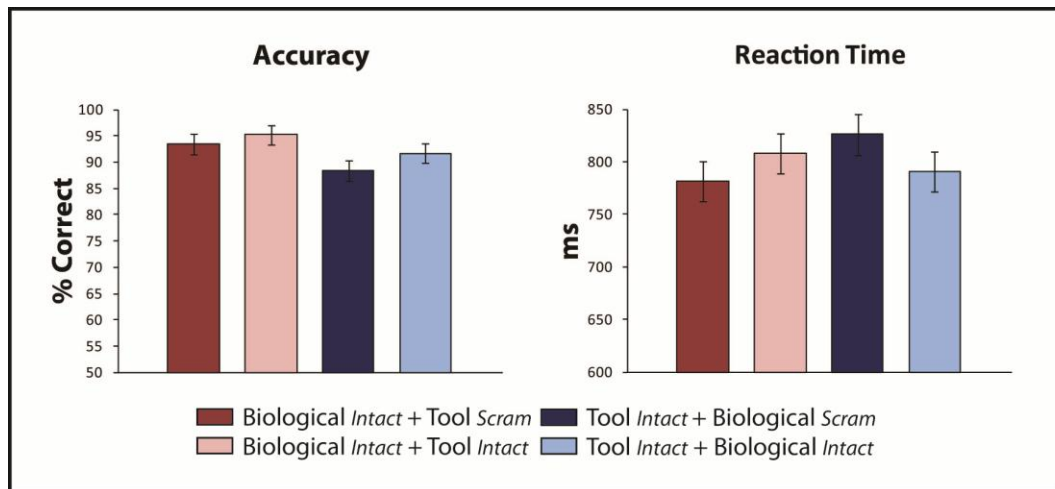
Figure 17: Experiment Four – Behavioral performance results

Cortical Surface-Based Whole-Brain Analysis

The convolved fMRI responses elicited by videos of point-light animations of

human and tool motion from each participant were mapped onto their cortical surface and

transformed into standard space for group analysis. Group-based fMRI responses were

then analyzed on an average surface using a mixed-effects ANOVA. Cortical regions

that showed a significant (p < 0.005 uncorrected; cluster bigger than 50mm2) main effect of motion category (Biological vs Tool) are listed in Table 3 and visualized on an inflated average cortical surface in Figure 18. These results are similar earlier findings (Safford et al., 2010) and the results of Experiment 1. As expected, the BOLD response of regions in the lateral temporal cortex showed a preference for motion category. There was a significantly greater activation of the biological motion relative to tool motion conditions in right LOTC, right STS, right MTG, left STS and left MTG ($p < 0.005$, uncorrected) for both the Intact plus Scram and Intact pus Intact conditions. In the left inferior temporal sulcus (ITS) a significantly greater response was observed to the Intact plus Scram and Intact plus Intact tool motion conditions compared with the Intact plus Scram and Intact plus Intact biological motion conditions ($p < 0.005$, uncorrected) (Figure 18).

Table 3: Experiment 4 – Cortical surface-based fMRI results: Talairach position of regions showing main effects of motion category and overlap condition for the responses to visual stimuli.
Values in the Max column correspond to the maximal value of –log10(p) significance. Bio, Biological; I, Intact; S, Scrambled; LH, left hemisphere; RH, right hemisphere; LOTC, lateral occipital temporal cortex; MFG, middle frontal gyrus; MTG, middle temporal gyrus; IPG, inferior parietal gyrus; IFG, inferior frontal gyrus; ITS, inferior temporal sulcus; STS, superior temporal sulcus; SPL, superior parietal lobule.

Region	Coordinates			Cluster size (mm2)	Max	Hemi
	x	y	z			
Bio > Tool						
LOTC	46.9	-69.5	9.4	446.2	5.913	RH
MTG	47.8	-54.4	14.0	184.23	4.503	RH
Dorsal Precuneus	7.5	-42.2	39.9	77.11	4.011	RH
IPG	42.6	-72.5	25.3	132.69	3.895	RH
Ventral Precuneus	22.1	-55.1	18.8	274.04	3.467	RH
STS	50.3	-42.9	5.4	67.98	3.407	RH
Posterior Cingulate	14.2	-41.2	43.9	66.16	2.780	RH
MTG	-41.3	-63.3	18.3	727.26	4.755	LH

