CORTICAL MECHANISMS FOR TRANSSACCADIC PERCEPTION OF VISUAL OBJECT FEATURES

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ABSTRACT

The cortical correlates for transsaccadic perception (i.e., the ability to perceive, maintain, and update information across rapid eye movements, or saccades; Irwin, 1991) have been little investigated. Previously, Dunkley et al. (2016) found evidence of transsaccadic updating of object orientation in specific intraparietal (i.e., supramarginal gyrus, SMG) and extrastriate occipital (putative V4) regions. Based on these findings, I hypothesized that transsaccadic perception may rely on a single cortical mechanism. In this dissertation, I first investigated whether activation in the previous regions would generalize to another modality (i.e., motor/grasping) for the same feature (orientation) change, using a functional magnetic resonance imaging (fMRI) event-related paradigm that involved participants grasping a three-dimensional rotatable object for either fixations or saccades. The findings from this experiment further support the role of SMG in transsaccadic updating of object orientation, and provide a novel view of traditional reach/grasp-related regions in their ability to update grasp-related signals across saccades. In the second experiment, I investigated whether parietal cortex (e.g., SMG) plays a general role in the transsaccadic perception of other low-level object features, such as spatial frequency. The results point to the engagement of a different, posteromedial extrastriate (i.e., cuneus) region for transsaccadic perception of spatial frequency changes. This indirect assessment of transsaccadic interactions for different object features suggests that feature sensitive mechanisms may exist. In the third experiment, I tested the cortical correlates directly for two object features: orientation and shape. In this experiment, only posteromedial extrastriate cortex was associated with transsaccadic feature updating in the feature discrimination task, as it showed both

saccade and feature modulations. Overall, the results of these three neuroimaging studies suggest that transsaccadic perception may be brought about by more than a single, general mechanism and, instead, through multiple, feature-dependent cortical mechanisms. Specifically, the saccade system communicates with inferior parietal cortex for transsaccadic judgements of orientation in an identified object, whereas as a medial occipital system is engaged for feature judgements related to object identity.

DEDICATION

I dedicate this dissertation to my parents.

Thank you for your unwavering support and constant encouragement

to push boundaries and achieve my best.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Overview

The ability to process and perceive information visually from the environment is the outcome of the carefully coordinated and elegant effort of two major components that form one system, i.e., the physical machinery that allows the uptake of visual sensory information and the neural/cortical processes that make sense of the information. In humans and non-human primates, such as macaque monkeys, this component comprises the eye: 1) the retina and its cellular constituents and 2) musculature that allows the movement and re-orientation of the eye. The latter component is composed of subcortical and cortical regions that have specific functions (e.g., superior colliculus; see Muñoz, 2002) to those that are more general-purpose regions (e.g., parietal cortex; Filimon, 2010).

Interacting with one's environment results in behaviour that is not restricted to movements of the head and body – rather, it is fine-tuned/supplemented by the controlled movements of the eyes. One of the fundamental reasons for eye movements, especially rapid eye movements or saccades, is to re-position the eye within the socket so as to allow the most relevant or desired aspects of the physical environment to be processed most directly by the fovea of the eye (the region with the highest concentration of cone cells and highest acuity). Thus, the ability to move the eyes several times per second permits fast-paced processing of the environment (Rayner, 1998). The visual information that reaches the fovea is then further processed in subcortical (e.g., lateral geniculate nucleus, LGN) and then, cortical (e.g., primary visual area, V1) regions.

A few studies have been able to identify the cortical components of the visual perception of object features across eye movements (specifically, saccades) such as object orientation (Prime, Vesia, & Crawford, 2011; Dunkley et al., 2016) and spatial frequency (Fabius et al., 2020). These two object features have been studied extensively, under conditions of fixation of the eyes, but the related cortical mechanisms when saccadic eye movements are produced have been little investigated. Thus, I endeavour to provide background information about these two object features, saccades and the *cortical* mechanisms responsible for their production, how saccades affect perception, the neuroimaging tools that we can use to answer questions about these processes, and the aims of this dissertation. For the sake of brevity, I will describe the studies fundamental to our understanding of each these topics, but will make reference to review articles that may provide further edification for the reader.

1.2 Visual features

For empirical purposes, the study of visual perception and actual action in our surroundings has involved one-dimensional (1D) and two-dimensional (2D) stimuli. The simplification of objects to their single components has been one approach to understanding how the visual system is able to process the rich information available to our retinas. Wherever possible, more invasive or in-depth assessments of more real-world stimuli (three-dimensional, 3D) have been used to identify the mechanisms involved in processing more ‘realistic’ objects (Snow et al., 2011). Almost all of these studies have assessed this while asking participants to maintain fixation of the eyes on a given spot

(dot, cross, etc.; Thaler et al., 2013). Here, I will focus on orientation and spatial frequency of objects, and what we have learned from psychophysical and physiological studies.

1.2.1 Object orientation

There are many objects with which we would like to interact in our environment. The ability to produce a successful reach toward or grasp of a desired object involves a number of processes that assess several object-related features, including its orientation. Grasping a pen or grabbing a mug first requires the identification of the object's orientation – is it tilted or vertical? Is it angled toward or away from you? These characteristics are important as they help to guide us in reaching our hands towards a given object and manipulating it, such as through a grasp. In the following subsection, I will discuss the psychophysical findings for how orientation is processed, as well as the relevant regions of the cerebral cortex.

1.2.1.1 Psychophysics

In 1967, Andrews assessed the ability to make judgements about whether the presented stimuli, or lines, were parallel and found that this can be accomplished very well. However, he suggested that this may not be a simple mechanism – this may require several regions dedicated to orientation processing or the interplay between multiple line detectors (Andrews, 1967). The visual system seems to be able to distinguish between object orientations easily, given that orientations of lines can be discriminated from as little as

0.3º from vertical (Westheimer et al., 1976; Regan & Beverly, 1985). Regan and Beverly (1985) demonstrated, with the use of sine-wave gratings, that discrimination of orientation is improved when the first and second stimuli are presented parallel to one another, but suffers when there is an angle difference of 10º-20º between the gratings (Regan & Beverly, 1985). On the other hand, detection diminishes when the first and second gratings are similarly oriented (Regan & Beverly, 1985). Using psychophysical data and computational modeling, Beaudot and Mullen (2006) proposed a model to help in understanding orientation discrimination, which suggests that this arises less from the sharpening of orientation tuning and more from assigning less weight to noisy sources of information about object orientation (also see Wilson & Regan (1984) and Regan & Beverly (1985)). Understanding how single features are assessed is an important step to further exploring how single features for multiple objects and multiple features for single objects are processed.

Visual search tasks have been utilized in order to understand the identification mechanisms of the features that make up entire objects ('primitives') (see Cavanagh et al., 1990). For example, Cavanagh et al. (1990) used a visual search task and discovered (1) that analysis of size and orientation is conducted in a parallel manner for all of the surface media tested (i.e., luminance, colour, texture, relative motion, and binocular disparity) and (2) asymmetry in search rate for orientation when stimuli are oblique and presented among vertical distractors (parallel search) or are vertical among oblique distractors (serial search). These results highlight the idea that the brain uses different 'strategies' (i.e., serial versus parallel processing) when faced with the simultaneous assessment of attributes of object surface (include luminance, colour, and texture for

example) or shape (include orientation, curvature, and lengths of edges for example) for instance.

Cavanagh et al. (1990) describe orientation as a surface feature - does this feature differ from other object features (e.g., size) in terms of processing? Are there quantifiable differences that arise for different aspects of objects? Faillenot et al. (1999) compared responses (reaction time and accuracy) to changes in orientation or size for 2D and 3D objects and found that, as one might have predicted, behavioural differences do exist. When reaction time was compared for 2D and 3D objects, there were no significant differences. However, accuracy was similar for both, but slightly worse than for the size change conditions. This adds another layer to the idea of mechanistic dissociation for dealing with different, multiple object features - the mechanisms used to assess changes in (2D and 3D) orientation may involve one set of regions or processes, whereas other features (such as size) may rely upon other networks or additional cortical components.

1.2.1.2 Cortical correlates

Neurophysiological recordings in cat striate cortex by Hubel and Wiesel (1959, 1962) provided the first view of orientation selective cortex. They showed in both cat and macaque monkey (striate) cortex that cerebral matter is subdivided into columns that show preferences for lines of specific orientations (Schiller et al., 1976a; Hubel et al., 1978). Although orientation processing may start (cortically) in striate cortex (visual area, V1), this information is processed in downstream regions based on the type of analysis,

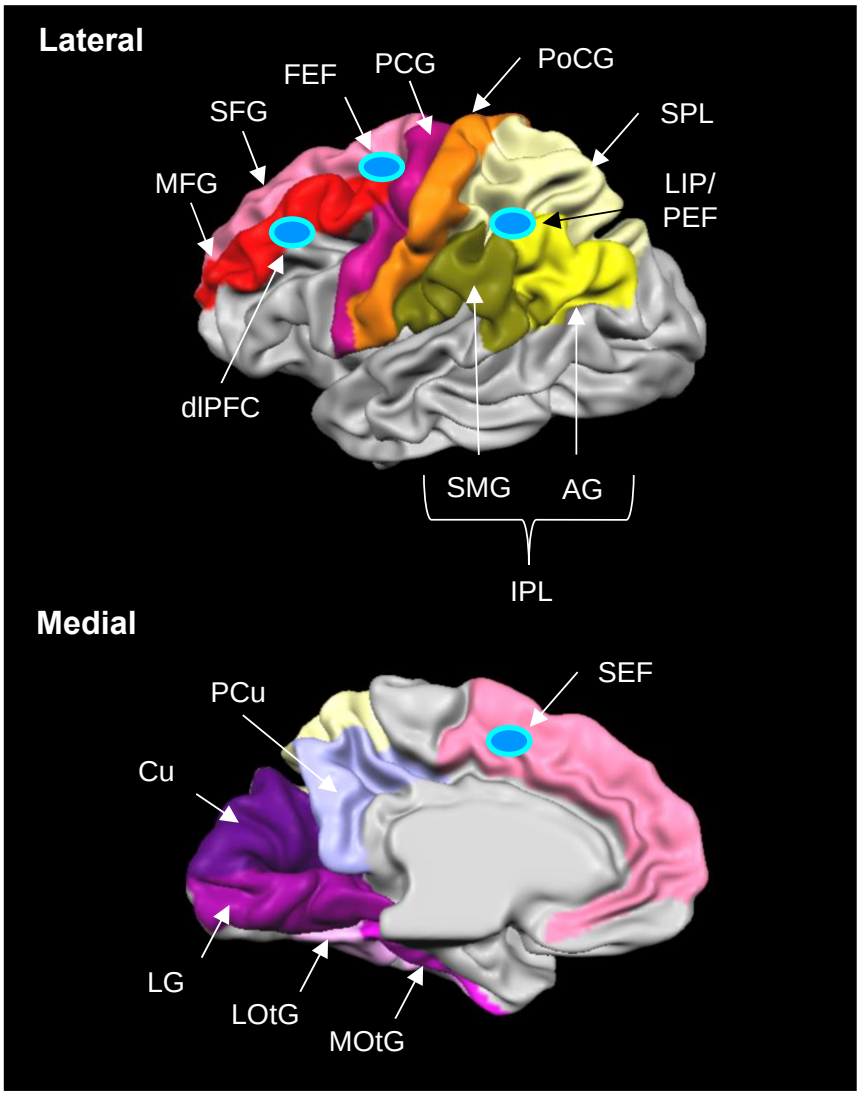

Figure 1.1. Select cortical regions. Lateral and medial views of a human hemisphere are shown (left). On the lateral view (above) are presented several key parietal and frontal regions (blue ovals). Posterior parietal cortex is divided into the superior parietal lobule (SPL) and inferior parietal lobe (IPL), which is further subdivided into supramarginal gyrus (SMG) and angular gyrus (AG). The blue oval depicts the parietal eye field (PEF; also known as the lateral intraparietal area, LIP). In frontal cortex, two blue ovals highlight the frontal eye field (FEF) and the dorsolateral prefrontal cortex (dlPFC). The medial view shows the occipital cortex, subdivided into more dorsal cuneus (Cu) and more ventral lingual gyrus (LG) (relative to the calcarine sulcus that divides them). It also shows more ventral extensions into lateral and medial occipitotemporal gyri (LOtG and MOtG, respectively). Dorsal from occipital cortex is medial parietal cortex, with visual emphasis on precuneus (PCu). More frontally is another saccade region, the supplementary eye field (SEF). Abbreviations: PoCG, postcentral gyrus; PCG, precentral gyrus; SFG, superior frontal gyrus; MFG, middle frontal gyrus. Inspired by Vingerhoets (2014).

perception (ventral stream) or action (dorsal stream) for example (Goodale & Milner, 1992).

One of the noted regions along the ventral stream that is involved in object orientation processing is visual area, V4 (Hinkle & Connor, 2002). When tested for response or tuning for 2D or 3D orientation, there were neuronal populations that showed preference for changes in orientation within the image plane, preference for 2D orientation (irrespective of changes in slant), as well as preference for 3D orientation (invariant across positions). Although downstream from V1, V4 is considered a somewhat early processing region (i.e., with respect to memory or decision-making regions for example). To find tuned response for 2D, as well as for 3D, orientation in V4, it is a striking result that shows both complex processing in an early-to-intermediate visual region and provides insight into the level of progression in bottom-up processing. Continuing along the ventral stream into higher-order occipitotemporal cortex (Fig. 1.1), such as posterior inferior temporal/TEO (macaque; Iwai, 1985; Tanaka et al., 1991), orientation processing expands past single line orientations. Lesion studies suggest that these regions are important for comparing oriented gratings (Orban et al., 1997; Vogels et al., 1997).

In the dorsal stream (Goodale & Milner, 1992), regions within parietal cortex, as understood from studies with parietal lesion patients, are associated with object orientation processing (but less so with object identification) (Faillenot et al., 1999). Neurophysiological recordings in macaque monkeys within the caudal component of the lateral section of intraparietal sulcus point to encoding of orientation for the longitudinal axis (Ohtsuka et al., 1995), as well as for flat surfaces in 3D space (Shikata et al., 1996).

In contrast to object recognition, which predominates in the ventral stream, dorsal parietal cortex is engaged for visuospatial encoding of objects and related features, such as orientation, in order to act upon the object (i.e., grasping; e.g., Faillenot et al., 1999; Murata et al., 2000; Gardner, Babu, Ghosh, et al., 2007; Gardner, Babu, Reitzen, et al., 2007). This information is crucial for visuomotor transformations that will ultimately allow an appropriate manipulation of the object, according to its specific features (e.g., orientation) (Jeannerod et al., 1995; Fattori, Raos, Breveglieri, et al., 2010). Although these two processing streams seem to be distinct (Ungerleider & Mishkin, 1982; Goodale & Milner, 1992), more recent perspectives suggest communication between them (Faillenot et al., 1999; Goodale & Westwood, 2004; Freud & Behrmann, 2020).

1.2.2 Spatial frequency

Another feature related to object processing is spatial frequency, which is defined as the number of alternating cycles of light and dark bars within a given grating that covers a certain visual angle (Blakemore & Sutton, 1969). For example, if alternating light and dark bars each occurs twice within a 2º grating, then that grating is said to have a spatial frequency of 1 cycle per degree (cpd). This is the number of repetitions of a pattern over a given distance. This is also a low-level object feature, like orientation, that is processed and influences our ability to perceive and interact with the world around us. In the following subsections, I will discuss psychophysical assessments of spatial frequency processing, as well as related cortical components.

1.2.2.1 Psychophysics

In order to probe how spatial frequency mechanisms are modulated, sine-wave gratings will be used (Blakemore & Sutton, 1969; Kitterle & Selig, 1991; Bex & Makous, 2002) (although other types of gratings, such as square-wave gratings have also been used; Tolhurst, 1972). Humans show near peak sensitivity for lower (2-4 cpd) spatial frequencies (sensitivity as a function of spatial frequency has an upside-down U shape; Campbell & Robson, 1968). Sensitivity to spatial frequencies <1cpd and 10cpd> drops off dramatically (Campbell & Robson, 1968). Lateral or surround inhibition causes a fall-off at low spatial frequencies (Hoekstra et al., 1974; Bex & Makous, 2002). On the other hand, attenuation of sensitivity for higher spatial frequencies has been explained in terms of optics of the eye and spatial summation (Campbell & Green, 1965; Bex & Makous, 2002). Sensitivity also decreases with visual field eccentricity as shown by Koenderink and colleagues (1978). How spatial frequency 'channels' might be distributed and show selectivity has been modeled using filters that try to mimic or approximate receptive fields (Marcelja, 1980; Daugman, 1980; Wilson & Gelb, 1984). These models have been fundamental in being able allow for inferences of detection (Watson & Ahumada, 1983), and discrimination (Wilson, 1985) of spatial frequency information.

1.2.2.2 Cortical correlates

Information about the spatial frequency of a grating (be it square-wave or sinusoidal, with the latter inducing more sensitive responses; Schiller et al., 1976b) reaches the cortex through the magnocellular (M) pathway or the parvocellular (P) pathway (Merigan, 1989;

Schiller et al., 1990). Low spatial frequency for black and white lines has been shown to be processed through the M pathway, whereas high spatial frequency and colour information is passed through the P pathway (Merigan, 1989; Schiller et al., 1990; Merigan et al., 1991). The organization of the input from the subcortical thalamus into primary cortex occurs in a structured manner.

The neuronal processing of spatial frequency information was first found within the cat striate cortex; therein, it was shown that there is columnar organization of cortex that is dedicated to the representation of orientation as well as adjacent columns that show processing of spatial frequency (Campbell et al. 1969; Maffei & Fiorentini, 1973). In macaque monkeys, this was shown using carbon labeled dye that was taken up during the processing of spatial frequencies of objects (Tootell et al., 1988). Using this methodology, Tootell et al. (1988) found that there appear to be columns for low versus high spatial frequencies (in blobs and interblobs, respectively; see Tootell et al., 1988). In addition, they confirmed that larger receptive fields occur for lower spatial frequencies and vice versa, and showed that spatial frequency sensitivity has an inverse relationship with visual field eccentricity (i.e., a lower spatial frequency processed in the fovea, a higher spatial frequency in peripheral cortical cells) (Schiller et al., 1976; DeValois et al. 1982; Tootell et al., 1988). Tootell et al. (1988) also found that the size of the centre of the receptive field defines the upper limit on spatial frequencies that can be processed, whereas the lower boundary is a function of lateral inhibition. Although the neuronal populations within striate cortex are carefully laid out for orientation versus spatial frequency, their processing mechanisms are interrelated (De Valois et al., 1982; Webster & De Valois, 1985).