Cingulate (isthumus)	-10.9	-55.9	14.6	299.04	4.307	LH
IFG	-44.8	30.5	-3.6	96.71	4.305	LH
Anterior STS	-49.6	-14.5	-14.5	99.78	4.064	LH
Temporal Pole	-30.9	-0.9	-34.0	128.01	3.992	LH
Lateral Occipital	-24.7	-86.6	9.5	109.33	3.539	LH
Posterior Cingulate	-10.1	-21.8	36.0	129.22	3.511	LH
Occipital Pole	-6.9	-96.7	11.6	55.15	3.163	LH
Middle STS	-52.0	-41.0	-1.0	64.69	2.852	LH
Tool > Bio						
Lateral Orbitofrontal	28.8	24.1	-2.8	69.04	3.152	RH
ITS	-47.2	-57.6	-3.4	573.44	6.359	LH
Supramarginal Sulcus	-43.2	-36.4	38.6	578.70	4.369	LH
Postcentral Sulcus	-52.0	-19.9	30.4	154.13	3.151	LH
I+I > I+S						
Fusiform Gyrus	42.3	-66.6	-8.7	521.48	5.413	RH
IFG	50.6	23.0	16.2	260.31	5.395	RH
LOTC	40.3	-60.9	10.7	816.30	5.123	RH
Precuneus	7.8	-53.8	44.1	112.91	4.644	RH
Rostral MFG	36.2	16.3	32.8	141.74	4.338	RH
IPS	24.0	-53.9	47.6	377.26	4.284	RH
Caudal MFG	38.0	42.0	8.7	121.73	3.855	RH
IPG	40.0	-66.8	25.9	188.80	3.526	RH
SPL	34.4	-48.8	36.9	61.22	3.160	RH
Parahippocampal	33.3	-17.6	-24.3	56.23	3.084	RH
IPS	17.4	-63.6	49.6	90.16	2.948	RH
Lateral Occipital	-41.5	-75.2	4.5	312.63	5.326	LH
Lateral Orbitofrontal	-34.5	24.6	-11.2	154.76	5.158	LH
IPS	-28.9	-64.3	26.0	688.59	5.099	LH
Anterior Fusiform	-36.3	-16.3	-21.6	133.03	5.078	LH
Fusiform	-42.9	-36.8	-17.4	315.51	4.873	LH
MTG	-60.4	-52.8	3.6	294.41	4.200	LH
IFG	-44.1	21.8	16.7	442.76	4.126	LH
Precuneus	-4.9	-61.5	33.4	106.37	3.201	LH
IFG	-44.3	29.0	-1.5	65.13	3.018	LH
MFG	-42.6	28.5	23.4	73.97	2.781	LH
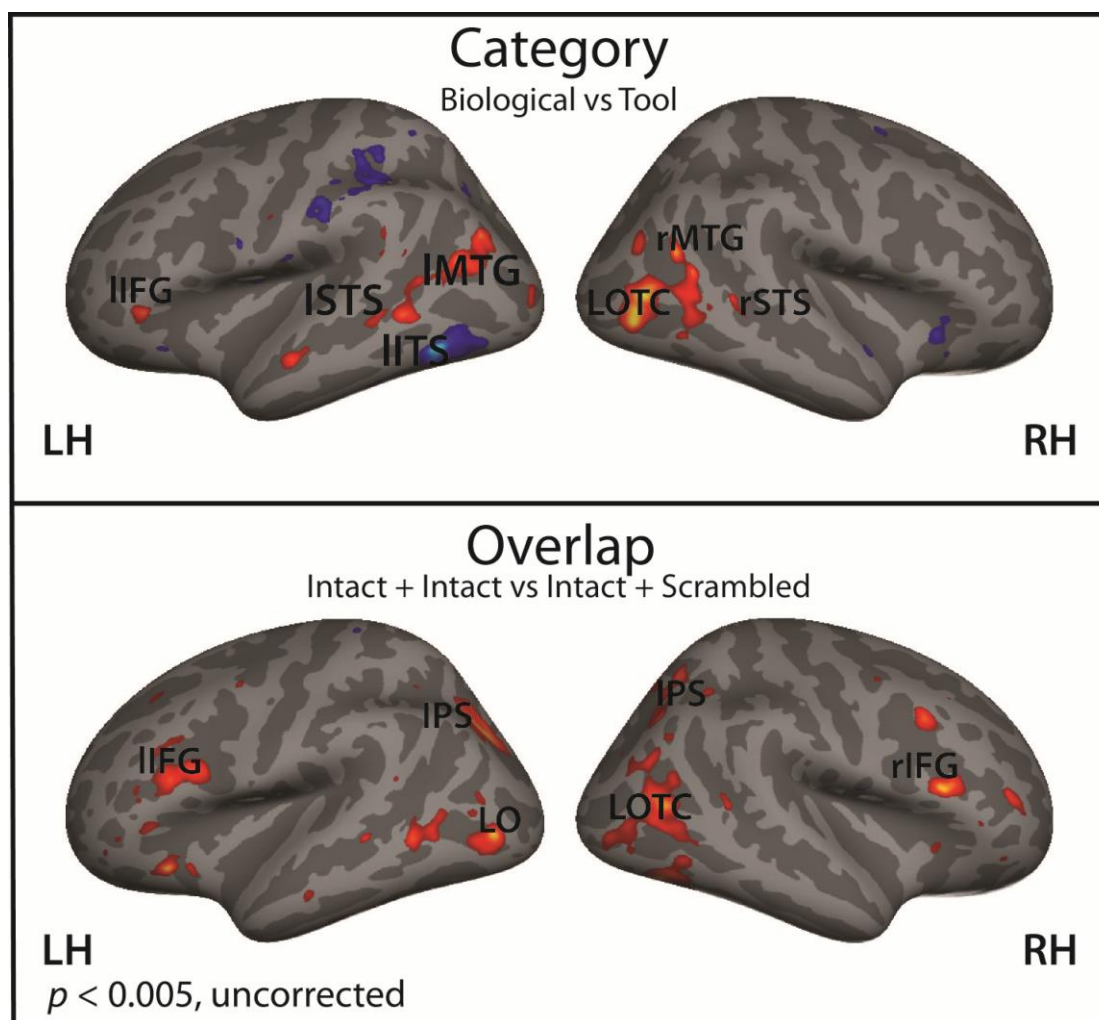
Figure 18: Experiment 4 – Cortical surface-based fMRI results displayed on inflated surface of the FreeSurfer fsaverage brain, responses to visual stimulation.