1.3 Saccades

The term ‘saccade’ that we now use to describe the fast eye movements that we make to re-orient our gaze to various, desired parts of our surroundings actually came from the jerky movements sometimes exhibited by horses (Leigh & Zee, 2005), and was coined by Javal (1879) and Landolt (1891). Although its origin lies in equine behaviour, Javal (1879) and Landolt (1891) repurposed the term to refer to the jerky movements of the eyes when reading. A great number of studies in the late 19th and early 20th centuries focused on the production of eye movements, and their various classifications, whilst reading because of the afterimages (ephemeral activation of retinal cells despite lack of or change in visual stimuli; Phillips, 2013) observed (Huey, 1900). Huey (1900) noted that, several years prior, there were suspicions that the occurrence of myopia (image falling anterior to retina, resulting in abnormal focusing and blurring; Saw et al., 1996) was a result of the specifics of the eye movements occurring during reading. Huey (1900) used tools and techniques used by Ahrens (1891) to track movements of the eye while participants read, and was able to provide very good measurements of eye movements and fixations during reading. However, these tools impacted eye muscles (Dodge, 1900). Thus, Dodge (1900) set out to provide an empirical and quantitative assessment of eye movements, which he did along the horizontal meridian. Among those eye movements, of particular interest here, are saccades, which were further defined by Yarbus (1967). The main types that can often be seen in saccade-related paradigms are: volitional, predictive, memory-guided, reflexive, express (Yarbus, 1967). Their observable features (i.e., latency, duration, velocity, accuracy) and the cortical regions involved in their production will be discussed in the following subsections.

1.3.1 Psychophysics

One of the first aspects of saccades that can be measured is the time it takes from the presentation of a ‘go’ cue to begin the eye movement until the onset of the eye movement, i.e., saccade latency (Leigh & Zee, 2005). In the healthy adult human, saccade latencies can range from 200 – 250 ms (Yang et al., 2002) (elsewhere, this figure has been a bit shorter, from 150 – 200 ms; Sharpe & Wong, 2005). However, differences may arise in saccade latencies that result from a variety of factors. The features of an object may affect how quickly a saccade can be produced such as luminance and size (Doma & Hallett, 1988; Groner & Groner, 1989). Attention has also been investigated with respect to its influence on the production of saccades (Leigh & Kennard, 2004). Precued attention (without a reflexive saccade), or covert attention (Rizzolatti et al., 1987; Walker et al., 1995), and correct/incorrect target cuing have been shown to affect saccade latencies, whereby cuing to a different than expected location (incorrect) elicits longer latencies than correct/congruent cuing (Van der Stigchel & Theeuwes, 2007). Saccade latencies have also been shown to differ for visual versus auditory stimuli for example, and are modality-dependent (Zambarbieri et al., 1982; Shelhamer & Joiner, 2003). Thus, they can reflect the influence of target characteristics, the accessibility of the underlying oculomotor system that elicits the saccade (Smith et al., 2004), and the effect of attention (especially when cuing is ‘correct’ or ‘incorrect’) (Leigh & Kennard, 2004; Van der Stigchel & Theeuwes, 2007).

In addition to saccade latency, duration, amplitude, and velocity have been characterized. Saccade duration is highly correlated with saccade amplitude, whereby longer saccade durations are observed for larger amplitudes and vice versa (Bahill et al., 1975; Abel et

al., 1983; Garbutt et al., 2003). Overall, saccade durations can range from 30 ms to 100 ms for amplitudes from 0.5º to 40º (Bahill et al., 1975; Smit et al., 1987; Smeets & Hooge, 2003). Average saccade velocities can range from 30 to 700 degrees/second (Bahill et al., 1975; Smit et al., 1987; Smeets & Hooge, 2003). Given the ballistic nature of the saccade, there is not much voluntary control over the duration of a saccade (Leigh & Kennard, 2004), though this can be affected by how alert or fatigued participants are (Bronstein & Kennard, 1987; McGregor & Stern, 1996) and target luminance (Bronstein & Kennard, 1987) for example. Saccade velocity can differ based on direction, and positions of the eye pre- and post-saccade (Leigh & Kennard, 2004). The relationship between saccade amplitude, duration, and velocity is referred to as the 'main sequence' and is described by exponential or power-function equations (Lebedev et al., 1996; Leigh & Kennard, 2004). However, deviations from these measurements in clinical populations have been noted (Rottach et al., 1997).

The last major feature of saccades is accuracy. Most saccades, especially in healthy adult humans, are accurate; although, they can be described as stopping just short of the target (hypometria) or just after the target (hypermetria) (Weber & Daroff, 1971). It can be influenced by object features such as luminance and size (Deubel, 1989). Different types of saccades also are associated with differences in accuracy, whereby visually-guided saccades show greater accuracy than do memory-guided ones (Opris et al., 2003). Lastly, fatigue and age are negatively correlated with saccade accuracy (prone to hypometria) (Abel et al., 1983).

1.3.2 Cortical correlates

There are two important features of saccades: the production or ‘pulse’ and the cessation or ‘step’. The first begins within a subcortical structure called the superior colliculus (SC) (Sparks & Mays, 1990). The latter occurs via brainstem ‘structure’ called the neural integrator (Sparks, 2002). (For a detailed review of the subcortical structures that are required for saccade production, please see Muñoz, 2002.) These subcortical structures are influenced by and have inputs from higher, cortical regions.

There are several regions within parietal and frontal cortex that have been demonstrated to guide or shape the production of saccades. In the parietal cortex is the parietal eye field (PEF; Fig. 1.1) (Müri et al., 1996). This region has been anatomically localized to the mid-posterior intraparietal sulcus (mIPS) (Müri et al., 1996; Vesia et al., 2010); although lateral/medial PEF locations have been noted (Medendorp et al., 2003; Cappadocia et al., 2018). The homologue in macaque monkeys is referred to as the lateral intraparietal area (LIP) (Andersen et al., 1992). Its function is to keep track of information obtained across saccades (e.g., target location) in order to plan an upcoming saccade (Andersen et al., 1992), as well as to promote saccadic accuracy to those targets in both memory-guided (Powell & Goldberg, 2000) and visually-guided saccades (Gaymard, Ploner, Rivaud, et al., 1998). It has also been associated with the production of reflexive saccades (Pierrot-Deseilligny, Rivaud, Gaymard, et al., 1991).

Within frontal cortex, there are three saccade-related regions. More laterally, at the junction of the posterior portion of superior frontal sulcus and precentral sulcus (Bruce & Goldberg, 1985) is the frontal eye field (FEF; Fig. 1.1). This region has been noted as

having a larger role in the generation of memory-guided saccades and a slightly less prominent role in producing visually-guided saccades (Pierrot-Deseilligny, Rivaud, Gaymard, et al., 1991; Gaymard, Ploner, Rivaud-Pechoux, et al., 1999). It is involved in producing voluntary saccades and processing visuospatial information (Gaymard, Ploner, Rivaud, et al., 1998; Schall, 2002; also see Sajad et al., 2020). More medially are located the cingulate eye field (CEF) and supplementary eye field (SEF; Fig. 1.1), the former of which is more involved in saccade sequences and memory-guided saccade production (Gaymard, Ploner, Rivaud, et al., 1998) and the latter is more concerned with motor commands for saccades and/or arm movement (Pierrot-Deseilligny, Israel, Berthoz, et al., 1993; Müri et al., 1994).

Although these regions have been defined due to their influence on and/or generation of saccades, they are not exclusive contributors to saccade production. There are well-described connections between parietal and frontal saccade regions (i.e., LIP and FEF; Schall, 1997; Schall & Thompson, 1999). There are also several connections between the frontal eye regions, such as FEF to SEF and CEF (Pouget et al., 2005). These connections are also mediated by a spatial working memory region (dorsolateral prefrontal cortex, dlPFC; Fig. 1.1) (Müri et al., 1996; Pierrot-Deseilligny, Müri, Nyffeler, et al., 2005). Lastly, these cortical connections also feed into subcortical regions that produce and modulate saccades (Sommer & Wurtz, 1998, 2001).

1.4 Spatial updating across saccades

When (retinal image) changes occur due to a change in eye position, the brain must be able to account for this and update the system. More formally, this process compares visuospatial information before and after a saccade, and is known as spatial updating (Funahashi, 2013). This process is able to account for changes to the image, so as to provide up-to-date and accurate information about the environment (Wang et al., 2006). Spatial updating is achieved through the combined and continuous assessment of retinal and extra-retinal signals (Colby & Goldberg, 1999), the latter of which alters the system to changes in eye movement amplitude and direction (Klier & Angelaki, 2008) which can help to influence the production of further eye movements toward various regions of the visual environment. Spatial updating is thought to play an important role in the perception of a constant visual world, despite the changing images on the retina with each intervening saccade (Merriam et al., 2003; Klier & Angelaki, 2008; Melcher & Colby, 2008). In the following, I will describe what has been learned from studies using psychophysical approaches, as well as the associated cortical components for spatial updating.

1.4.1 Psychophysics

Given the detailed visual information the retina receives with each saccadic eye movement, it is natural to ponder the level of updating from one fixation to the next. Irwin et al. (1988, 1990) investigated how much information gets transferred across each rapid eye movement and found that the visual image is, in fact, not updated in a point-by-point manner. In terms of object features, visual form has been shown to be updated or

remapped across saccades (Melcher, 2007), as well motion (Melcher & Fracasso, 2012), and attention to multiple objects (Melcher, 2009; Rolfs et al., 2011). Wolfe and Whitney (2015) used images of faces and showed that the perceived level of affect in the post-saccadically presented neutral face was shifted away from the initially presented face. These results allowed them to conclude that remapping may be occurring at the object-level, with less of a focus on the specific feature components (Wolfe & Whitney, 2015). However, the specifics of the detail that is brought from one fixation to the next via spatial updating is still under investigation.

Is visual information attached to an imaginary reference frame that is kept constant within space or world coordinates? Is it encoded relative to objects in the world (i.e., allocentric) or relative to the viewer (i.e., egocentric)? The ability to view our surroundings as constant, despite the jarring change in retinal input from one fixation to the next, the debate about how visual information is encoded is ongoing. In a virtual reality (VR) design, Wang et al. (2006) investigated the ability of human participants to identify locations of a range of objects. Their logic was that, if encoding occurs allocentrically, only the participant's position and orientation need to be updated and not the location of the objects, whereas in an egocentric reference frame, the location of objects is coded in terms of the participant, which should result in set size-dependent results. Their results support the egocentric model, as localization errors increased with an increase in set size. These findings suggest that this process is fundamental to our ability to navigate our environment (Simons & Wang, 1998; Wang & Spelke, 2000) by keeping track of how visual information has changed across the retina, but also how the environment has shifted relative to changes in orientation and position (Wolbers et al., 2008), allowing us

to store object and spatial-related signals across saccades. The debate about how information about the world is encoded and what is updated across saccades is ongoing (Vuong et al., 2019; Fabius et al., 2020; see Melcher & Colby, 2008; Mathôt & Theeuwes, 2011).

1.4.2 Cortical correlates

Spatial updating is manifested as a change in activation of one neuronal population to another, typically related to movement of a target to a new, future location (Muñoz, 2002). This is accompanied by or a result of receiving a copy of the eye motor command (corollary discharge or efference copy) (Duhamel, Colby, & Goldberg, 1992; Sommer & Wurtz, 2004). This allows for the updating of visual sensory information such as through a subcortical to cortical pathway that extends from SC to thalamus to FEF (Sommer & Wurtz, 2004).

In order to best uncover the cortical regions involved in remapping, tasks requiring the production of a single saccade to a target (single-step) or two saccades (double-step) have pointed to the parietal lobe as a potential target or region (Duhamel, Goldberg, Fitzgibbon, et al., 1992; Heide et al., 1995; Medendorp et al., 2003). Further scrutiny of the parietal lobe and its relationship to remapping has pointed to a saccade-generating region discussed previously (see subsection 1.3.2), LIP in macaques and PEF in humans (Duhamel, Colby, & Goldberg, 1992). Given its ability to respond to changes in eye position and visuospatial information as a result of saccadic eye movements, it is an excellent first candidate for spatial updating. This process has also been shown

separately in visual regions upstream of parietal cortex, such as in visual areas V2 and V3 (Nakamura & Colby, 2002; Merriam et al., 2007), as well as downstream in frontal regions such as FEF (Goldberg & Bruce, 1990). It has also been shown for specific object features such as motion within ventral intraparietal area, VIP (Duhamel, Colby, & Goldberg, 1998) and object identification within anterior intraparietal area, AIP (Sakata et al., 1995). Thus, spatial updating involves the efforts of early visual, more complex visuospatial transformation parietal regions, and/or frontal eye regions at the cortical level.

1.5 Transsaccadic perception for object features

As shown from research on eye movements during reading, several saccadic eye movements are generated per second (Rayner, 1998). As indicated, the reason for the re-orientation of the eye is to re-direct what visual information from the environment falls on the retina, specifically the fovea where the highest level of detail can be obtained (Rayner, 1998; Muñoz, 2002). However, because the visual image changes with each fixation, there is a replacement of information from one eye movement to the next. In order to create a 'map' of the spatial environment (Wang et al., 2006), visual information gained from one fixation must be visuospatially encoded and spatially updated, retained, and compared with/fused with information from the next fixation as a result of a saccade (McConkie & Zola, 1979; Irwin, 1991; Henderson, 1997; Prime, Vesia, & Crawford, 2011; also see Sajad et al., 2020). In the following subsections, I will highlight information about transsaccadic perception obtained from psychophysics studies, the cortical regions involved, and predictive computational models.

1.5.1 Psychophysics

Just as for spatial updating (see section 1.4), it is important to determine the distinct components of transsaccadic perception. There are three main such components: 1) sensory processing / encoding, 2) maintenance in memory, and 3) updating and integration with new sensory information (Helmholtz, trans. 1963; McConkie & Zola, 1979; Irwin, 1991; Henderson, 1997; Prime, Vesia, & Crawford, 2011).

The type of information that is processed or attended to (Cavanagh et al., 2010; Rolfs et al., 2011; Stewart & Schütz, 2018a) has been demonstrated to occur for multiple object features (Luck & Vogel, 1997; Walker & Cuthbert, 1998; Lee & Chun, 2001; Vogel et al., 2001) and entire objects as well (Wolfe & Whitney, 2015). In terms of specific features, Melcher (2007) tested for transsaccadic integration of shape, tilt, and contrast, and found effects for the former two features. Prime, Niemeier and Crawford (2006) used a line intersection task with an intervening saccade and determined that object orientation is another feature that is updated. Lastly, even dynamic object features such as motion have been shown to be encoded and updated across a saccade (Melcher & Morrone, 2003; Melcher & Fracasso, 2012; Turi & Burr, 2012). In terms of how this information is encoded or laid out mentally, Melcher and Colby (2008) suggest that this information is remapped and encoded relative to their corresponding locations (this topic is still being debated; see O'Regan, 1992; Irwin, 1993; Bridgeman et al., 1994; Golomb, 2019).

Just like any other process, there is a finite amount of resources available to the system. Similarly, when probed to determine how much information (in terms of single items) can be remembered across saccades, it has been consistently found that approximately 3-4

items can be retained in transsaccadic memory (Irwin, 1992; Irwin & Gordon, 1998; Irwin & Zelinsky, 2002; Prime, Tsotsos, Keith, et al., 2007; Prime, Vesia, & Crawford, 2008). Similarly, when presented among a variable set size, 3-4 objects could be remembered for luminance, colour, and orientation (Prime, Tsotsos, Keith, et al., 2007).

How quickly does this process happen? Several studies found that it can take as long as the saccade latency (Wolf & Schütz, 2015; Stewart & Schütz, 2018a) or longer (Ganmor et al., 2015), whereas others still (Bellebaum & Daum, 2006; Fabius, Fracasso, & Van der Stigchel, 2016) showed that it can happen in tens of milliseconds post-saccade. Overall, it is a very rapid process that is unsurprisingly dependent on the saccade latency, which can be influenced by a variety of factors (see subsection 1.3.1).

1.5.2 Cortical correlates

In order to determine the regions of the brain that are involved in transsaccadic integration, several methodological approaches have been used, including neurophysiological approaches, transcranial magnetic stimulation (TMS), and functional magnetic resonance imaging (fMRI). The more invasive of the techniques, neurophysiological recordings, has been helpful in identifying specific neuronal populations within a given cortical region. This allowed Subramanian and Colby (2014) to record from an area within intraparietal sulcus, LIP, and show that there are saccade-related integration responses for change in object features, specifically shape. The involvement of parietal cortex (wherein LIP/PEF is found; Fig. 1.1) in transsaccadic integration was also supported using TMS (which can act to create a temporary virtual

lesion and inactivation of the targeted region) in a task where comparisons of pre- versus post-saccadic presentations of oriented sinusoidal gratings were made (Prime, Vesia, & Crawford, 2008). Thus, parietal cortex plays a role in visuospatial transformation and integration (Pierrot-Deseilligny, Müri, Nyffeler, et al., 2005; Culham & Valyear, 2006) for saccade-related movements (though this has also been shown for hand and arm movements; see Filimon, 2010). Using fMRI, it was suggested that object orientation can be compared and updated across a saccade which may occur in a particular parietal region within right supramarginal gyrus (SMG; Fig. 1.1; Dunkley et al., 2016).

Transsaccadic integration was also found outside of parietal cortex. Specifically, integration of object orientation across saccades was suggested to occur in early visual cortex (Malik et al., 2015) and FEF (Prime, Vesia, & Crawford, 2010). A higher order area, dlPFC, was also shown to be involved in keeping track of, updating and integrating object orientation information across saccades (Tanaka et al., 2014). Taken together, these findings suggest that a specific, well-coordinated network of visuospatial transformation parietal regions, saccade- and working-memory frontal regions are involved in the sensory processing, maintenance, and integration of object feature information.

1.5.3 Models

In order to allow for prediction of future results about how the cortical system will operate for the integration of object features across saccades, computational models have been created, especially to explain peri-saccadic behaviour (observable actions during saccades) (Hamker et al., 2011). These models have been based on findings from tasks

that involve changes of locations of targets during saccades that seem to be mislocalized (i.e., changes that occur during the production of the saccade are not noticed and not updated into the saccade plan, so targets are mislocalized and errors are produced) (Hamker et al., 2011). These computational models converge on the idea that the receptive field for a particular fixation and future fixation is modulated in a dynamic manner, but the factors that contribute to the updating of signals therein remain to be further explored (see Hamker et al., 2011). One recent model investigated receptive field behaviour across time for spatial updating for saccade and smooth pursuit – continuous target tracking – and found that the former uses predictive remapping mechanisms, whereas the latter involves continual gaze-centered updating (Mohsenzadeh et al., 2016).

1.6 Grasping

In addition to perceiving an object, we may wish to manipulate or interact with an object (Bütepage et al., 2019). The ability to reach out and grasp an object, known as prehension, comprises two key phases: 1) transport (moving the arm and hand through space to reach toward the desired object) and 2) grasping (shaping the hand in order to match well the features of the object, such as its shape and orientation) (Jeannerod, 1984; also see Monaco, Buckingham, Sperandio, et al., 2016). The first component is largely determined by the ability of the visual and motor systems to interact in order to determine where the hand is versus where it must land. The latter component is produced by implicated joints and muscles, in addition to object processing. In this section, I will first

discuss the behavioural components associated with grasping and then, provide a condensed description of the associated cortical regions.