Importantly, consistent with previous findings (Safford et al., 2010 and

Experiment 1), these responses were dependent on selectively attending to the preferred

motion category; when biological motion was present but attention was directed to the

tool motion (Tool Intact plus Biological Intact condition), the responses in the biological

motion preferring regions (e.g., bilateral STS and MTG) were significantly reduced

compared to when attention was directed toward biological motion (Biological Intact plus Tool Scram and Biological Intact plus Tool Intact conditions) ($p < 0.005$ uncorrected). Likewise, when tool motion was present but attention was directed to the biological motion (Biological Intact plus Tool Intact condition), the responses in tool motion-preferring regions were significantly lower compared with when attention was directed toward tool motion (Tool Intact plus Biological Scram and Tool Intact plus Biological Intact conditions) ($p < 0.005$ uncorrected).

Also consistent with earlier findings, in addition to showing a greater response to biological motion than to tool motion, there were also regions that showed a main effect of overlap (Intact plus Intact vs Intact plus Scram); these are listed in Table 3 and visualized on an inflated average cortical surface in Figure 18. This effect was observed in bilateral inferior frontal gyrus (IFG) and intraparietal sulcus (IPS) as well as right LOTC and a left lateral occipital (LO) region ($p < 0.005$ uncorrected).

Timecourse of Category-Selective ROIs

Based on the surface-based analysis of cortical responses to video presentation ROIs were identified that showed object-motion category preferences. Regions in the right STS and right LOTC showed greater responses to biological motion conditions while a region in the left ITS was defined by greater response to the tool motion conditions. Time courses of the average event-related BOLD response extracted from these ROIs are shown in Figure 19. The time course extracted from the right STS shows a significant difference between biological and tool motion conditions at 6 seconds following video onset t(14) = 2.37, $p < 0.05$; however, there were no object motion

category differences in the responses at any point prior to stimulus presentation. Similarly, the right LOTC showed greater response to tool motion conditions between 6 and 10 seconds following video onset but again no differences during the expectation period. The time course from the left ITS also showed category effects following video presentation with a significantly greater response to tool motion compared to biological motion at 2 s $t(14) = 2.23$, $p < 0.05$, and 4 s, $t(14) = 2.09$, $p < 0.05$, following video onset; but once more no such differences were evident during the pre-stimulus expectation period.
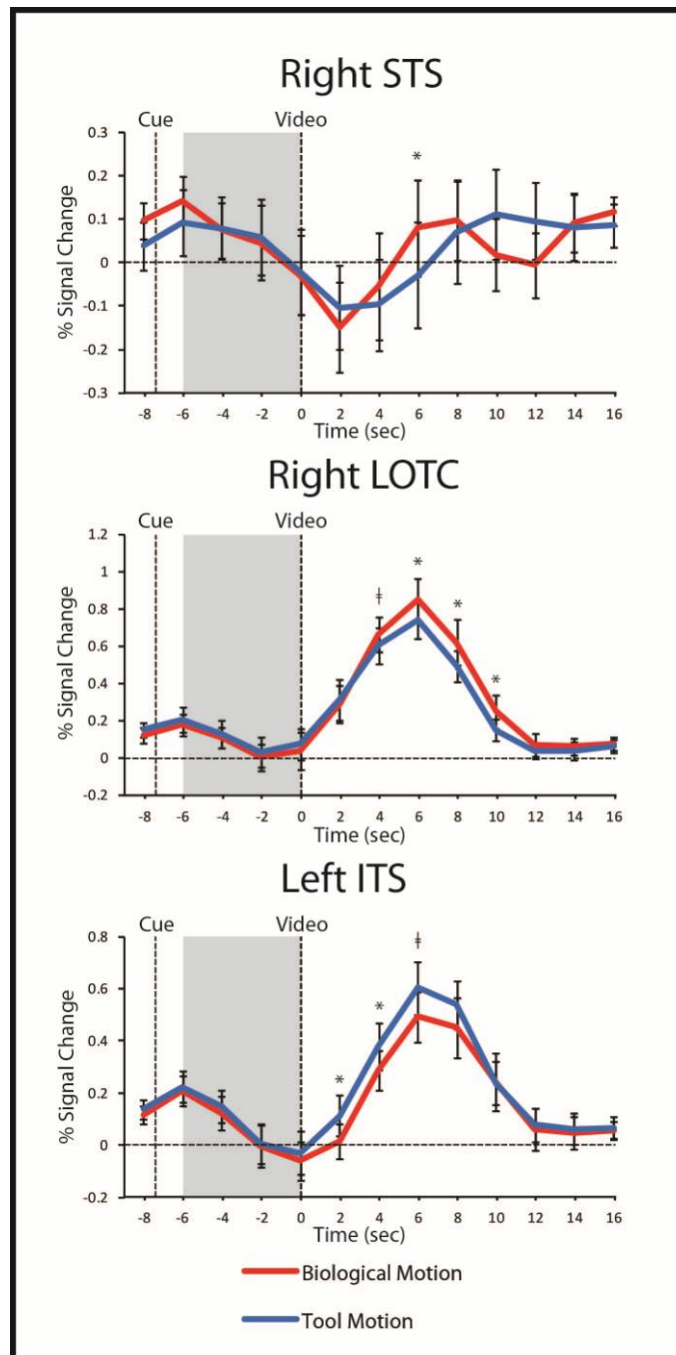
Figure 19: Experiment 4 – Time courses of event-related averages in biological motion-selective (right STS and LOTC) and tool motion-selective (left ITS) regions for trials with a 6-sec ISI. (* indicates *p* < 0.05; ǂ indicates *p* < 0.07) The gray shaded area in each panel indicates the 6 sec expectation period.

Discussion

The goal of experiment four was to examine the influence of categorical expectations on the pattern of baseline neural activity in the absence of visual stimulation using event-related fMRI. Here, centrally presented videos of point-light biological and tool motion were spatially overlapping with intact or scrambled versions of the other motion type and participants were instructed to attend to one motion category or the other. Category specific attentional cues were given several seconds prior to video onset and this information was maintained through an expectation period. The cortical responses during this expectation period were examined for category-specific attention related baseline increases. While there were significant attentionally modulated differences in the BOLD signal between biological and tool motion conditions following stimulus presentation, there were no category differences observed during the expectation period.

The results from this experiment did not support the notion that pre-stimulus neuronal activity is influenced by object-based attention. An alternative account, that pre-stimulus baseline increases reflect primarily spatial information (McMains et al., 2007), seems more likely. Several previous experiments have shown that spatial attention yields pre-stimulus enhancement of activity in cortical regions that represent the attended location (Kastner et al., 1999; Luck, Chelazzi, Hillyard, & Desimone, 1997; Sylvester et al., 2008, 2009). An experiment by McMains and colleagues (2007) confirmed and extended such findings by showing that attention to peripherally presented visual stimuli led to baseline increases but that there were no differences in these baseline signals for expectation of different stimulus features (color and motion). The results

reported here give further support to this claim that baseline increases do not reflect the stimulus preference of a visual area. Although it was not directly tested here, this type of pre-stimulus attentional facilitation appears to be driven by spatially specific expectations about where in the visual field target stimuli will subsequently appear.