1.6.1 Psychophysics

Movements of the hand can be largely divided into two types: prehensile (hand moves in order to fully or partially make contact with and hold an object) and non-prehensile (objects are manipulated without grasping by hand) (Napier, 1956). In prehensile movements, which will be the focus here, the hand moves toward the desired object, which is associated with an initial high velocity movement of the hand and an opening of the hand (Rosenbaum et al., 2006). During the transportation phase, fingers tend to move more than does the thumb, where maximum aperture occurs in the latter half of the transport movement (Jeannerod, 1984) (even later on if the object is large; Marteniuk et al., 1990). The first part of transportation involves a fast phase where the fingers stretch out, whereas the second part is a much slower phase during which the fingers start to close (Jeannerod, 1984). Shortly before the wrapping of the fingers around the object, the fingers close in a manner that is consistent with the characteristics of the object, such as the size and shape (Jeannerod, 1984). This behaviour occurs under conditions with and without visual feedback – in the former, reaches are longer than when vision is not available, whereas in the latter, reaches are less accurate (Jeannerod, 1984; Prablanc et al., 1979).

In order to carefully position and mould the fingers to the desired, graspable object, one of the distinctions that has to be accomplished is between object perception and

recognition, as the former will determine where in space the object may be found so as to be able to navigate towards it, whereas the latter is important for the particular configuration that the hand must assume in order to grasp the object well (Creem & Proffitt, 2001). The function or meaning of an object may also influence how an object is manipulated (Klatzsky et al., 1987; Greeno, 1994). This points to Gibson's (1966) idea of affordance (further discussed in e.g., Goldstein, 1981; Gibson, 2000; Jones, 2003), which suggests that interaction with objects in the environment is the result of a careful consideration of factors that deal with personal requirements (body, size, etc.) and environmental components (Gibson, 1977 as cited in Greeno, 1994; Tucker & Ellis, 2001). An object can be interacted with via one of two types of grip: power (an object is held within the palm of the hand, with the fingers partially flexed and opposed by the force of the thumb) or precision (a pinching of an object with the opposing forces of the thumb and remaining fingers) (Napier, 1956; Landsmeer, 1962). (Evolutionary explanations for the development of the power versus precision grip have been offered elsewhere (Young, 2003; King et al., 2015).) The types of object properties that can influence grasp include shape (Goodale et al., 1994; Eloka & Franz, 2011), orientation (Paulun et al., 2016; Scharoun et al., 2016; Klein et al., 2019), and weight (Paulun et al., 2016; Klein et al., 2019).

1.6.2 Cortical correlates

According to the dual visual pathway theory (Ungerleider & Mishkin, 1982; Goodale & Milner, 1992), there is a ventral pathway that extends from primary visual cortex (V1) into

inferior temporal cortex and is responsible for recognition and identification of objects (‘perception’ pathway), as well as a dorsal pathway that extends from early visual cortex (V1) into parietal cortex and functions to process and/or produce actions such as grasping (‘action’ pathway). The latter pathway has been further parsed into dorsolateral (grasping) and dorsomedial (reach coding) streams (Jeannerod et al., 1995; Caminiti et al., 1998; Culham et al., 2003; Culham & Valyear, 2006; see Turella & Lingnau (2014) for more information).

In the dorsolateral pathway, there are two main cortical regions at play: the anterior intraparietal sulcus (AIP in macaque, aIPS in humans; Fig. 1.1; Murata, Gallese, Luppino, et al., 2000; Brochier & Umiltà, 2007; Gardner, Babu, Ghosh, et al., 2007; Gardner, Babu, Reitzen et al., 2007; Baumann et al., 2009) and area F5 (macaque)/ventral premotor cortex (PMv; human) (Murata, Fadiga, Fogassi, et al., 1997; Raos et al., 2006; Fluet et al., 2010; Turella & Lingnau, 2014). aIPS has been shown to have increased firing in neurons when grasping occurs in light and/or dark conditions, as well as while viewing objects that can be grasped (Murata, Gallese, Luppino, et al., 2000; Brochier & Umiltà, 2007). F5/PMv neurons have also been found to code for grasping of objects, based on grip type and object shape (Raos et al., 2006). This region has also been found to interact with other parts of cortex, such as somatosensory and dorsal premotor cortex, and through aIPS will eventually interact with primary motor cortex (M1; precentral gyrus; Fig. 1.1) in order to produce the desired action (Rizzolatti & Luppino, 2001; Brochier & Umiltà, 2007).

The dorsomedial pathway comprises two regions within posterior parietal cortex, (visual area V6A, or superior parieto-occipital cortex, SPOC (Fattori, Gamberini, Kutz, et al., 2001; Fattori, Kutz, Breveglieri, et al., 2005; Bosco et al., 2015) and midintraparietal area (MIP; macaque; Colby & Goldberg, 1999) / midintraparietal sulcus (mIPS; human; Johnson et al., 1996; Prado et al., 2005), and dorsal premotor cortex (PMd; Caminiti et al., 1991). This pathway has been associated with reach planning and arm positioning during the transport portion of the reach-to-grasp (Vesia et al., 2010; Vesia et al., 2017).

The further division of the dorsal 'action' pathway into a dorsolateral and a dorsomedial stream has been recently been debated (Goodale & Westwood, 2004; Turella & Lingnau, 2014). Although the original view or model of the division of reaching/grasping has suggested a separation of reach-related components versus grasp-related components, there have been findings within multiple regions (V6A (Fattori, Raos, Breveglieri, et al., 2010; Fattori, Breveglieri, Raos, et al., 2012), PMd and AIP for example (Lehmann & Scherberger, 2013)) that argue against a rigid separation of regions dedicated to reaching and grasping. The idea that the 'pathways' may interact or not be as separate as once thought is given weight by the recent amendment to the previous model of the two-stream visual system (Goodale et al., 1994; Goodale & Westwood, 2004; Milner & Goodale, 2008).

1.7 Functional magnetic resonance imaging

Determining which cortical regions may be involved in a given task in humans without having to resort to invasive approaches is possible through the use of several

neuroimaging techniques, including functional magnetic resonance imaging (fMRI). This technique was preceded by positron emission tomography (PET) – a technique that uses the injection of a radionuclide in small quantities that has a fast decay rate, but can only be administered a specific number of times per year (de Beeck & Nakatani, 2019) - which has largely been replaced by fMRI (Corbetta, 1993), for which there are no known risks (with some restrictions; de Beeck & Nakatani, 2019). I will discuss the theory behind fMRI, as well more specific applications relevant to this dissertation, including fMRI adaptation and functional connectivity analysis.

1.7.1 General theory

FMRI utilizes the change in blood flow to a region of the brain that is active as its measurement, i.e., the blood oxygenation-level dependent (BOLD) signal. The idea is that, if a particular region of the brain is active in response to a particular stimulus or task, it will use the oxygen in the red blood cells in nearby vasculature (Buxton et al., 2004). After this rapid consumption of oxygen, there will be a rush of new oxygen in oxygenated blood cells in the area (Buxton et al., 2004). The level of oxygenation in local blood flow for the cerebral cortex can be modeled in the form of a hemodynamic response function (Friston et al., 2000; Buxton et al., 2004; Lindquist & Wager, 2007). This response is said to be event-related, as it is an indirect measure of a direct response to a given stimulus or event (Buxton et al., 2004).

On average, the hemodynamic response is comprised of an initial dip in the BOLD signal as a function of time, which has been suggested to be due to the decrease in oxygenation

due to initial consumption (Yacoub et al., 2001), an increase in response for a duration of 4-6 s (Bandettini et al., 1992), and a post-stimulus undershoot (Chen & Pike, 2009; for review, see van Zijl et al., 2012). Although this 4-6 s response may seem slow, it is able to display the dynamic nature of cortical activity in response to short event periods (on the order of hundreds of milliseconds; Buxton et al., 2004). The curve of the BOLD response can be altered if several events occur during a trial that happen in less than the average hemodynamic response duration (Pollman et al., 2000) which is an important factor to consider when creating event-related fMRI paradigms (Buckner, 1998).

1.7.2 Relevant methodological approaches

FMRI paradigms can be adapted or designed in such a manner so as to allow the experimenter to better pinpoint activation in response to stimuli or events. One such direction is fMRI adaptation (fMRIa; Fig. 1.2), which involves the presentation of a stimulus followed by (1) the presentation of the same/similar stimulus or (2) the presentation of a different stimulus (Fig. 1.2; Grill-Spector & Malach, 2001; Kar & Krekelberg, 2016). If the BOLD signal that reflects the repeated presentation of the stimulus is greater for (1) than (2), this is known as repetition enhancement (Segaert et al., 2013). On the other hand, if the BOLD signal for the repeated stimulus is greater for (2) than (1), this is referred to as repetition suppression (Grill-Spector & Malach, 2001; Segaert et al., 2013). Either of these effects, if found within a particular cortical region, suggest that that area may be sensitive to the stimulus or event being tested. In contrast, if the BOLD signal is the same in both (1) and (2), when subtracted, there will be no

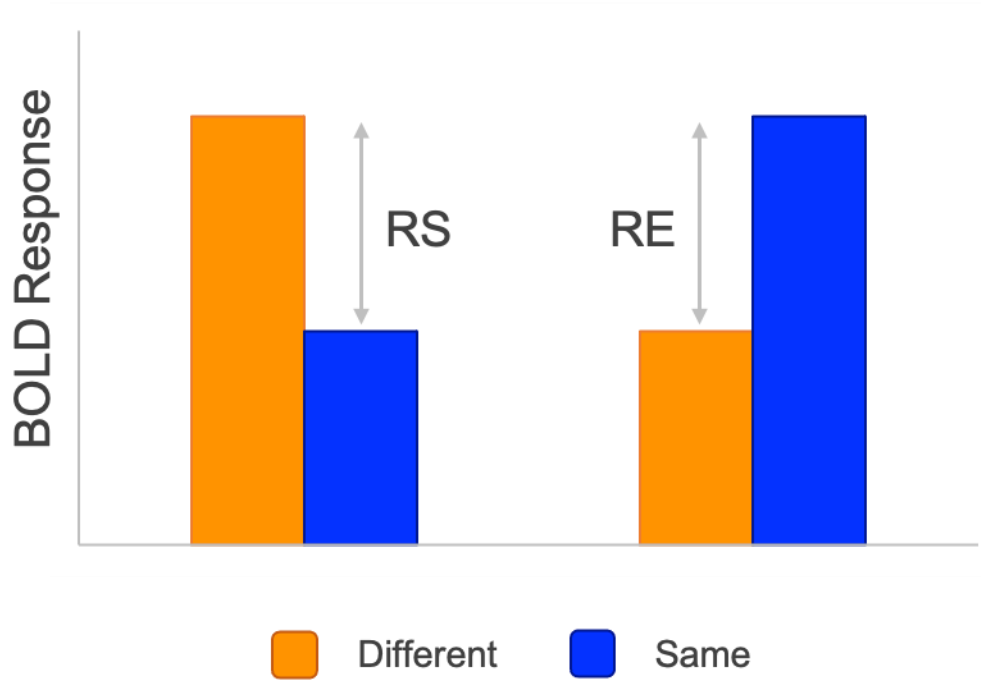

Figure 1.2. FMRIa effects, repetition suppression (RS) and enhancement (RE) depicted in graphical format. Repetition suppression is depicted in the set of bars on the lefthand side, where BOLD activity is greater for trials associated with change in a stimulus property (Different condition) compared with trials in which the stimulus property is repeated (Same condition) across re- presentations of the stimulus. In contrast, repetition enhancement, depicted in the set of bars on the righthand side, reflects BOLD for trials with a repeated stimulus property that is greater than for trials with a change in the chosen property across stimulus presentations.

difference, suggesting that the region is likely not modulated by or sensitive to what is being tested (Grill-Spector & Malach, 2001).

Another way of understanding cortical mechanisms relies on the assessment of communication between regions. This involves the analysis of time courses of the BOLD response for particular regions-of-interest (ROIs), or seeds, relative to other brain regions (Friston et al., 1997; O'Reilly et al., 2012). This is referred to as functional connectivity analysis, whereby relationships between regions (with a given start seed region) are analyzed in a manner that presents results as a function of a given task, or usually at rest (Greicius et al., 2009). Functional connectivity analysis applied to data acquired over a short period of time during rest with fMRI has allowed experimenters to determine specific networks of cortical regions, such as the default mode network (Greicius et al., 2009) and dorsal attention network (Fox et al., 2005). However, because there are also event-related fMRI tasks, there are specific functional connectivity approaches that can account for task-related changes (O'Reilly et al., 2012; Schröder et al., 2020). One such tool can provide information about interactions between cortical regions, as well as the direction of information flow which is referred to as dynamic causal modeling (Friston et al., 2003). Another approach that allows for the elucidation of task-based effects is through psychophysiological interaction (PPI) analysis (Friston et al., 1997; Schröder et al., 2020) – although this technique is limited in its ability to indicate the direction of information flow.

1.8 Aims and hypotheses

To date, we have learned a considerable amount of information about the visual and motor systems that allow us to perceive, keep track of, and interact with objects in our surroundings (Irwin, 1996; Prime, Tsotsos, Keith, et al., 2007; Prime, Vesia, & Crawford, 2008; Prime, Vesia, & Crawford, 2010; Cavina-Pratesi et al., 2010). The subcortical and cortical regions responsible for the production of saccades (see Muñoz, 2002) have been well-documented, as well as regions responsible for the encoding and updating of hand/arm-related activity (see Filimon, 2010). We have also learned from psychophysical studies the parameters of the type and quantity of information that is encoded within fixations, how it is retained and integrated with information from future fixations (Luck & Vogel, 1997; Prime, Tsotsos, Keith, et al., 2007), and how splitting or redirection of attention can affect this process (Cavanagh et al., 2010; Rolfs et al., 2011; Stewart & Schütz, 2018a). However, no study has yet investigated how the oculomotor system and grasping interact when saccades are produced. In addition, although it is known where object orientation is processed (Hubel & Wiesel, 1959, 1962; Dunkley et al., 2016) and that it can be updated across saccades (Prime, Tsotsos, Keith, et al., 2007; Prime, Vesia, & Crawford, 2008; Prime, Vesia, & Crawford, 2010), there is little information about how these processes differ (or not) for other object features.

Despite what we know about object orientation processing (Hubel & Wiesel, 1959, 1962) and that it can be updated across saccades (Prime, Tsotsos, Keith, et al., 2007; Prime, Vesia, & Crawford, 2008, 2010; Dunkley et al., 2016), I first attempted to fill in the gap that connects these processes with another modality (i.e., motor – grasping). Based on previous findings for transsaccadic perception of object orientation (Dunkley et al., 2016), I hypothesized that there may be a single cortical mechanism for transsaccadic

perception, where parietal cortex may serve a special role. To investigate this, I set out to identify the cortical regions that are involved in the updating of object orientation across saccades when participants have to grasp a rotatable 3D object. I predicted that regions previously suggested to be involved in transsaccadic integration of object orientation (i.e., right SMG; Fig. 1.1; Dunkley et al., 2016) and parietal regions that perform visuomotor transformations (i.e., those regions that can account for saccade, grasp actions; see Filimon, 2010) would be involved in the updating of orientation information across saccades when participants are required to execute a grasp. I found that this was, indeed, the case, i.e., right SMG and parietal regions (aIPS and SPL; Fig. 1.1) were involved in the remapping of orientation information for grasping.

Another question to ask in this line of investigation relates to the cortical regions recruited to update different object features across saccades. I investigated whether parietal cortex acts as a more general transsaccadic integrator, not just across modalities, but also across object features. Of the isolated object features that have been tested previously (see subsection 1.5.1), spatial frequency has only recently been mentioned (Fabius et al., 2020). It is one of the earliest features that is processed (V1; De Valois et al., 1982), just like object orientation (Hubel & Wiesel, 1959, 1962). Due to the few studies that have been conducted to investigate the cortical activity associated with transsaccadic perception of object features, there is little reason to anticipate that transsaccadic updating would require the use of a variable, separate feature network. Thus, I hypothesized that, if transsaccadic perception involves a general-purpose mechanism, the updating of spatial frequency across saccades may also involve parietal cortex, in particular right SMG (Dunkley et al., 2016). If this is not the case, then I would anticipate

early visual regions as being involved due to the early processing of this feature in striate and extrastriate cortex (Nakamura & Colby, 2002). The results here point toward transsaccadic interactions in early visual (cuneus, LG; Fig. 1.1) cortex for spatial frequency, with additional saccade-related regions in parietal (precuneus; Fig. 1.1) and frontal (FEF; Fig. 1.1) cortex. These findings suggest that transsaccadic perception may not tap into a single, general purpose system for any one object feature; rather, transsaccadic perception may rely upon several feature-dependent updating mechanisms.

One consistent aspect of these studies, as well as the one conducted by Dunkley et al. (2016), is that a single object feature is tested each time. Presumably, if multiple features were tested, I would expect to observe the feature-specific transsaccadic cortical mechanisms. In other words, if object orientation was modulated, all else being equal, I would expect to see SMG being engaged for a perceptual task (and any additional modality/motor related regions). If spatial frequency can act to relay information about object identity for example (Valyear et al., 2006), perhaps a change in identity/shape may also recruit extrastriate cortex (cuneus/LG, as in the second experiment here; Baltaretu et al., 2021a). Thus, using 2D stimuli, I used a direct test of object orientation versus shape change (as a way of communicating object identity change) for fixations or saccades to probe the dissociable nature of transsaccadic perception mechanisms. I hypothesized that changes in object orientation across saccades would recruit SMG, whereas (if spatial frequency represents an underlying characteristic, related to object identity) shape changes should recruit extrastriate (cuneus/LG) cortex. Saccade-related regions were found primarily in occipital and parietal cortex, with extrastriate (cuneus)

cortex showing additional feature-related effects. This more direct test of transsaccadic perceptual mechanisms for different object features also reflects the idea of separate cortical mechanisms.

This dissertation describes the experiments that have tried to address if: 1) parietal cortex has a potential general-purpose role in transsaccadic perception and 2) object feature-specific transsaccadic cortical mechanisms exist. In Chapter 2, I will describe and discuss the findings from the fMRI study on transsaccadic perception of object orientation for grasping. This chapter will serve to explore the cortical system involved for the coordination of the saccade and grasp systems. Chapter 3 will provide a description and discussion of the results for the transsaccadic perception of another object feature, spatial frequency. Here, I will delve into the considerations of spatial frequency of an object within the realm of transsaccadic interactions. Chapter 4 will concentrate on the results of investigations into transsaccadic perception of multiple object features, namely object orientation and shape. The findings from this final study will serve to open discussions surrounding transsaccadic perception and whether it employs a singular, general mechanism or several, feature-specific mechanisms. Finally, in Chapter 5, I will provide further discourse on the following: 1) summary of the findings from the three studies, 2) the contribution of those findings to transsaccadic literature, 3) address some remaining unanswered questions, and 4) potential applications and future directions.

CHAPTER 2

PARIETAL CORTEX INTEGRATES SACCADE AND OBJECT ORIENTATION SIGNALS TO UPDATE GRASP PLANS

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2.1 Abstract

Coordinated reach-to-grasp movements are often accompanied by rapid eye movements (saccades) that displace the desired object image relative to the retina. Parietal cortex compensates for this by updating reach goals relative to current gaze direction, but its role in the integration of oculomotor and visual orientation signals for updating *grasp* plans is unknown. Based on a recent perceptual experiment, we hypothesized that inferior parietal cortex (specifically supramarginal gyrus; SMG) integrates saccade and visual signals to update grasp plans in additional intraparietal / superior parietal regions. To test this hypothesis in humans (7 females, 6 males), we employed a functional magnetic resonance adaptation paradigm, where saccades sometimes interrupted grasp preparation toward a briefly presented object that later reappeared (with the same/different orientation) just before movement. Right SMG and several parietal grasp regions, namely left anterior intraparietal sulcus (aIPS) and bilateral superior parietal lobule (SPL), met our criteria for transsaccadic orientation integration: they showed task-dependent saccade modulations and, during grasp execution, they were specifically sensitive to changes in object orientation that followed saccades. Finally, SMG showed enhanced functional connectivity with both prefrontal saccade regions (consistent with oculomotor input) and aIPS / SPL (consistent with sensorimotor output). These results support the general role of parietal cortex for the integration of visuospatial perturbations, and provide specific cortical modules for the integration of oculomotor and visual signals for grasp updating.

2.2 Introduction

We inhabit a dynamic visual environment, where the brain must simultaneously compensate for both *afferent* (externally-driven) and *reafferent* (internally-driven) sensory events, often using internal *efference* copies of our own motion (Sherrington, 1918; Sperry, 1950; von Holst & Mittelstaedt, 1950; Helmholtz, trans. 1963). For example, parietal cortex plays an important role in updating reach goals in response to both unexpected changes in object location (Pisella et al., 2000) and internally-driven changes in eye position (Batista et al., 1999; Khan et al., 2005). This internal compensation, likely using saccade efference copies, allows more precise aiming (Vaziri, 2006; Dash et al., 2016) and reaches toward targets that are no longer visible (Henriques et al., 1998; Fiehler et al., 2011). However, successful object manipulation also requires grasping: shaping of the hand to fit specific object attributes like shape and orientation (Jeannerod, 1984; Fabbri et al., 2016; Desmurget & Prablanc, 2017). In order to successfully coordinate reach transport and grasp (Castiello, 2005; Marotta et al., 2006), intended grasp location and orientation must remain linked and updated during saccades (Crawford et al., 2004; Fan et al., 2006). However, to date, the cortical mechanisms for *transsaccadic grasp updating* have not been studied.

Transsaccadic grasp updating could recruit the mechanisms for transsaccadic perception: the comparison and integration of visual information across visual fixations (Irwin, 1996; Prime, Tsotsos, Keith, et al., 2007; Melcher & Colby, 2008). Transcranial magnetic stimulation (TMS) studies suggest that the frontal eye field (FEF) provides the saccade efference copy for transsaccadic integration in posterior parietal cortex (PPC) (Prime, Vesia, & Crawford, 2010, 2011). A recent functional magnetic resonance imaging

(fMRI) study showed that inferior parietal cortex (specifically, the supramarginal gyrus, SMG) is sensitive to transsaccadic changes in visual stimulus orientation (Dunkley et al., 2016). Human SMG may be an expansion of primate lateral intraparietal cortex, which contains saccade, visual feature, and spatial updating signals (Gnadt et al., 1988; Subramanian & Colby, 2014). Since the inferior parietal cortex is thought to mediate perception and action (Goodale & Milner, 1992; Rizzolatti & Matelli, 2003), we hypothesized that SMG might also play a role in transsaccadic updating of grasp orientation, using efference copy input from the FEF.

Successful grasp also requires the updating of sensorimotor plans. Several parietal regions have been implicated in the visuomotor transformations for grasp, including the anterior intraparietal sulcus (aIPS) (Murata et al., 2000; Monaco et al., 2010), superior parietal cortex (SPL) (Culham et al., 2003; Filimon et al., 2009), and superior parieto-occipital cortex (SPOC) (Gallivan et al., 2011; Rossit et al., 2013). TMS experiments suggest that SPOC is involved in early visuomotor transformations for reach goals (Vesia & Crawford, 2012; Monaco et al., 2014). Of these regions, the more anterior intraparietal regions have specifically been implicated in updating grasp in response to external visual perturbations (Glover et al., 2005; Le et al., 2014; Janssen & Scherberger, 2015). However, it is not known if any part or all of these regions are specifically involved in transsaccadic grasp updating.

Based on this literature, we hypothesized that SMG and the parietal grasp network provide the visuomotor coupling for transsaccadic grasp updating, by integrating visual features with saccade signals from FEF. To test this model, we merged two previous event-related fMRI paradigms for transsaccadic integration (Dunkley et al., 2016) and

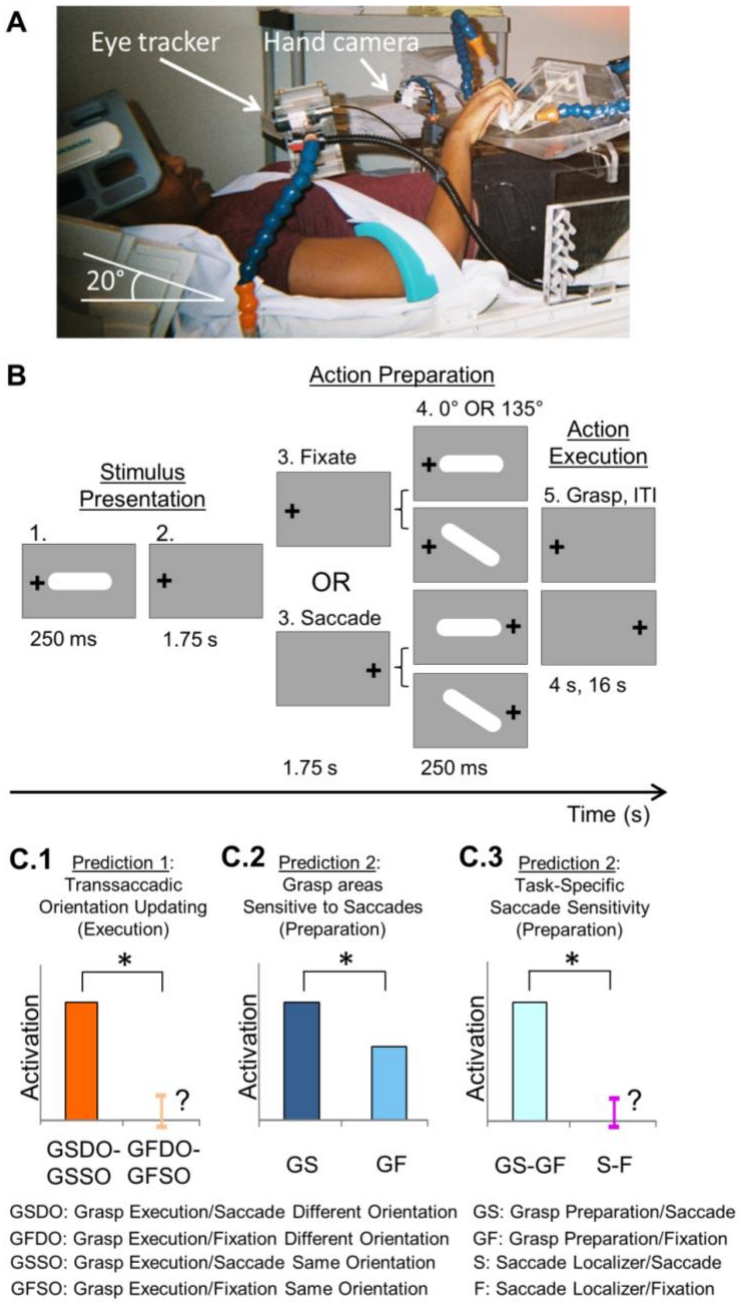


Figure 2.1. Experimental set-up, paradigm, and predictions. A. Set-up of the experiment, showing participant lying supine on MRI table with head tilted at 20° under the head coil, along with MRI-compatible eye tracker for right eye and hand tracker. Participants rested their hand on the abdomen in a comfortable position and were asked to transport their hand to the platform to grasp an oriented 3D bar only when required to do so; a strap across the torso was used to ensure minimal-to-no movement of the shoulder and arm during transportation of the hand to the platform. The blue stalk above the platform was used to illuminate the central grasp object, whereas those to the left and right contained LEDs and were used to ensure fixation of gaze. B. Stimuli and task. An example of an

initial trial condition is shown (0° grasp bar, gaze left) followed by the four possible conditions that might result: Fixate / Different Feature, Fixate / Same Feature, Saccade / Different Feature, and Saccade / Same Feature. Each trial lasted 24 seconds and was comprised of three major phases: 1) Stimulus Presentation, during which the grasp object was illuminated in one of two possible orientations (0° or 135°) and gaze could be left or right; 2) Action Preparation, when participants maintained fixation on the same LED as in the previous phase (Fixate condition) or they made a saccade to the opposite LED (Saccade condition) – the object was illuminated a second time at the end of this phase and was presented either in the Same orientation as in phase 1 (0° if the initial was 0° or 135° if the initial orientation was 135°; Same condition) or at a Different orientation (0° if the initial was 135° or vice versa; Different condition); and 3) Action Execution, which required participants to grasp the oriented object within 4 s and then, return to rest (only the first 2 s were used for analysis). This was followed by an intertrial interval of 16 s. C. The possible predictions for sensitivity to saccade signals in grasp regions in three conditions. C.1. The first prediction suggests that, during the Action Execution phase, cortical regions that specifically update object orientation across saccades should show a greater difference in activity between the Same and Different Orientation conditions in the Grasp Saccade condition, as compared with the Same – Different Orientation difference in the Grasp Fixate condition (GSDO, GSSO, GFDO, GFSO, respectively). C.2. The second prediction indicates that, if a grasp region is modulated by saccade signals, the BOLD activity should be greater for the Saccade condition (Grasp Saccade condition, GS), as com-pared with the Fixate condition (Grasp Fixation condition, GF). C.3. The third prediction tests whether modulations due to saccade signals during the grasp Action Preparation phase (C.2) are specific to grasp-related activity. This predicts a greater difference be-tween the Saccade and Fixate conditions in the grasp experiment compared to a separate saccade localizer that only required participants to either saccade between our two LEDs or fixate on one of the LEDs ((Grasp Saccade - Grasp Fixate) - (Saccade – Fixate); (GS – GF) – (S – F)).

grasp planning (Monaco et al., 2014) (Fig. 2.1B). We then applied a specific set of criteria to identify regions involved in the integration of eye position and visual orientation signals for grasp updating: 1) these regions should be specifically sensitive to transsaccadic changes in required grasp orientation plans (Fig. 2.1 C.1), 2) they should show saccade modulations during grasp preparation (Fig. 2.1 C.2), and 3) these modulations should become progressively more grasp task-specific as the sensorimotor transformation advances (Fig. 2.1 C.3). Finally, during grasp updating, these regions should show stronger functional connectivity, both with each other and the cortical saccade generator, during saccades as compared to fixation.

2.3 Materials and methods

2.3.1 Participants

To determine the appropriate number of participants (human) required for a sufficient effect size/ level of power in this study, we reviewed the most relevant previous literature and then did a power analysis. The current experimental design was based on our previous fMRI studies of transsaccadic memory (Dunkley et al., 2016) and grasp orientation (Monaco et al., 2014). Thirteen participants were analyzed in the Dunkley et al. (2016) study and 14 in the Monaco et al. (2014) study. We have found previously that an additional motor response in the experiment increases the cortical activation in the posterior parietal regions of interest for this study (Chen et al., 2014; Cappadocia et al., 2018), so we based our power analysis on the Monaco et al. (2011) study and chose their region of interest that was closest to the posterior parietal activation that we expected. Specifically, we used the effect size (1.27, Cohen’s d) from their left posterior intraparietal

sulcus (pIPS) activation, along with the following parameters: 1) two-tailed t-test option, 2) an α value of 0.05 (we had planned for one contrast), and 3) a high power value (0.98). Using these values in G*Power (Faul et al., 2009), we calculated that 13 participants would provide a sufficient actual power value (0.987).

In order to obtain a reliable dataset of 13 participants (after the exclusion criteria described in the analysis section below), we had to test seventeen participants. These were all graduate students from York University, Toronto, Ontario, Canada, experienced with performing visual experiments and with no known neurological disorders and normal or corrected-to-normal vision. These participants (7 females, 6 males) were all right-handed and were aged 26.5 +/- 3.7 years (from 22 to 32). All participants provided written consent and were compensated financially for their time. The York University Human Participants Review Subcommittee approved all experiments.

2.3.2 Experimental set-up and stimuli

Participants were asked to fill out an MRI screening form. Upon passing MRI screening, participants were informed about the task. Once they felt comfortable with what the experiment entailed, they were asked to assume a supine position on the MRI table, with their head in a six-channel coil tilted forward at a 20° angle (in order to allow for direct visibility of the objects) (Monaco et al., 2014). To obtain a complete signal, we also placed a four-channel coil anteriorly on the head (Monaco et al., 2014).

This experiment was conducted in complete darkness. In our set-up, we had red fixation light emitting diodes (LEDs) for participants to focus on during the entire duration of a trial. A fixation LED was placed to the left and right of the central stimulus (between

10-12° from the center of the stimulus to each LED; (Monaco et al., 2014)). There was also a white LED that was used to illuminate the stimulus only when participants would grasp at a particular time point in each trial (Fig. 2.1A, B). These LEDs were mounted onto a rotatable platform that was placed above each participant's pelvis. LEDs were held in place by MRI-compatible rigid tubes (which were made of many units to allow for movement of the overall tube in order to position the LEDs accordingly).

The stimulus that participants had to grasp was a six-degree long bar with rounded ends (Fig. 2.1A, B) and centered on the platform. The bar could be rotated, but two MRI-compatible pins were placed in the surrounding area to ensure that the bar could only be oriented horizontally (0°) or obliquely (135°).

For each participant, right eye position was recorded using an infrared camera affixed to the right side of the MRI table (Fig. 2.1A). Eye movement signals were recorded using iViewX software (SensoMotoric Instruments) for offline analysis. We recorded, using a hand camera (Fig. 2.1A), the reaching and grasping movements of participants during each trial of every run.

Lastly, in order to reduce any motion artifacts in the imaging data, participants' upper arm and shoulder were immobilized using an MRI-compatible belt that was strapped down across their torso. Participants reached with their right hand and pivoted only from their elbow joint, with only the minimal rotation of the shoulder joint. Their right arm was supported with foam padding and sand bags to provide a comfortable height from which the arm could reach and grasp the object for the duration of the experiment. We also made sure that the addition of the padding was appropriate and allowed participants to reach and grasp the object appropriately.

2.3.3 General paradigm/procedure

2.3.3.1 Experiment

We used an event-related fMRI design to identify cortical regions involved in updating grasp orientation across saccadic eye movements. Specifically, we developed a behavioral paradigm that combined elements of 1) a transsaccadic orientation memory study, where participants viewed a briefly-presented sine-wave grating, made a saccade, and then had to judge if a second visual stimulus had the same or different orientation (Dunkley et al., 2016) and 2) a grasp orientation study, where the orientation of a grasp stimulus could remain the same or change just before the reach (Monaco et al., 2011). First, participants were placed in the MRI bore and a comfortable reach distance was determined for placement of the grasp stimulus by moving the platform along the MRI table. Participants were then trained to reach and grasp this bar stimulus (see previous) in response to a specific 'go' signal (Fig. 2.1A, B). At the beginning of each reach trial, participants rested their arm, bent at the elbow, on their abdomen in a position that was within comfortable reaching distance of the stimulus. Participants were instructed to use all digits of their right hand to grasp the center of the object (Fig. 2.1A). Upon completing the grasp, participants returned their arm to the same resting position as prior to the reach.

Each trial started with the illumination of one of the two LEDs to the right and left of the central target. Then, the central target was illuminated for 250 ms. The target could be oriented at 0° or 135° (pseudorandomized and counterbalanced within and across runs). Participants were required to keep fixating for another 1.75 s. This first two-second phase was referred to as the '*Stimulus Presentation*' phase (Fig. 2.1B). After this period,

participants kept fixating on the same LED for another 1.75 s ('Fixate' condition) or made a saccade to the other LED, which would be illuminated while the previous LED would be extinguished ('Saccade' condition). (Note that fixation occurred for the entirety of a trial only for Fixation trials, which were intermingled with Saccade trials.) Following this 1.75 s period, the object was illuminated for 250 ms. This was referred to as the '*Action Preparation*' phase (Fig. 2.1B), when participants were expected to retain stimulus location and orientation information, and use this to prepare for a movement (Monaco et al., 2011; Chen et al., 2014; Cappadocia et al., 2018). The object could now be oriented in the same orientation as in the first illumination/presentation ('Same Orientation' condition, e.g., 0° orientation first and then, another 0° orientation; same for the 135° orientation) or a different orientation as compared to the first ('Different Orientation' condition, e.g., 0° orientation first, followed by a 135° orientation, and vice versa). Participants were then given 4 s to reach out to grasp the object in its final orientation as described above ('*Action Execution'* phase) while still fixating the illuminated LED. Following this phase, the LED was set up for the next trial and participants had 16 s to rest while maintaining fixation (intertrial interval, ITI), so as to allow the BOLD signal to return to baseline. The illumination of the stimulus marked the beginning of each trial, whereas the end of the 16 s period of relaxation marked the end of the trial.

In order to create the different orientation conditions, one experimenter rotated the stimulus as needed in the scanner room, but out of the participant's view and in complete darkness. To reduce the possibility of participants predicting Different versus Same orientation based on sound feedback, the experimenter moved the stimulus away and back to its required orientation (also during Same Orientation conditions).

The design of the experiment consisted of a 2 (Gaze Position: Fixate or Saccade) x 2 (Gaze Fixation Location: Left or Right) x 2 (Object Orientation: 0° or 135°) design. This produced eight condition types, which were repeated four times within one run. There were six runs in total. As mentioned previously, the condition types were pseudorandomized and intermingled within each run and across runs.

Compared to our previous study (Dunkley et al., 2016), we used a shorter stimulus period (total of 2 s for each stimulus presentation) in order to match an acquisition time of 2 s, and to ensure a reasonably long run/ experiment (given that a long ITI is needed to allow the BOLD to return to baseline). Recent studies have suggested that this transsaccadic integration can occur on the order of tens of ms (Prime, Vesia, & Crawford, 2008; Dunkley et al., 2016; Stewart & Schütz, 2019). In addition, we chose a fixed ITI (no jitter) because we did not investigate response timing in this study and we wished to maximize our statistical power in order to detect transsaccadic integration signals (Dunkley et al., 2016).

2.3.3.2 Saccade localizer

To determine which regions are involved in the production of saccadic eye movements, we used a localizer that had a sequence similar to that of the experimental runs. This localizer comprised alternating periods of fixation and saccadic eye movements. First, a baseline of activity would be established as a result of participants fixating the illuminated LED for 18 s (two runs total of data were collected, where participants fixated the left LED first and right LED second, or vice versa). Then, every second for 6 s, the LEDs would alternate in illumination, resulting in saccades. After this, participants would then fixate

the initial LED for 16 s. This fixation-saccade sequence was repeated eight times in the localizer run. There was a last fixation period of 18 s.