In contrast to these results, other researchers have demonstrated categorical expectation related baseline increases (Esterman & Yantis, 2010). What factors might be the basis for this discrepancy? One possible explanation is that the nature of expectation may have differed between experiments. While use of gradually cohering images could have made the level of expectation more perceptual in the previous experiment, in the current experiment categorical expectation occurred on more of a semantic or cognitive level. The cognitive processes occurring during the expectation period in the experiment described here could reflect more of an encoding and maintenance of working memory rather than an attention related preparatory mechanism. Additionally, in the experiment by Esterman and colleagues, although anticipatory category effects occurred prior to reliable visual information, these effects did not emerge until the point at which participants expected the noise display to begin develop into a coherent image. Thus, perhaps in the case of category-specific expectation top-down signals reflect facilitation the neural activity associated with visual processing of the stimuli, rather than a preparatory mechanism. This category anticipation effect is perhaps a different mechanism that the baseline increases due to spatial attention. Therefore, it seems justified that in this experiment top-down influences on category-specific visual cortical regions occurred only when visual information was present.

A general principle of the biased competition model is that competition is controlled by multiple biasing mechanisms, including bottom-up stimulus-driven effects and top-down influences generated by cognitive demands (Beck & Kastner, 2009). One proposed mechanism through which top-down biasing signals are implemented is through enhancement of baseline activity according to a task specific template, which reflects the allocation of attention (Desimone & Duncan, 1995). The evidence provided by this experiment indicated that, in the case of object-based attention, effects of top-down, attentional biasing are observed only in response to visual stimulation.

CHAPTER 7: SUMMARY & GENERAL DISCUSSION

Summary

This dissertation described a series of four experiments that examined the role of attention in biological motion perception. These experiments made use of a biological motion identification task using point-light animations of human actions and tool motion. Observers were able to quickly and easily identify the actions of the moving human figure or tool in these stimuli. However, under the more challenging perceptual conditions afforded by the experimental manipulations, differences in behavioral performance and neural activity were observed, and these differences reflect attentional modulation of biological motion processing. By monitoring behavioral and event-related fMRI responses to biological motion under different attentional conditions, results illustrated a number of related conclusions which serve to better characterize the involvement of selective attention in the neural mechanisms underlying biological motion perception.

Specifically, the findings from the experiments reported in this dissertation allow for the following conclusions:

1. Biological motion perception is modulated by selective attention. The evidence provided by these experiments is in agreement with earlier findings (Safford et al., 2010) and support a role of attention in the cortical mechanisms underlying biological motion perception. When object-based

attention was directed toward competing visual information – in this case tool motion – the neural response to biological motion was reduced compared to when the biological motion stimuli was the focus of participants' attention. Likewise, when tool motion was present but attention was directed toward overlapping biological motion, the fMRI response of a tool motion selective region, located in the left ITG, was reduced.

2. In addition to the effect of attentional modulation of object-motion category selective responses, lateral occipital-temporal and parietal regions show increases when participants had to segregate the attended motion category from the intact version of the unattended object relative to segregation from scrambled motion. This fMRI response likely reflects the greater attentional demands required to discriminate between two objects in the overlapping stimulus conditions. A psychophysiological interaction analysis showed that under these conditions of conflict, parietal regions interact with other regions in the fronto-parietal attention control network, including the IFG (Corbetta & Shulman, 2002), to modulate activity in STS. These results support the suggestion that the attentional modulation observed in STS may be, at least in part, driven by top-down influences received via the parietal lobe.

3. The spatial proximity of simultaneously presented conflicting visual information influences performance on biological motion identification, seemingly by reducing competition as objects are separated. Experiment two showed that there was improved performance when biological motion stimuli

were separated from tool motion stimuli compared to when the two stimuli were overlapping and competition was greatest. These findings provide evidence for the idea that the role of attention in processing biological motion is to resolve competition when stimuli fall within the same RF (Desimone & Duncan, 1995). Importantly though, there were no differences observed between separating the objects into the same hemifield or different hemifields. While it is largely accepted that the RFs of neurons responsible for processing biological motion stimuli are as large as a whole hemifield (Grossman et al., 2000; J. C. Thompson & Baccus, 2012), these results could indicate that RFs are as small as a quadrant. Alternatively, these results might not actually be due to moving the competing objects into separate RFs, but rather could suggest that there is something special about the segregation process involved when the stimuli are overlapping.