2.3.3.3 Imaging parameters

We used a 3T Siemens Magnetom TIM Trio magnetic resonance imaging (MRI) scanner. The functional experimental data were acquired using an echo-planar imaging (EPI) sequence (repetition time [TR]= 2000 ms; echo time [TE]= 30 ms; flip angle [FA]= 90 degrees; field of view [FOV]= 192 x 192 mm, matrix size= 64 x 64 with an in-slice resolution of 3 mm x 3 mm; slice thickness= 3.5 mm, no gap) for all six functional runs in an ascending and interleaved manner. For the saccade localizer, an EPI sequence was also used to acquire the data sequences (repetition time [TR]= 2000 ms; echo time [TE]= 30 ms; flip angle [FA]= 90 degrees; field of view [FOV]= 192 x 192 mm, matrix size= 64 x 64 with an in-slice resolution of 3 mm x 3 mm; slice thickness= 3.5 mm, no gap). Along with functional data, a T1-weighted anatomical reference volume was acquired using an MPRAGE sequence (TR= 1900 ms, FA= 256 mm x 256 mm; voxel size= 1 x 1 x 1 mm^3). For each volume of anatomical data obtained, 192 slices were acquired. For the experimental task, we collected 395 volumes of functional data for the experimental runs, where each volume comprised 35 slices. For the saccade localizer, we collected 98 volumes of functional data, where each volume comprised 35 slices.

2.3.4 Analysis

2.3.4.1 Behavioural data

We monitored eye position during the experiment and analyzed it offline, to verify that participants fixated on the appropriate LED and did not make any additional, unnecessary saccades during trials. Any trials showing inappropriate fixation or saccades were removed from additional analysis. Similarly, video data were analyzed offline to determine if the participant grasped the object at the required time. Any trials during which any anomaly in grasping occurred (i.e., participant grasped the object too early or too late, etc.) were removed from further analysis by being designated as confound predictors in the general linear model (see below). On this basis, eight trials across all participants (0.003%) were removed from the entire data set (two trials each were excluded from two participants and one trial from another four participants).

2.3.4.2 Functional imaging data: experimental

A general linear model (GLM) was created for each run for each participant. A predictor was used as a baseline for the period of fixation at the beginning and the end of each run ("Baseline"), accounting for the first 18 s of each run and the 16 s intertrial interval. The initial 2 s *(Stimulus Presentation* phase) during which the object was illuminated and participants had to fixate an LED was assigned a predictor that indicated the location of the fixation LED ("Adapt_LVF" and "Adapt_RVF" if the fixation was on the right LED or left LED, respectively; left and right visual field for LVF and RVF, respectively). The subsequent *Action Preparation* phase (2 s) was assigned one of four predictors: "Sacc_DiffFeature", "Sacc_SameFeature", "Fix_DiffFeature", or "Fix_SameFeature" for when participants made a saccade or fixated and, for each of these, whether the orientation of the object was the same (Same Orientation condition) or different (Different

Orientation condition). The *Action Execution* phase was divided in two 2-s phases. There were four predictors for the first 2 s of the grasp event. These predictors were based on the direction of the preceding saccade and upon whether the orientation of the object that was being grasped was the same in the *Action Preparation* phase as in the *Stimulus Presentation* phase (Same Orientation condition) or different (Different Orientation condition). Thus, the four predictors were: “Motor Execution_Sacc_DiffFeature”, “Motor Execution_Sacc_SameFeature”, “Motor Execution_Fix_DiffFeature”, and “Motor Execution_Fix_SameFeature”. The following 2 s of the *Action Execution* phase were provided a “Motor Execution” predictor. These predictors comprised each GLM for each participant (BrainVoyager QX 2.8, Brain Innovation). Each predictor variable was convolved with a haemodynamic response function (standard two-gamma function model). GLMs were modified through the addition of confound predictors for eye movement or hand movement errors. If a GLM had more than 50% of the trials being modelled in the confound predictor, the GLM for that run was not included in the overall population level GLM (random effects GLM, RFX GLM).

Additionally, functional data for all runs across all participants were preprocessed (slice time correction: cubic spline, temporal filtering: <2 cycles/run, and 3D motion correction: trilinear/sinc). Data for runs that had abrupt motion of over 2 mm were excluded from the RFX GLM and additional analysis. As a result, four participants’ data were excluded because more than half of the runs were unusable due to abrupt, excessive head motion of over 2 mm. From the remaining 13 participants, 8 additional runs were removed (i.e., 256 trials out of a possible 2496 across the 13 participants, or 10.3%). The anatomical data was transformed to a Talairach template (Talairach &

Tournoux, 1988) and the functional data from the remaining 13 participants were coregistered using gradient-based affine alignment (translation, rotation, scale affine transformation) to raw anatomical data. Functional data were smoothed using an FWHM of 8 mm.

2.3.4.3 Functional imaging data: saccade localizer

For the preprocessing of functional data for the localizer, see above section. On the basis of excessive head motion (>2 mm), one person's data was completely excluded, half of the data were excluded for a second person (runs where initial fixation was on the left), and half were excluded for a third person (runs where initial fixation was on the right). Using the remaining functional data, we ran an RFX GLM on the data for each of the localizers. For the saccade localizers, we had three predictors: a 9 s "Baseline" predictor, a 16 s fixation "Fix" predictor, and a 6 s saccade "Sacc" predictor. The results of the saccade localizer were used to identify which areas are involved in saccade production in our task specifically (Figs. 2.2B, 2.4B).

2.3.4.4 Experimental design and statistical analysis

BrainVoyager (BrainVoyager QX 2.8, Brain Innovation) was used for the analysis in this study. For each analysis we derived data from the most appropriate experimental phase (*i.e., Action Preparation* phase*, Action Execution* phase), i.e., when the relevant brain events would be expected. This included volumetric map contrasts for general grasp and saccade activation (Grasp Fixation – Baseline; Grasp Saccade – Fixation) from the *Action Preparation* phase (Fig. 2.2), as well as more the specific hypothesis tests described

below. Note that this experiment was not designed to temporally separate BOLD signals from our task phases, so they could be influenced by other task phases, but these additional signals should cancel in our specific hypothesis tests.

In the above contrasts, the volumetric maps had p-values Bonferroni corrected according to the number of contrasts that were applied to the same dataset (i.e., $p<0.25$ for two contrasts, corrected from $p<0.05$). in addition, cluster threshold correction was applied to these data using the plugin provided by BrainVoyager that implements Monte Carlo simulations (Forman et al., 1995). In order to qualitatively visualize the data (Figs. 2.2-2.5), we superimposed the surviving clusters onto the 'inflated brain rendering of an example participant' for each analysis. Since this process often results in small anatomic distortions, we sometimes also include transverse slice renderings below in key points (Fig. 2.3A). Note that these data are only provided for visualization purposes: the following describes the objective procedures that we used for anatomic localization and hypothesis testing.

2.3.4.5 Localization of sites of interest

We hypothesized that 1) several specific cortical areas are involved in transsaccadic updating of grasp plans (see Introduction), and 2) to qualify for this role, they must pass three specific predictions (Fig. 2.1C). In order to apply these predictions to specific sites, we first used the contrast [(Grasp Saccade Different Orientation – Grasp Saccade Same Orientation) – (Grasp Fixation Different Orientation – Grasp Fixation Same Orientation)], with a t-statistic of 2.2 ($p<0.048$), as implemented in BrainVoyager, to the *Action Execution* phase. This was designed to provide a preliminary dataset related to cortical

signals that are feature modulated in a saccade-specific manner. Again, cluster threshold correction was applied to these data. In the Results section, we refer to the regions that survive as 'clusters of activation' (i.e., Fig. 2.3A).

Next, to localize specific anatomic sites within these clusters, we decreased the p-values applied to the data until only peak voxels of activation remained within each of the clusters (Frost & Goebel, 2012; Lührs et al., 2016). These peak voxels were then used to determine the Talairach coordinates shown in Table 2.1. These coordinates were then fed into BrainVoyager Brain Tutor (BrainVoyager Brain Tutor 2.5, Brain Innovation) to provide an initial estimate of the anatomic name of each 'site', which were then confirmed against previous conventions in the literature (see Table 2.1). We then re-adjusted the thresholds to select active voxels within a maximum 1000 mm^3 cubic area surrounding the peak voxel(s). The selected areas were then used to test our specific predictions (see next subsection).

2.3.4.6 Hypothesis testing

Once the sites of interest were determined, they were used to test our specific predictions (Fig. 2.1C). Here, we used BrainVoyager to select a sub-cluster of activation around each peak voxel and extract the corresponding β-weights. We then plotted these β-weights in 'bar graph' format that allowed direct visual comparisons to our predictions. For each prediction, the p-value (0.05) was Bonferroni corrected for the number of t-tests conducted (i.e., relative to how many sites were tested).

First, we tested if the overall statistical results of the volumetric map contrast described above [(Grasp Saccade Different Orientation – Grasp Saccade Same

Orientation) – (Grasp Fixation Different Orientation – Grasp Fixation Same Orientation)] from the *Action Execution* phase held up for the specific anatomic coordinates selected as our sites of interest, using their β-weights for direct comparison to prediction 1 (Fig. 2.1, C.1). In other words, we confirmed if these specific sites of interest showed the same saccade-specific stimulus orientation modulations as the entire cluster. We then used their active voxels to extract β-weights from two additional *Preparatory Phase* contrasts (when saccades occurred) in order to test predictions 2 and 3: saccade-related activation (Grasp Saccade – Grasp Fixation) to test prediction 2 (Fig. 2.1 C.2), and task-specific saccade-sensitivity [(Grasp Saccade – Grasp Fixation) - (Localizer Saccade – Localizer Fixation)] to test prediction 3. In other words, we tested if these sites were modulated by saccades in our task, and if those modulations were task-specific. Lastly, for each test of our predictions, t- and p-values, as well as effect size (calculated Cohen's d, using G*Power (Faul et al., 2009)) are provided.

2.3.4.7 Functional connectivity: psychophysiological interaction analysis

Finally, in order to determine the network of cortical regions that interact to update saccade signals during the grasp preparation, we conducted psychophysiological (PPI) analysis (Friston et al., 1997; McLaren et al., 2012; O'Reilly et al., 2012) on data derived from right SMG (seed region) from the *Action Preparation* phase. We used three predictors: 1) physiological component (z-normalized time courses obtained from the seed regions for each participant for each included run), 2) psychological component (predictors of the model were convolved with a haemodynamic response function), and 3) psychophysiological interaction component (multiplication of z-normalized time

courses with task model in a volume-by-volume manner). For the task model produced for the psychological component, the Saccade predictors were set to a value of '+1', whereas the Fixation predictors were set to a value of '-1'; all other and baseline predictors were set to a value of '0'. Single design matrices (SDMs) were created for each participant for each included run. These were subsequently included in an RFX GLM (Friston et al., 1997) in order to determine functional connectivity between right SMG with each of these and associated sites.

2.4 Results

2.4.1 Task-related grasp and saccade modulations

Various studies have shown that humans can remember stimulus properties for several seconds, and use these to plan action until a 'go' signal is provided (Chen et al., 2014; Cappadocia et al., 2018). Our goal here was to examine the influence of a saccade on these signals, especially when it interrupts a change in the external world. To test this, we used a task (Fig. 2.1B) with three key phases: *Stimulus Presentation* (which begins with the original grasp stimulus orientation), *Action Preparation* (which included a saccade in 50% of trials, and ends with a Different or Same stimulus orientation that also acts as a 'go' signal), and *Action Execution* (where the actual reach and grasp occurs). By design, we expected brain activation to be dominated by: 1) visual signals during the *Stimulus Presentation* phase, 2) grasp preparation, saccade, and spatial updating signals during the *Action Preparation* phase, and 3) grasp motor signals and (in the case of Different stimulus orientations) grasp orientation updating during the *Action Execution* phase of this task. As noted in the Methods, our experiment was not designed to distinguish the

temporal events in this sequence (Cappadocia et al., 2017), but for each analysis we maximized the relevant signal by deriving data from the most appropriate task phase.

We begin with an overview of the activation derived from the *Action Preparation* phase (between 1st and 2nd stimulus; Fig. 2.1B), where one might expect to find events most closely related to the saccade-related updating of the original grasp stimulus. First, we derived the overall task-related activity from this phase, by contrasting Grasp Fixation trials against their baseline activity (Fig. 2.2A). This revealed activation in a parietofrontal network, including right SMG and several well-established reach/grasp regions: aIPS, lateral SPL (lSPL), precentral gyrus (PCG; corresponding to primary motor cortex), and dorsal / ventral precentral sulcus (PCSd/ PCSv; likely portions of these regions corresponding to dorsal and ventral premotor cortex, respectively) (Culham et al., 2003; Galletti et al., 2003; Castiello, 2005). In short, the initial stimulus (and likely subsequent events) evoked massive activity in the grasp network. To detect if these task-related signals were also modulated by saccades, we compared Grasp Saccade trials to Grasp Fixation trials derived from the *Action Preparation* phase (Fig. 2.2B*,* sky blue regions), and compared this to activity from our saccade localizer task (Fig. 2.2B, fuchsia regions). These two contrasts produced overlap in some cortical regions (e.g., right frontal cortex and SMG), but saccades also produced extensive superior parietal and occipital modulations in the grasp task, including aIPS and adjacent portions of SPL (Murata et al., 2000; Culham et al., 2003; Filimon et al., 2009; Monaco et al., 2010). However, these additional modulations could be related to various functions, such as updating reach *goals* (Batista et al., 1999; Khan et al., 2005), general aspects of eye-hand coordination (Vesia & Crawford, 2012), or expected sensory feedback (Culham & Valyear, 2006). To identify

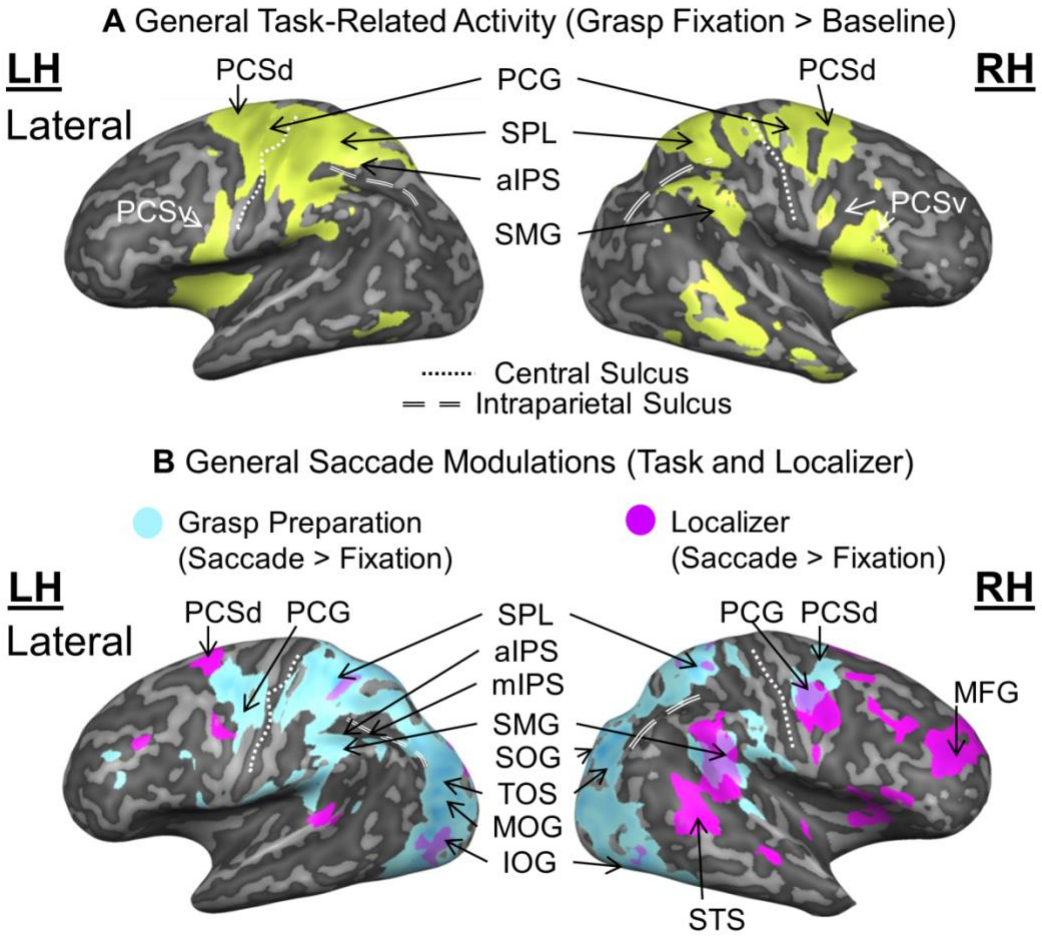


Figure 2.2. Overview of general grasp task-related activity (A) and saccade modulations (B), derived from the Action Preparation phase. **A.** Shown are inflated brain renderings of an example participant (left and right hemispheres from the lateral view, respectively). An activation map obtained using an RFX GLM (n=13) is shown for the contrast, Grasp Fixation > Baseline (chartreuse). *Abbreviations*: PCSd: dorsal precentral sulcus, PCSv: ventral precentral sulcus, PCG: precentral gyrus, aIPS: anterior intraparietal sulcus, SPL: superior parietal lobule, SMG: supramarginal gyrus. **B.** Activation maps for a Saccade > Fixate contrast obtained using an RFX GLM (n=13) on grasp experiment data (sky blue) and on a separate saccade localizer (fuchsia) were overlaid onto inflated brain renderings from an example participant (left and right hemispheres shown in the lateral views). *Abbreviations:* PCSd: dorsal precentral sulcus, PCSv: ventral precentral sulcus, PCG: precentral gyrus, SPL: superior parietal lobule, aIPS: anterior intraparietal sulcus, mIPS: middle intraparietal sulcus, SMG: supramarginal gyrus, SOG: superior occipital gyrus, TOS: transverse occipital sulcus, MOG: middle occipital gyrus, IOG: inferior occipital gyrus, STS: superior temporal sulcus.

specific *transsaccadic grasp updating* activity, we used our *a priori* predictions (Fig. 2.1 C.1, 2, 3), to localize and test specific sites of interest, as described in the Methods and shown in the following analyses.

2.4.2 Interactions between saccade and orientation sensitivity

If our participants incorporated original object orientation into short-term memory and used this for grasp planning (Monaco et al., 2011; Chen et al., 2014), their brains should 1) update this information across saccades (Melcher & Colby, 2008; Dunkley et al., 2016), and 2) update this again when they saw the final object orientation (Wolf & Schütz, 2015; Fornaciai et al., 2018). Thus, the cortical response to the second stimulus should be modulated by the orientation of the first stimulus (Monaco et al., 2011), and some of these modulations should depend on changes in eye position. Specifically, we predicted that these sites should show an increased response to orientation changes in the Grasp Saccade condition and little or no increase in the Grasp Fixation condition (Fig. 2.1 C.1). Alternatively, if participants ignored the initial stimulus and waited for the final stimulus to plan the grasp, these modulations should not occur.

Based on previous literature, we hypothesized that this might involve both right SMG (Dunkley et al., 2016) and the intra/superior parietal grasp network (Glover et al., 2005; Le et al., 2014). To test this, we had to localize specific sites of interest and apply our three predictions (Fig. 2.1C). As a first step, we identified cortical regions that were sensitive to changes in grasp orientation (Different versus Same Orientation) that follow saccades. Specifically, we used a voxelwise contrast applied to the trials wherein a saccade or fixation occurred (i.e., (Grasp Saccade Different Orientation - Grasp Saccade

Same Orientation) - (Grasp Fixation Different Orientation - Grasp Fixation Same Orientation)). Then (as described in the Methods) we applied a cluster thresholding algorithm to isolate specific clusters of activation. This yielded four separate clusters of activation, spanning left and right anterior PPC (Fig. 2.3A). This suggests that several regions within anterior PPC show saccade-specific sensitivity to grasp stimulus orientation changes, but does not yet provide the anatomic specificity required to test our hypotheses.