4. The cortical responses to biological motion stimuli were also influenced by the spatial separation between competing objects. In experiment three, when unattended tool motion was separated from overlapping biological motion the responses in STS increased, consistent with the idea that the competitive interactions between the objects was reduced when the stimuli fell within separate RFs. However, as with the behavioral results, the amount of increased BOLD response did not scale with further separation between the objects (same hemifield vs different hemifield configurations). These findings, thus, lend two possible explanations: either the pattern of responses

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is due to a reduction in competition as the stimuli move into separate RFs and RFs are smaller than was originally considered, or if RFs really are as large as a hemifield, the effects are due to the involvement of a unique, and more demanding, segregation process when stimuli are overlapping.

5. The responses observed in STS when biological motion was not the focus of attentional selection indicate that spatial attention also plays a role, as there was a reduction in the response to biological motion when it was separated from tool motion. In the separated conditions, in addition to being the unattended object, biological motion also appeared outside the attended location. This result likely indicates involvement of a spatial attention component in addition to object-based attention which was emphasized by the task and is consistent with recent evidence that suggests that spatial and object-based attention interact with each other to facilitate coherent perception (Kravitz & Behrmann, 2011).

6. The activity recorded from other cortical regions was also influenced by the spatial separation between simultaneously presented object motion. Motion sensitive area MT+ showed a pattern of activation similar to STS with overall greater responses to attended biological motion as well as effects of spatial configuration. This biological motion selective activation is likely due to the overlap between area MT+ and the extrastriate body area (EBA) (Peelen et al., 2006).

7. Expectations regarding the category of to-be-attended motion stimuli did not preactivate the cortical regions ultimately responsible for processing such visual information. The results of experiment four showed that there were no differences in baseline activity observed when attention was directed toward either biological or tool motion. While there has been some evidence of category expectation-related differences prior to stimulus presentation (Esterman & Yantis, 2010), these results were unsuccessful at replicating such findings and are consistent with the suggestion that pre-stimulus baseline increases exclusively reflect orienting of spatial attention (McMains et al., 2007).

General Discussion

Selective Attention Plays a Role in Biological Motion Perception

Biological motion, like other "special" stimuli such as faces that have a certain amount of ecological or social relevance, appears to have privileged access to visual processing resources (Shi et al., 2010; Thornton & Vuong, 2004) and perception seems to occur effortlessly. Accordingly, this ease of recognition led earlier accounts to describe biological motion perception as a bottom-up, attention-free process (Giese & Poggio, 2003; Johansson, 1973). However, although perception of these complex stimuli may seem effortless, it is not an attention free process.

Especially under conditions of high task difficulty, such as with degraded stimuli (Parasuraman et al., 2009) or in a cluttered environment with competing items present (Cavanagh, 2001; Safford et al., 2010), attentional resources are required for efficient

processing of biological motion. These attentional requirements are most apparent in tasks involving complex, perceptually demanding tasks such as those that necessitate integration of multiple signals (ie. form and motion) or when stimuli must be selected from an array of distracters. It has been demonstrated that coherent biological motion perception involves integration of form and motion cues (Baccus et al., 2009; J. C. Thompson & Baccus, 2012). When this integration becomes more difficult, such that detection involves global integration across space and time , the task becomes more attentionally demanding (Thornton et al., 2002). Perhaps, then, one role of attention is to facilitate the integration of these cues under challenging circumstances. Similarly, when point-light biological motion stimuli are presented along with distracting visual information (Cavanagh, 2001; Safford et al., 2010), attention is required, seemingly to bias processing resources in favor of the selected item.

Taken together with the earlier behavioral and neuroimaging evidence, the experiments presented here provide further credence for critical involvement of attention in biological motion perception. As measured by event-related fMRI, responses in the cortical areas that are involved biological motion perception, particularly the STS, are modulated by attention such that BOLD responses are reduced when task demands select against human motion. Additionally, not only is the cortical response to biological motion modulated as a function of whether or not the observer is selectively attending to biological motion, but when conflicting, task-irrelevant information is presented farther away (or at least not overlapping), performance improves, as demonstrated by experiment two, and cortical responses are increased, as demonstrated by experiment three.

There has been some debate about whether any stimulus category can truly be processed at the level of object representations without the need of attention. Certain classes of stimuli, including those that have considerable ecological significance such as real-world scenes human bodies, and faces, appear to have privileged access to processing (Downing, Bray, Rogers, & Childs, 2004; Reddy & VanRullen, 2007; Rousselet, Fabre-Thorpe, & Thorpe, 2002), and this privileged access seems to be related to the existence of specialized processing streams for a given stimulus category (Downing et al., 2001; Kanwisher & Yovel, 2006). However, given that biological motion also has neural mechanisms specialized for processing and, as is presented here, at least under some circumstances, is reliant on attention, these two features (selective neural population and processed free of attention) of a given stimulus class may not necessarily co-occur. Perhaps there is really no stimulus category that can truly be processed completely free of attention (Nakayama & Joseph, 1998). If the task can be made sufficiently difficult, attention related effects on performance and neural activity could be observed even for these "special" classes of stimuli.

The Biased Competition Model of Attention and Biological Motion

The biased competition model proposes that simultaneously presented objects compete for processing resources and that attention is necessary to resolve this competition by biasing the response in favor of the selected stimuli (Desimone & Duncan, 1995). An important principle of this theory is that the competitive interactions that occur among simultaneously presented visual information are strongest at the level of the RF, such that the mutually suppressive interactions are maximal when stimuli fall

within the same RF.   Therefore, the degree of spacing between stimuli should influence the level of competitive interactions and, accordingly, such findings have been demonstrated for both task performance and the underlying cortical mechanisms. Increasing the distance between items improved performance on dual-task, matching (VanRullen et al., 2005) and visual search tasks (Reddy & VanRullen, 2007) involving pictures of faces and natural scenes. Similarly, fMRI experiments comparing the responses to sequentially and simultaneously presented stimuli have shown that varying the size and degree of spatial separation between stimuli influenced the level of competition and that this modulation was related on the size of the RFs in each particular cortical region (Kastner et al., 2001).

The experiments discussed in this dissertation partially support this hypothesis with better performance and increased BOLD response when stimuli are not overlapping and biological motion is the focus of attention. However, the findings that there were no further enhancements to performance or cortical activation when stimuli were separated into distinct visual hemifields compared to when the objects were separated but remained in the same hemifield, makes it unclear whether these effects are truly due to moving the stimuli into separate RFs. An alternative explanation is that the segregation process involved when stimuli are overlapping is somehow different from when they are separated.

When biological motion was not the focus of object based attention, separating the two objects had the opposite effect on the response in STS compared to when biological motion was attended. Directing attention to tool motion resulted in further

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reduction of the response in STS with separation. In these conditions, biological motion was moved outside the locus of spatial attention in addition to being unselected by object-based attention. This finding indicates that there was some involvement of spatial attention; yet, this result is still consistent with attention serving to bias responses in favor of the attended category. It was initially hypothesized that diminished competition in the separated conditions would be evident as reduced suppression of the response to unattended biological motion. It was thought that responses would be more similar to when biological motion was attended. However, as the biological motion remains outside the focus of object-based selection in these attend-to-tool motion conditions, the further reduction in activation of biological motion sensitive regions reported in experiment three are actually consistent with attention serving to improve the quality of the perceptual representation of the selected item. This pattern of results is a demonstration of spatial and object-based attention functioning in an integrative manner to facilitate efficient selection and processing of task-relevant information (Kravitz & Behrmann, 2011).

Another prediction of the biased competition model is that top-down influences, such as task demands, bias processing resources in favor of the neural representation of the attended stimuli. One way that this bias could be instantiated is through pre-activation of the brain regions that will ultimately process the stimuli according to an internal 'template' (Desimone & Duncan, 1995). There is substantial evidence that, even in the absence of any visual stimulation, effects of attention related facilitation are observed. That directing attention toward a location increases neural baseline activity in

cortical areas that represent that specific region in space has been demonstrated with both single-cell physiology (Luck et al., 1997) and human neuroimaging studies (Kastner et al., 1999; McMains et al., 2007; Sylvester et al., 2008, 2009). Additionally, expectations regarding specific features (Chawla et al., 1999; Shulman et al., 1999) and even object categories (Chelazzi et al., 1993; Esterman & Yantis, 2010) have been shown to selectively increase anticipatory activity in neurons that are specifically responsive to the same stimulus properties.