2.4.3 Site localization and anatomic coordinates

To localize specific anatomic sites for our subsequent analysis, we identified the peak voxels of PPC clusters described in the previous section, and then extracted their Talairach coordinates (Table 2.1). According to BrainVoyager Brain Tutor (BrainVoyager Brain Tutor 2.5, Brain Innovation), these peak voxels correspond to right SMG, left aIPS, and left/right SPL, which we further identified as left mSPL (a medial portion of left superior parietal lobule), and right lSPL (a lateral portion of right superior parietal lobule, slightly postero-lateral to right aIPS). This was confirmed against previous literature (Tunik et al., 2008; Singhal et al., 2013; Dunkley et al., 2016). These sites have been indicated as black/white dots superimposed on the voxel clusters in Figure 2.3A, and will henceforth be referred to as ‘putative transsaccadic grasp updating sites’. Note that in the following two hypothesis sections, it is only the active voxels immediately surrounding these sites (within a 1000 mm^3 cubic area) that were analyzed (see Methods).

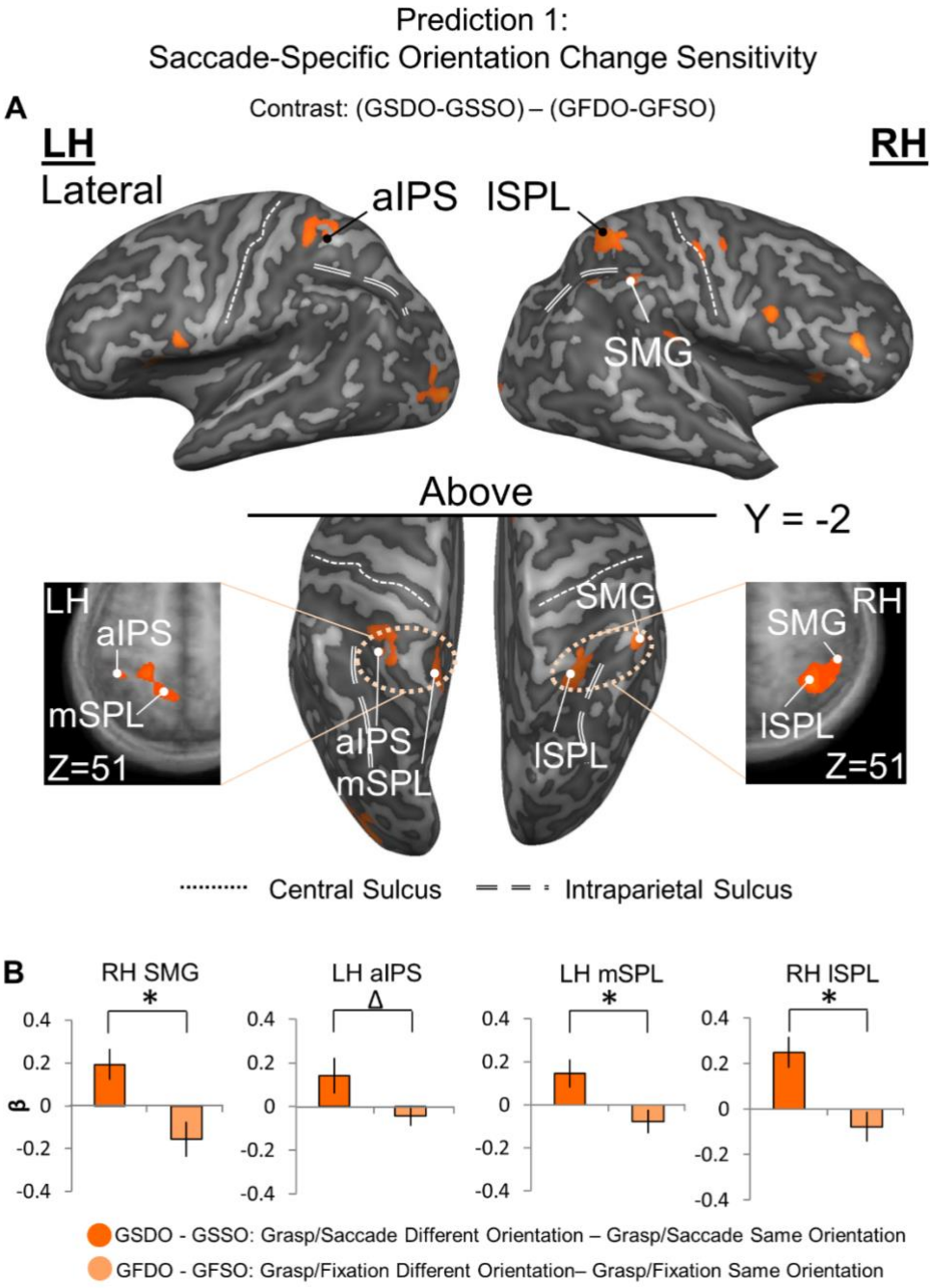


Figure 2.3. Localizing (A) and testing (B) sites for prediction 1: saccade-specific orientation change sensitivity. **A.** Voxelwise statistical map overlaid onto inflated brain rendering of an example participant obtained using an RFX GLM (n=13) for Different > Same in the Grasp Saccade (GS) condition as compared with the Grasp Fixate (GF) condition, derived from the *Action Execution* phase. Top panels show the lateral views of the inflated brain rendering on which can be seen activation in right lateral superior lateral lobule (lSPL) and supramarginal gyrus (SMG; black/white dots correspond to peak voxels of activation). In the middle, bottom panels, the top view of the left and right hemispheres

can be seen, which display activation also in the left anterior intraparietal sulcus (aIPS) and medial SPL (mSPL). The left and rightmost panels contain transverse slices through the average brain of all the participants onto which the activation in these four regions can be viewed in more detail. These results (that the final motor plan was modulated by the initial stimulus orientation) contradict the notion that participants waited for the second stimulus orientation to begin action planning. Instead, they show that an orientation-specific action plan was formed immediately, and then updated when the second stimulus was presented. **B.** Bar graphs of β-weights plotted for the difference between the Grasp Saccade Different and Same Orientation conditions (dark orange) versus the difference between the Grasp Fixation Different and Same conditions (light orange). The small, variable Grasp Fixation results are analogous to the results of sensory adaptation studies, where both repetition suppression and enhancement effects have been observed. Data were extracted from the active voxels in the transsaccadic sites shown in A. To quantitatively test prediction 1, we performed *a priori*-motivated repeated-measures t-tests; given that there are four areas and therefore, four t-tests to be conducted, the significance level p-value (0.05) was Bonferroni corrected (0.05/4 = 0.0125). Statistical tests were carried out on β-weights extracted from active voxels of these sites in order to test Prediction 1. Values are mean ± SEM analyzed by repeated measures t-tests. (Please see Results for specific statistical values.) * indicates a statistically significant difference between the GS and GF β-weights (i.e., that the p-value obtained is less than the Bonferroni corrected p=0.0125). ∆ indicates an uncorrected significant difference between the GS and GF β-weights (i.e., that the p-value obtained is less than the original significance level p=0.05, but is not less than the Bonferroni corrected p=0.0125).

Table 2.1 Putative names, Talaraich coordinates, and active voxels within 1000 mm^3 for each site of interest extracted from the Action Execution phase.

Site	**Talairach coordinates**						**Active Voxels**	**References**
Name	x	y	z	Std x	Std y	Std z	*n* voxels	
LH aIPS	-38	-41	53	2.3	1.6	1.9	217	Tunik et al., 2008; Singhal et al., 2013
LH mSPL	-13	-51	54	2.4	2.3	2.7	642	Tunik et al., 2008; Filimon et al., 2009
RH SMG	49	-40	48	2.0	2.2	2.1	361	Dunkley et al., 2016
RH lSPL	35	-49	53	2.8	2.8	2.7	875	Tunik et al., 2008; Filimon et al., 2009

2.4.4 Prediction 1: saccade-specific orientation sensitivity

Prediction 1 (Fig. 2.1 C.1) was that our putative transsaccadic grasp updating sites should be more sensitive to changes in grasp stimulus orientation that occur across a saccade, as opposed to fixation. [Note that we have already shown this for the voxel clusters used to localize these sites (Fig. 2.3A), so here we are simply confirming this for data derived from these specific anatomic coordinates (right SMG, left aIPS, left mSPL, and right lSPL), and converting the data into a bar-graph format for direct comparison with our prediction (Fig. 2.1 C.1).] To do this, we extracted β-weights from the active voxels including and surrounding the peak voxel(s) of these sites, again from the *Action Execution* phase. Figure 2.3B shows the orientation change sensitivity of these variables (Different – Same) for each of our four sites, contrasting the Saccade condition against the Fixation condition.

As expected, each followed the predicted pattern: higher orientation change sensitivity following saccades versus fixation. For statistical analysis of these data, we used an α value of 0.05; we tested prediction 1 for our four transsaccadic grasp updater sites, so resulting p-values were adjusted for multiple comparisons and assessed against a Bonferroni p-value of 0.0125 (0.05/4) for statistical significance. All four sites showed significant saccade-specific responses to changes in stimulus orientation ($t(12)_{SMG}= 3.30$, $p_{SMG}=0.0032$, effect size= 0.92; $t(12)_{aIPS}= 2.34$, $p_{aIPS}=0.019$, effect size= 0.65; $t(12)_{lSPL}= 5.49$, $p_{lSPL}=0.000069$, effect size= 1.52; $t(12)_{mSPL}= 3.04$, $p_{mSPL}=0.0051$, effect size= 0.84). These p-values remained significant after correction for multiple comparisons, with the exception of one site: aIPS. However, the original cluster associated with aIPS (Fig. 2.3A)

did survive cluster threshold correction, and this was a key component of our hypothesis, so we retained this site for further analysis.

2.4.5 Predictions 2 and 3: site-specific saccade modulations and task specificity

To examine the influence of saccades on our putative transsaccadic grasp updating sites, we performed additional contrasts. Figure 2.4 shows 1) the overall activity over baseline during the Fixation condition (Fig. 2.4A), and 2) saccade modulations in both our task and saccade localizer (Fig. 2.4B), derived as in Figure 2.2B. The location of our putative transsaccadic grasp updating sites are indicated by the four black dots superimposed on the contrasts. All four sites (right SMG, left aIPS, and bilateral SPL) fell within these task-related regions of activation, as well as within or bordering on, regions of saccade modulation in the localizer task (Fig. 2.4B). We then used the sites of interest defined in Figure 2.3A to extract β-weights from the latter data, to directly test prediction 2 (greater activation during saccades compared to fixation) and prediction 3 (greater modulation during the grasp task than during saccades alone, i.e. task-specific saccade modulations).

Figure 2.4C shows the application of prediction 2 on β-weights extracted from grasp-related activity in Figure 2.4B. All four sites showed significantly higher activity in the presence of saccades (t-test statistics were assessed against a Bonferroni corrected p-value of 0.0125 (0.05/4=0.0125) for multiple comparisons for the four transsaccadic sites separately for each of the predictions, 2 and 3), although SMG did not survive correction for multiple comparisons ($t(12)_{SMG}$= 2.08, p_{SMG}=0.030, effect size= 0.58; $t(12)_{aIPS}$= 3.85, p_{aIPS}=0.0011, effect size= 1.07; $t(12)_{lSPL}$= 4.53, p_{lSPL}=0.00034, effect size=

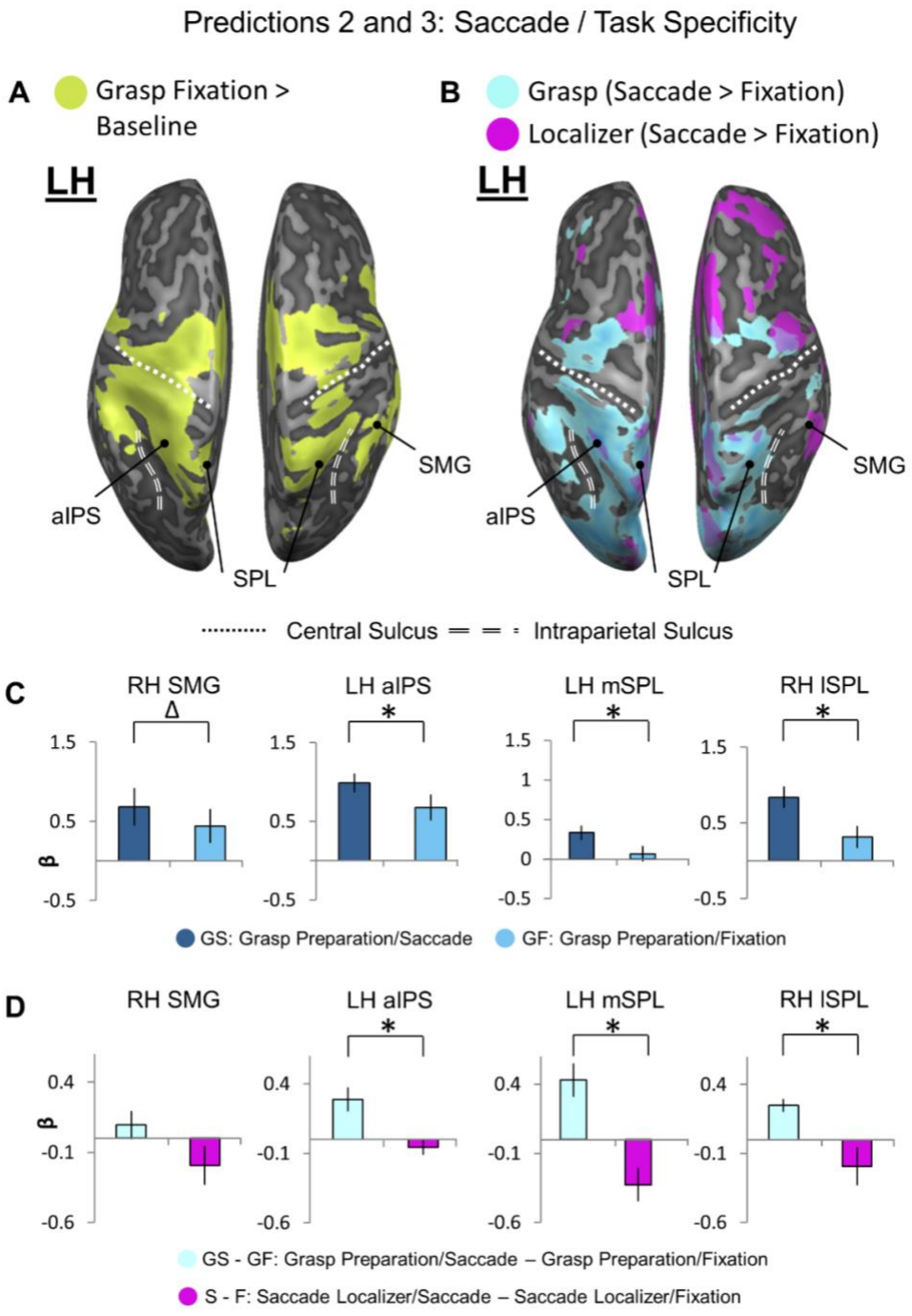


Figure 2.4. Location of putative transsaccadic reach updating sites (from Fig. 3) superimposed on general grasp regions (A) and saccade modulations (B) derived from the *Action Preparation* phase, followed by tests for predictions 2 (C) and 3 (D). **A.** Shown is an inflated brain rendering of an example participant (left and right hemispheres viewed

from above, respectively). An activation map obtained using an RFX GLM (n=13) is shown for the contrast, Grasp Fixation > Baseline (chartreuse). The four putative transsaccadic grasp updating sites (depicted as black dots) from Figure 3 are superimposed on this activation. aIPS: anterior intraparietal sulcus, mSPL: medial superior parietal lobule, lSPL: lateral superior parietal lobule, SMG: supramarginal gyrus. **B.** Activation maps for a Saccade > Fixate contrast obtained using an RFX GLM (n=13) on grasp experiment data (sky blue) and on a separate saccade localizer (fuchsia) were overlaid onto an inflated brain rendering from an example participant (left and right hemispheres shown from a bird's eye view). These overlaid activation maps allow for comparison of which cortical sites respond to saccade signals in a grasp task-specific manner. *Abbreviations:* aIPS: anterior intraparietal sulcus, mSPL: medial superior parietal lobule, lSPL: lateral superior parietal lobule, SMG: supramarginal gyrus. **C.** Bar graphs of β-weights plotted for Grasp Saccade (GS) conditions (dark blue) versus Grasp Fixation (GF) conditions (light blue) from all 13 participants. Data were extracted from active voxels from the transsaccadic sites, the peak voxels of which are represented by the black dots above in A and B in order to test prediction 2. To quantitatively test prediction 2, we performed *a priori*-motivated repeated-measures t-tests; given that there are four areas and therefore, four t-tests to be conducted, the significance level p-value (0.05) was Bonferroni corrected (0.05/4 = 0.0125). (Please see Results for specific statistical values.) Values are mean ± SEM analyzed by repeated measures t-tests. **D.** Bar graphs of β-weights plotted for Grasp Saccade conditions (pale blue) versus Grasp Fixation conditions (magenta). Data were extracted from the transsaccadic sites shown in Fig. 2A and B, which were compared for only the ten participants whose data were analyzed for the saccade localizer. Statistical tests were carried out on β-weights extracted from the active voxels of these areas in order to test prediction 3. Values are mean ± SEM analyzed by dependent t-test. To quantitatively test prediction 3, we performed *a priori*-motivated repeated-measures t-tests; given that there are four areas and therefore, four t-tests to be conducted, the significance level p-value (0.05) was Bonferroni corrected (0.05/4 = 0.0125). (Please see Results for specific statistical values.) * indicates a statistically significant difference between the GS and GF β-weights (i.e., that the p-value obtained is less than the Bonferroni corrected p=0.0125). ∆ indicates an uncorrected significant difference between the GS and GF β-weights (i.e., that the p-value obtained is less than the original significance level p=0.05, but is not less than the Bonferroni corrected p=0.0125).

1.26; $t(12)_{mSPL}$= 7.27, p_{mSPL}=0.0000050, effect size= 2.02).To test the task specificity of these modulations, we applied prediction 3, i.e., we tested if our putative updating sites showed saccade modulations during the grasp task, but not during saccades alone (Fig. 2.4D). In this case, only aIPS and bilateral SPL showed significant task specificity ($t(12)_{SMG}$= 1.34, p_{SMG}=0.11, effect size= 0.43; $t(12)_{aIPS}$= 3.58, p_{aIPS}=0.0030, effect size= 1.14; $t(12)_{lSPL}$= 3.44, p_{lSPL}=0.0037, effect size= 1.09; $t(12)_{mSPL}$= 3.12, p_{mSPL}=0.0062, effect size= 0.99). This suggests a progression of grasp task-specificity from SMG to the more superior motor regions.