Here, experiment four aimed to determine whether expectations regarding object motion categories (biological or tool motion) would result in selective baseline increases in the cortical areas that are selective for biological or tool motion stimuli. The findings show that, while the time courses of the BOLD signal showed category differences following stimulus presentation, there were no differences that were related to expectation of a specific motion category. Thus, the evidence presented here does not support the hypothesis that category expectations lead to anticipatory facilitation, but rather is consistent with other findings that pre-activation is driven by attention to a given spatial location (McMains et al., 2007). While other researchers have found such category specific expectation effects (Esterman & Yantis, 2010), these might be qualitatively different from the baseline increases due to spatial attention as they appear only when observers expect a visual image to begin to appear. Taken together, these results indicate that with regard specifically to object-based attention, top-down facilitation seems to involve regionally specific enhancement of the responses that are evoked, rather than influencing neural activity prior to any stimulus.

Replicability and the Use of fMRI

It is important to note that the experimental effects on cortical activity described in this dissertation were observed using fMRI. While there is evidence that the BOLD fMRI signal reflects synaptic activity and has been specifically related to local field potentials (Goense & Logothetis, 2008; Logothetis, 2003; Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001; Logothetis & Wandell, 2004), it remains an indirect measure of neural activity and there has been some criticism about the validity and replicability of fMRI effects. Importantly, one of the main findings of the line of research presented here, that biological motion selective responses in lateral temporal cortex are modulated by object-based selective attention, seems to be quite persistent and when taken along with a previous study using a similar task (Safford et al., 2010) has been replicated a total of four times. Additionally, this earlier experiment by Safford and colleagues also showed similar effects using ERPs, which is a more direct measure of cortical electrical activity. The generalizability of these effects is evident in that the tasks used in these experiments were similar and used similar stimuli, but they were not identical. For example, in the first experiment by Safford and colleagues a block design was used and the 1-back task involved matching each action to the previous one but did not require the high-level identification that was necessary for the three more recent experiments presented here. That such similar results would be replicated with related but not identical tasks in independent samples speaks to the robustness of this effect as well as the utility of fMRI as a tool for studying cognition and the associated brain activity.

Implications and Future Directions

The results of the four experiments discussed in this dissertation provide a basis for understanding of the function of selective attention in biological motion perception. However, there are some remaining questions that future experiments might seek to address.

As was discussed in the introduction, patients with neuropsychiatric disorders including ASD and schizophrenia experience deficits in both attention and biological motion perception. The co-occurrence of these impairments indicated that they might be somehow linked. The evidence supplied by these experiments support the notion that a relationship does exist between biological motion and attention. To better understand how this relationship is played out in the manifestation of these disorders, future experiments could directly test the association in patients with a paradigm similar to those used in this dissertation. Such experiments could compare the pattern of results to those presented here using healthy participants and potential differences would be useful in developing a better understanding for the nature of the disorders.

The improved performance and increased cortical activity with separated the configurations observed in experiments two and three suggest that selective attention acts to bias processing resources in favor of biological motion when it is the focus of attention. However, due to the lack of differences between same and different hemifield configurations, the soundness of this interpretation is uncertain. An alternative explanation for these findings is that it is more difficult to segregate object motion from the background when it is overlapping with another object than when the background consists of only noise, possibly due to effects of crowding independent of influences of

attention. To better establish that these effects are attentionally based, additional research could examine performance levels under varied attention conditions, for example using a dual task paradigm. If this configuration effect is driven by attention then when less attentional resources are available (high-load) the effect may be stronger compared to low-load conditions.

Alternatively, another way to address this question is to employ a task similar to the paradigm used in experiments two and three, but include a configuration where stimuli are close together, but not overlapping. Such a design could distinguish between the possible explanations for the current findings by testing whether the RFs truly are smaller than originally considered. If results of within quadrant separation are more similar to the overlapping conditions than the outside quadrant separation, this would indicate that the RFs of the neural populations involved really are as small as a quadrant. However, if the results are more similar to those when the objects are moved into separate quadrants, this would indicate that the differences observed in the current experiment are due to the nature of the segregation process when stimuli are overlapping.

An additional experiment that would give further credibility to the evidence presented here could make use of transcranial magnetic stimulation (TMS). TMS operates by stimulating neural populations to induce a temporary lesion by introducing noise into neural processes. This is a major advantage as it allows researchers to draw conclusions regarding the necessity of specific brain regions for particular cognitive processes, rather than simply establishing correlational relationships, as is the case with other neuroimaging techniques. TMS could be applied to an attentional control region,

for example the SPL region that was identified by the experiments discussed here, during a biological motion identification task under high and low levels of visual clutter. TMS induced disruption SPL should have more of an impact on performance in a high clutter environment compared to lower clutter. Such an experiment could serve to support the current fMRI findings and demonstrate the causal role of parietal regions on attentional modulation during biological motion perception.

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