2.4.6 Functional connectivity of SMG with saccade and grasp sites

Our analyses so far have confirmed our perceptual updating result for SMG (Dunkley et al., 2016), and extended this function to sensorimotor updating in aIPS and SPL for grasp; but, do these sites participate in a coherent functional network for grasp updating? Based on our previous finding that right SMG is active for perceptual orientation updating (Dunkley et al., 2016), and its re-appearance in the current grasp task, we hypothesized that SMG is a key hub for updating visual orientation across saccades, and that it would communicate with both saccade regions (for signal input) and grasp regions (for signal output) during our grasp task. To do this, we identified a seed site within the right SMG using our independent saccade localizer data, and performed a psychophysiological interaction (PPI) analysis to examine which sites showed increased functional connectivity for Saccade as compared with Fixation trials with SMG derived from data aligned with the *Action Preparation* phase (Fig. 2.5A-C). This resulted in three sites that survived cluster threshold correction: right PCSd (likely a portion corresponding to FEF),

left medial, superior frontal gyrus (likely the supplementary eye field, SEF), and SPL (including a cluster that overlaps with aIPS).

2.5 Discussion

In this study, we set out to identify the cortical regions associated with updating grasp plans during changes in gaze direction and/or object orientation. We reasoned that, in order to perform this function, the brain would have to integrate saccade signals in regions sensitive to visual orientation and/or grasp orientation updating. To identify these sites, we applied three specific criteria: specific transsaccadic sensitivity to orientation changes, sensitivity to intervening saccades versus fixation, and task specificity in these saccade modulations, at least in the more superior parietal grasp motor sites. We found four sites that met these criteria: right SMG, a site previously implicated in transsaccadic orientation perception (Dunkley et al., 2016), and three more

dorsal sites that are associated with grasp correction (Prime, Vesia, & Crawford, 2008; Vesia et al., 2010). Finally, with the use of task-related functional connectivity analysis with seed site SMG, we identified a putative network for saccades that includes parietal and prefrontal regions.

2.5.1 Transsaccadic updating of object orientation for grasp

Here, we hypothesized that SMG (Dunkley et al., 2016) would contribute to feature updating for grasp execution, whereas some part of other regions involved planning/updating grasp orientation (Murata et al., 2000; Monaco et al., 2014, 2015) would also be involved in the transsaccadic updating of orientation for grasp preparation. To test this, we compared orientation change specificity for saccades versus fixation during *Action Execution*, and found four sites (right SMG,

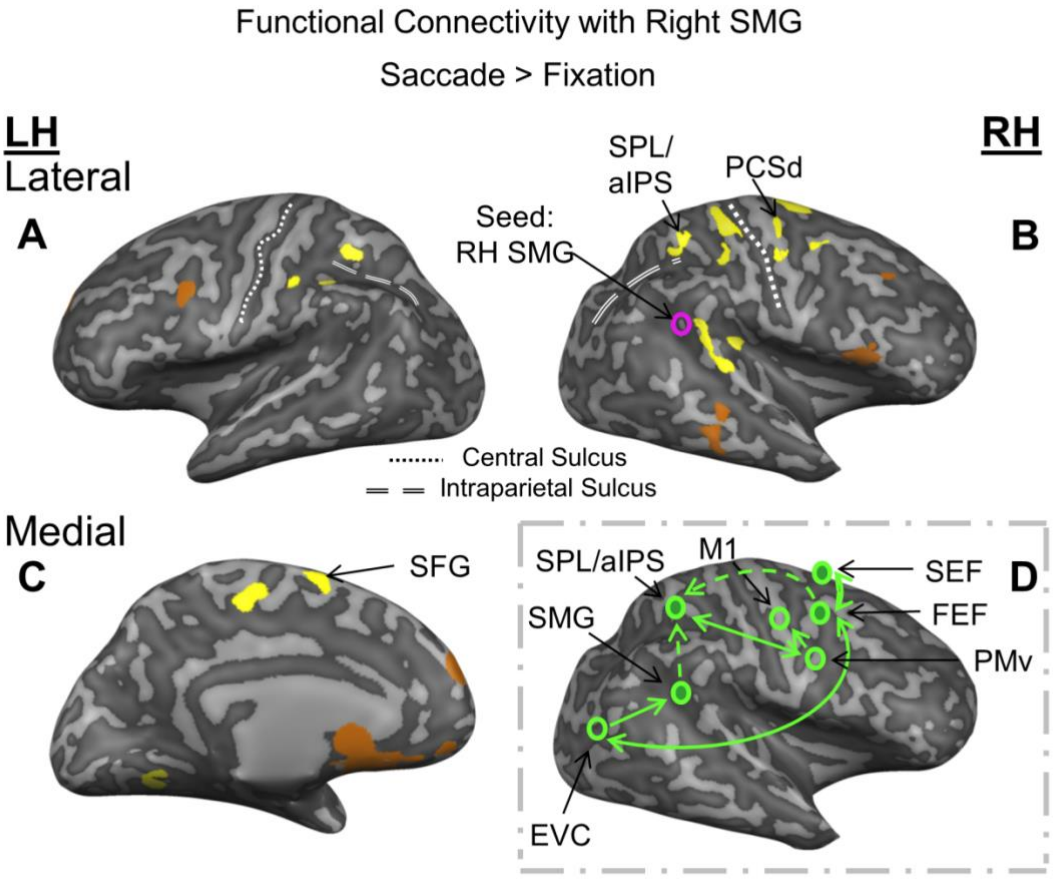


Figure 2.5. Functional connectivity network involved in transsaccadic updating of grasp orientation. **A-C.** Using a Saccade > Fixation contrast (from the *Action Preparation* phase) and the right supramarginal gyrus (SMG) as a seed region obtained from the separate saccade localizer, psychophysiological interaction is shown in the activation maps (yellow for positive correlation; copper for negative correlation) overlaid onto the inflated brain renderings of an example participant. Right frontal eye field (FEF), SPL (that extends into the anterior intraparietal sulcus, aIPS) and left supplementary eye field (SEF) show significant, cluster-corrected positive correlation with right SMG. Only sites that passed a $p<0.05$ and cluster threshold correction are labeled. **D.** A potential network for the communication between right SMG and other saccade and grasp regions.

left aIPS, and bilateral SPL) that fit this criterion and passed our standard statistical criteria. (Note that our right lSPL site was similar to left aIPS, but positioned more laterally and posterior.) We further found that all of these sites were modulated by saccades, although the motor task specificity of these modulations was clearer in aIPS and SPL. Finally, the laterality of these responses was consistent with our hypothesis, i.e., right SMG being consistent with the general role of right parietal cortex in spatial awareness (Perry & Zeki, 2000), whereas left aIPS was opposite to the motor effector uses (the right hand). This supports a general-purpose role for right SMG in the transsaccadic updating of object orientation, and adds a more unique role for aIPS and SPL in updating grasp orientation.

SMG is a region that has largely been implicated in perception tasks, such as those requiring spatial processing of orientation (Kheradmand et al., 2015) and visual search (Eimer et al., 2011), or those requiring crossmodal spatial attention (Macaluso et al., 2000). In contrast, SPL possesses both saccade and grasp-preshaping signals (Filimon et al., 2009; Gallivan et al., 2011), making this an ideal site to update grasp plans. Our anterior SPL grasp updating sites excluded more posterior grasp areas like SPOC (Gallivan et al., 2011; Rossit et al., 2013), consistent with the idea that the latter is concerned with setting initial reach goals (Vesia et al., 2010; Vesia & Crawford, 2012), whereas the former anterior areas are involved in updating those goals (Glover et al., 2005; Le et al., 2014; Janssen & Scherberger, 2015). These updated signals might then be relayed to PMd (Tanné-Gariépy et al., 2002; Davare, 2006), which possesses both reach-only and intermingled saccade-reach populations of neurons (Filimon et al., 2009). Finally, aIPS is sensitive to object orientation information for grasp (Murata et al., 2000;

Brouwer et al., 2009; Glover et al., 2012; Vesia et al., 2017). aIPS appeared twice in our analysis: first in Figure 3, near the coordinates provided in some previous studies (Medendorp et al., 2003; Gallivan et al., 2011; Monaco et al., 2011) and second, clustered with SPL in our network analysis (Fig. 2.5). It is thought that populations of neurons in aIPS may process object features such as its orientation in order to ultimately shape and orient the hand to match the object's shape and orientation (Monaco et al., 2014). Information related to grasping is then proposed to travel to PMv to engage specific reach/grasp-related neuronal populations to generate motor commands (Davare, 2006; Davare et al., 2009; Filimon et al., 2009). Thus, our result appears to be consistent with the known functions of these regions, and extends our understanding of how these functions might be linked to update grasp signals in the presence of saccades.

2.5.2 A putative network for transsaccadic updating of grasp plans

An important goal for this study was to understand how distributed cortical regions might work as a network to update grasp plans during saccades. Based on the computational requirements of this function, we hypothesized that such a network should involve: 1) regions specific to transsaccadic updating of orientation features, 2) saccade regions for oculomotor input, and 3) and grasp updating regions for motor output. Given our previous (Dunkley et al., 2016) and current results, we hypothesized that right SMG would play the first role (i.e., here, it would update object features across saccades during the *Action Preparation* phase so that these could be spatially integrated with new visual information for *Action Execution*), and chose this as the seed site for our functional connectivity analysis. As described in the Introduction, we expected prefrontal saccade regions to play

the second role, and parietal grasp regions to provide the final role (based on our current results, aIPS/SPL). Indeed, this analysis revealed a functional network for saccades versus fixation involving right SMG, right SPL, right aIPS, right PCSd, and the left superior frontal gyrus. Taken together with the overlapping sites that fit the previous three criteria, this suggests a saccade-dependent network with the specific properties needed for updating grasp orientation.

PPI analysis does not provide directionality, but based on the functional requirements of the task and known physiology of these regions, we conceptualized this network as shown in Figure 2.5D. PCSd likely corresponds to the right FEF (Luna et al., 1998; Krauzlis, 2005). The FEF is a key component of the cortical saccade generator (Krauzlis, 2005), and is known to provide feedback to earlier visual areas (Moore & Armstrong, 2003; Hamker, 2010). The superior frontal gyrus likely corresponds to the supplementary eye field (Grosbras et al., 1999; Krauzlis, 2005), which has reciprocal connections with FEF. Thus, FEF/SEF could be the source of saccade signals for SMG and the entire network. As discussed above, aIPS (Gallivan et al., 2011) and SPL are implicated in grasp planning / corrections, show saccade signals (Filimon et al., 2009; Filimon, 2010), and of course were already implicated in transsaccadic grasp updating in our other analyses. Thus, this putative network appears to possess all of the signals and characteristics that one would expect to find in a transsaccadic updating circuit during grasp preparation.

Eye-hand coordination is relatively understood in terms of the transport component of reach, but little is known about the integration of saccade and visual signals for updating grasp configuration across eye movements. We set out to identify a putative human grasp

updater and found a remarkably consistent cluster of regions including SMG and aIPS/SPL, (likely) receiving oculomotor inputs from prefrontal eye fields. This network provides the necessary neural machinery to integrate object features and saccade signals, and thus ensure grasp plans remain updated and coordinated with gaze-centered reach transport plans (Batista et al., 1999; Khan et al., 2005). These new findings have several general implications: First, this circuit might explain some of the various symptoms of constructional apraxia resulting from damage to the posterior parietal cortex (Heilman et al., 1986; Sirigu et al., 1996). Constructional apraxia is a disorder affecting complex manual tasks that involve the coding and updating of multiple objects (Smith & Gilchrist, 2005; Russell et al., 2010). Second, the role of the inferior parietal cortex in both transsaccadic perception (Dunkley et al., 2016) and grasp updating supports the notion that inferior parietal cortex (a very late phylogenetic development) has high-level visuospatial functions for both ventral and dorsal stream vision (Goodale & Milner, 1992). Finally, the various roles of specific parietal modules in spatial updating (Klier & Angelaki, 2008), visual feedback corrections (Medendorp et al., 2003), and (here) a combination of the two for action updating, support a general role for parietal cortex for detecting, differentiating, and compensating for internally and externally induced spatial perturbations.

CHAPTER 3

OCCIPITAL CORTEX IS MODULATED BY TRANSSACCADIC CHANGES IN SPATIAL FREQUENCY: AN FMRI STUDY

Baltaretu, B.R., Dunkley, B.T., Stevens, W.D., & Crawford, J.D. (in press). Occipital cortex is modulated by transsaccadic changes in spatial frequency: An fMRI study. *Scientific Reports*.

3.1 Abstract

Previous neuroimaging studies have shown that inferior parietal and ventral occipital cortex are involved in the transsaccadic processing of visual object orientation. Here, we investigated whether the same areas are also involved in transsaccadic processing of a different feature, namely, spatial frequency. We employed a functional magnetic resonance imaging paradigm where participants briefly viewed a grating stimulus with a specific spatial frequency that later reappeared with the same or different frequency, after a saccade or continuous fixation. First, using a whole-brain Saccade > Fixation contrast, we localized two frontal (left precentral sulcus and right medial superior frontal gyrus), four parietal (bilateral superior parietal lobule and precuneus), and four occipital (bilateral cuneus and lingual gyri) regions. Whereas the frontoparietal sites showed task specificity, the occipital sites were also modulated in a saccade control task. Only occipital cortex showed transsaccadic feature modulations, with significant repetition *enhancement* in right cuneus. These observations (parietal task specificity, occipital enhancement, right lateralization) are consistent with previous transsaccadic studies. However, the specific regions differed (ventrolateral for orientation, dorsomedial for spatial frequency). Overall, this study supports a general role for occipital and parietal cortex in transsaccadic vision, with a specific role for cuneus in spatial frequency processing.

3.2 Introduction

The visual system tracks both low-level (e.g., orientation, spatial frequency) and high-level (e.g., objects, faces) components of our visual surroundings through space and time (Suzuki & Cavanagh, 1995), despite the interruption of several saccades (rapid eye

movements) per second (Irwin, 1991; Melcher, 2005). To do this, visual features must be encoded, retained, updated, and integrated across saccades (Rayner, 1998; Melcher, 2009), through a process called transsaccadic perception (Irwin, 1991; Rayner et al., 1980; Irwin et al., 1983; Henderson et al., 1987). As argued elsewhere (Prime, Niemeier, & Crawford, 2006; Prime, Vesia, & Crawford, 2011; Melcher & Colby, 2008), transsaccadic perception likely incorporates mechanisms for both visual working memory (Courtney et al., 1996; Luck & Vogel, 1997) and spatial updating (Klier & Angelaki, 2008; Funahashi, 2013). However, the specific *neural* mechanisms for human transsaccadic feature perception are not well understood.

When saccades occur, both object locations and their associated features shift relative to eye position. It is well established that human posterior parietal cortex (PPC; specifically, the mid-posterior parietal sulcus) is involved in transsaccadic spatial updating, i.e., the updating of object *location* relative to each new eye position (Medendorp et al., 2003; Merriam et al., 2003; Khan et al., 2005; Morris et al., 2007). Recently, we found that inferior PPC (specifically, right supramarginal gyrus; SMG) is also modulated by transsaccadic comparisons of object orientation (Dunkley et al., 2016). Specifically, when a circular grating was presented, followed by a saccade and then presentation of a grating with a different orientation, SMG showed *repetition suppression* (compared to presentation of the same stimulus in the same orientation). Conversely, a ventrolateral occipital area (‘putative V4’) showed *repetition enhancement*. Both observations suggest underlying cortical activity modulations specific to transsaccadic interactions of object orientation.

Consistent with these findings, transcranial magnetic stimulation (TMS) of PPC (just posterior to SMG) disrupted transsaccadic memory of multiple object orientations (Prime, Vesia, & Crawford, 2008, 2010), and TMS over occipital cortex disrupted gaze-centered updating of object orientation (Malik et al., 2015). SMG activity was also modulated during transsaccadic updating of object orientation for grasp, along with other parietal sensorimotor areas. Whereas SMG was always saccade-modulated, the sensorimotor grasp areas were only saccade-modulated when a grasp was planned (Baltaretu et al., 2020). Functional connectivity analysis suggested that these areas also communicated with the frontal/supplementary eye fields, possibly providing the motor signal that drives the updating (Prime, Vesia, & Crawford, 2010; Baltaretu et al., 2020). These findings implicate both occipital cortex and PPC in the transsaccadic updating of *both* object location and orientation.

Importantly, it is not known if these neural mechanisms generalize to other stimulus features. One might expect PPC to be involved in other aspects of transsaccadic feature memory and integration, because of its general role in spatial updating (Medendorp et al., 2003; Bellebaum et al., 2005; Merriam & Colby, 2005); however, the specific mechanisms might differ. SMG seems to play a specialized role for high-level object orientation in various spatial tasks (Taylor et al., 2011; Kheradmand et al., 2013). Likewise, extrastriate cortical areas show specialization for processing different features (Van Essen, 1995; Nakamura & Colby, 2002). Thus, while SMG and ‘putative V4’ might play a general role in transsaccadic updating of all visual features, it is equally possible that the brain engages different cortical networks for transsaccadic processing of different features, as it does during prolonged visual fixations (Faillenot et al., 2001; Baumann et al., 2008).

To address this question, we used an event-related fMRI paradigm, similar to Dunkley et al. (2016), where participants briefly viewed two successive 2D spatial frequency grating stimuli, either while continually fixating the eyes, or interleaved by a saccade to the opposite side, and then judged whether the two gratings were the same or different. But here, we modulated spatial frequency, rather than orientation (Fig. 3.1a,b). Using a hypothesis-driven approach (Baltaretu et al., 2020), we first performed a whole-brain analysis to identify cortical regions that were modulated by saccades during the task (Fig. 3.2, prediction 1). As in our previous experiment (Baltaretu et al., 2020), we also compared these modulations to activation in a simple saccade task, to see if they were task-specific. We, then, tested if sites of peak activation within these regions showed feature-specific modulations (Fig. 3.2, prediction 2). Based on our previous experiments (Dunkley et al., 2016; Baltaretu et al., 2020), we expected repetition *suppression* in PPC (prediction 2a) and *enhancement* in occipital cortex (prediction 2b), whereas frontal cortex was not expected to show (directional) feature-related modulations. As a secondary issue, we also tested if these areas showed task specificity (or not) compared to our previous study (Baltaretu et al., 2020). Our results support the general role of occipital and parietal cortex in transsaccadic visual processing (Dunkley et al., 2016), with similar parietal task specificity (Baltaretu et al., 2020), but suggest that different, more dorsomedial areas are involved for processing spatial frequency.

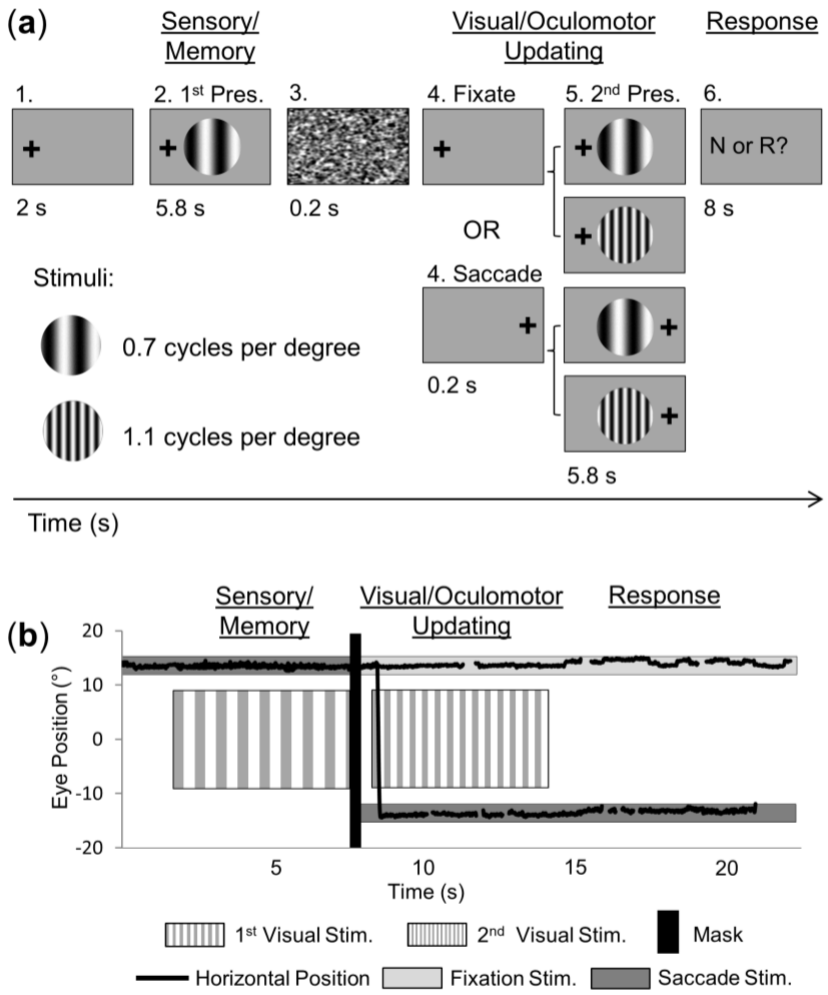


Figure 3.1. Experimental paradigm and eye movement traces. **a.** An example trial is shown (0.7 cycles per degree, cpd, left fixation) with the four possible conditions: Fixation Same, Fixation Different, Saccade Same, and Saccade Different. Each 22 s trial had three major phases: 1) *Sensory/Memory,* for the first presentation of the stimulus at one of the two possible spatial frequencies (0.7 or 1.1 cpd) while gaze could be to the left or right; 2) *Visual/Oculomotor Updating*, for the second presentation of the stimulus at the same spatial frequency (e.g., 0.7 cpd for first and second stimulus presentations; *Same* condition) or different (e.g., 0.7 cpd for first presentation and 1.1 cpd for second stimulus presentation, or vice versa; *Different* condition) while participants maintained fixation on the same cross (*Fixate* condition) or made a directed saccade (*Saccade* condition); and 3) *Response*, for the button press response period where an indication of whether the spatial frequency across the two stimulus presentations was the same ('R') or different ('N'). **b.** An example eye position trace (º) for an example fixation and saccade trial. In this figure, each of the two trials started with initial fixation on the right (13.5º from centre), then diverged after the initial presentation of the stimulus (1st visual stimulus) and mask (black vertical bar), whereby gaze remained fixed for the fixation trial or moved to the other fixation cross position (-13.5º from centre) for the saccade trial, where it remained after the second stimulus presentation (2nd visual stimulus), and button press period.

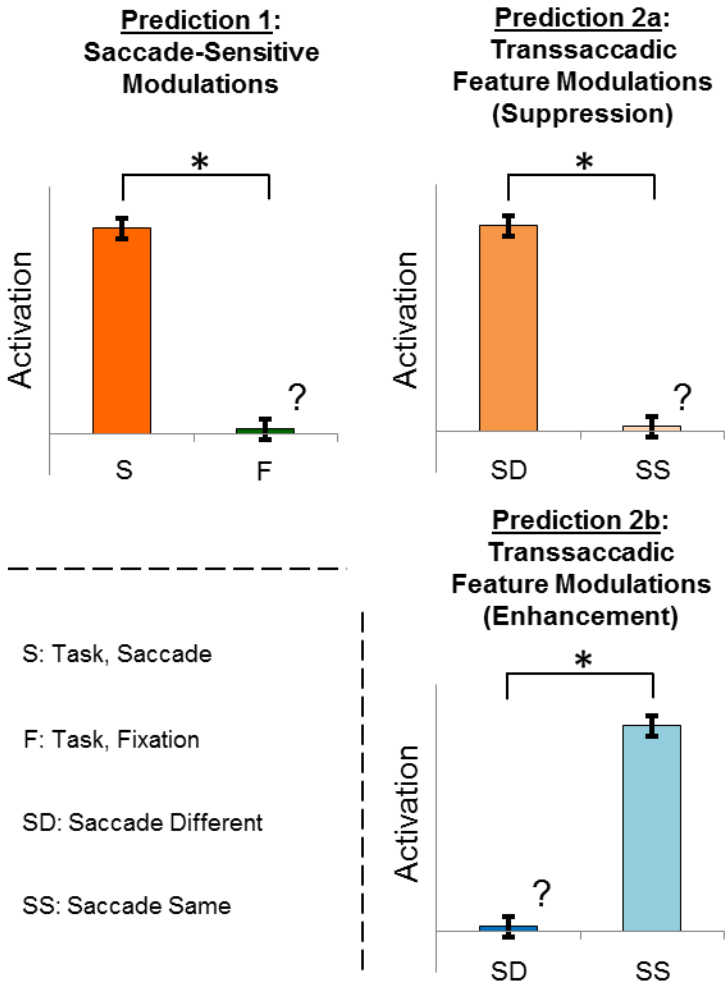


Figure 3.2. Predictions used to test saccade- and feature-specificity. Prediction 1: The saccade-related effects in this region should be larger in the *Saccade* condition than the *Fixation* condition, within the experimental task (i.e., (Saccade – Fixation); S, F, respectively). Prediction 2a: Parietal areas should show transsaccadic feature repetition *suppression* (Dunkley et al., 2016; Baltaretu et al., 2020)*, i.e.,* a larger response for a change in spatial frequency than a repetition, following an intervening saccade (i.e., (Saccade/Different > Saccade/Same); SD, SS, respectively). Prediction 2b: Alternatively, occipital areas have been known to show transsaccadic repetition *enhancement* (Dunkley et al., 2016), whereby there should be a larger response for a repetition in spatial frequency than for changes, following an intervening saccade (i.e., (Saccade/Same > Saccade/Different)) (Microsoft PowerPoint v16.44; www.microsoft.com).

3.3 Results

Overall, our task (Fig. 3.1) produced widespread activation in brain areas related to vision, visual memory, and eye movements during the initial *Sensory/Memory Phase* (Fig. 3.S1; see Appendix) and *Visual/Oculomotor Updating Phase* (Fig. 3.S2; see Appendix). To test our hypotheses, we focused on the *Visual/Oculomotor Updating* phase of our task, i.e. the period after the first stimulus presentation, starting at the time when a saccade occurred and a second stimulus (either Same or Different) appeared (Fig. 3.1a). As in our recent study (Baltaretu et al., 2020), we used an analysis pipeline that began with a whole-brain voxelwise contrast to identify regions of interest, followed by further hypotheses testing on peak sites-of-interest. In this dataset, saccade modulations were more robust than feature modulations, so we used a *Saccade* vs. *Fixation* contrast (Fig. 3.3) to identify regions that qualify for prediction 1 (Fig. 2). This was then used to localize specific sites-of-interest to test prediction 2 (Fig. 3.2), i.e., feature interactions (Figs. 3.4, 3.5, 3.6). Additionally, we used a simple saccade motor task to test if these areas are automatically driven by saccade signals (as observed previously in SMG), or are only activated by saccades in a task-specific fashion (Baltaretu et al., 2020). An *a priori* power analysis suggested that 14 participants were required for the voxelwise contrasts used in this pipeline (see Methods: Power analysis). To obtain this level, we continued testing participants (21 in total), until 15 of these passed our behavioural inclusion criteria for fMRI analysis (see Methods: Behavioural data and exclusion criteria).

3.3.1 Prediction 1: saccade modulations

3.3.1.1 Whole-brain analysis. The first step in our analysis was a whole-brain voxelwise

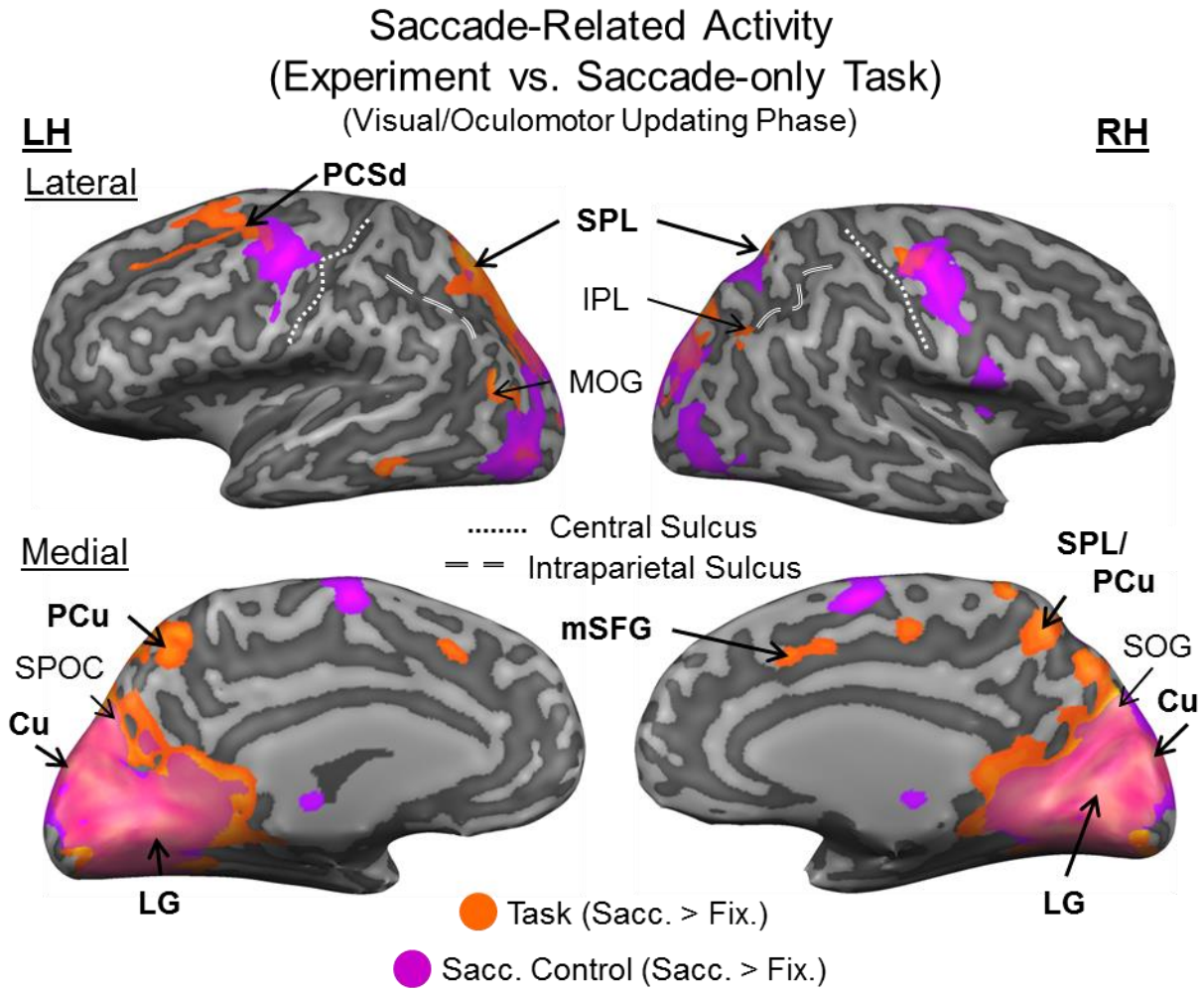


Figure 3.3. Saccade-related effects during experimental task vs. independent saccade task. Voxelwise statistical maps from an RFX GLM for Saccade > Fixation in the experimental task (n=15; orange; FDR ($q < 0.05$) and cluster correction) versus the control task (n=12; fuchsia; FDR ($q < 0.05$) and cluster correction) are overlaid onto inflated cortical surface renderings of example participant (left hemisphere on the left, right hemisphere on the right; upper panels showing the lateral views, and lower panels showing medial views) (BrainVoyager QX v2.8; www.brainvoyager.com). There is substantial overlap in activity in medial occipital regions for task and saccade control (for example, cuneus, Cu, lingual gyrus, LG, and superior occipital gyrus, SOG). However, experimental task-specific saccade modulations can be observed in particular parietal (precuneus, PCu, and superior parietal lobule, SPL) and frontal saccade regions (medial superior frontal gyrus, mSFG – likely pre-supplementary eye field; dorsal precentral sulcus, PCSd – likely frontal eye field). (Bold regions are those that are subsequently tested against prediction 2.)

contrast (*Saccade* > *Fixation*; Figs. 3.2, 3.3) on fMRI data derived from the *Visual/Oculomotor Updating* phase of our experimental task. The resulting group data are shown in Fig. 3.3 (orange; n=15), overlaid on a representative anatomical scan in 'inflated brain' coordinates (note that while visually convenient, this convention results in small spatial distortions). This contrast revealed extensive cortical activation spanning occipital and parietal cortex, with some additional activation in frontal cortex. Also shown is the *Saccade* > *Fixation* contrast (fuchsia) from an independent saccade control task (n=12), where participants simply made saccades back and forth between two points (see Methods). Note that, overall, saccade modulations were much more widespread in the experimental task, suggesting that additional saccade interactions were required for the more complex visual processing and response required in this task (Baltaretu et al., 2020).

3.3.1.2 Sites-of-Interest. The second step in this analysis was to determine specific cortical coordinates for our hypothesis tests. To do this, we localized the sites of peak activation within the occipital and parietal lobes from our experimental transsaccadic task. This resulted in 1) two frontal sites: right medial superior frontal gyrus, mSFG, and left dorsal precentral sulcus, PCSd, 2) four parietal sites: bilateral superior parietal cortex (SPL) and bilateral precuneus (PCu), and 3) four occipital sites: bilateral lingual gyrus (LG) and cuneus (Cu). These sites are shown in Figures 3.4a, 3.5a, and 3.6a respectively, overlaid on anatomical slices (less susceptible to distortions). Coordinates and supporting references for these sites are shown in Table 1. Note that, by definition, each of these sites passed our prediction 1 (Saccade > Fixation), so were next tested on prediction 2.

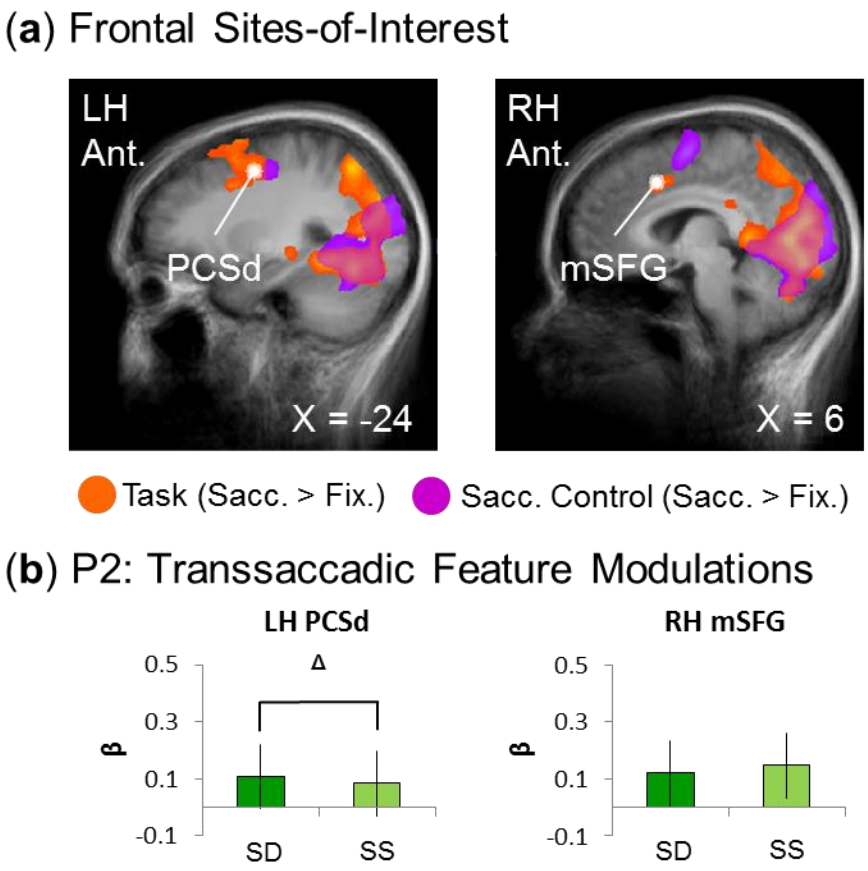


Figure 3.4. Testing feature sensitivity in frontal sites-of-interest. **a.** The sites-of-interest in frontal cortex were localized and are visualized on the slices of the averaged brains of all (n=15) participants. (These regions are superimposed onto activation maps from an RFX GLM for the experimental transsaccadic data (n=15; orange) and from the separate saccade control task (n=12; fuchsia) (BrainVoyager QX v2.8; www.brainvoyager.com).) The white dots represent peak voxels of each frontal site-of-interest. The left panel shows the left dorsal precentral sulcus (PCSd) and the right panel shows the right medial superior frontal gyrus (mSFG). **b.** We tested feature sensitivity in frontal regions, though with no particular directional hypothesis, for spatial frequency (experimental task data; n=15). Results indicate that there is a trend toward statistical significance ($p < 0.10$) for feature sensitivity in left PCSd, with no effect in right mSFG. Overall, this supports a more general saccade-related role for frontal regions in transsaccadic tasks, like this one. Bar graphs show mean β-weights ± SEM analyzed using two-tailed repeated measures t-tests.

3.3.2 Prediction 2: transsaccadic feature modulations

3.3.2.1 Frontal cortex. Figure 3.4a provides an overview of the frontal cortex data used to test our hypotheses, showing *Saccade* > *Fixation* modulations during the updating portion of our experimental transsaccadic task (orange) and for reference, the same contrast from the saccade control task (fuchsia). The white arrows/dots indicate the sites of peak activity used for further testing including right mSFG and left PCSd, likely corresponding to pre-supplementary eye fields and frontal eye fields respectively (Table 1). Caudal PCSd appears to overlap with a region of control task activation, whereas mSFG is anterior to another region of the control task (Figs. 3.3, 3.4a). For further hypothesis testing, we used BrainVoyager (BrainVoyager QX v2.8, Brain Innovation) to create spheres (radius= 5 mm) around these peaks and then, extracted β-weights from those spheres to test our feature modulation prediction (Song et al., 2006; Baltaretu et al., 2020; Tsushima et al., 2020). Since transsaccadic feature modulations were not expected in frontal cortex, we applied a two-tailed repeated-measures t-test (Prediction 2a/2b, n = 15). There was a trend toward feature modulation in left PCSd (Fig. 3.4b; $p < 0.10$; Table 3.1), but neither site reached significance (Fig. 3.4b; Table 3.1), consistent with the notion that these frontal areas are primarily involved in the saccade motor aspects of such tasks (Goldberg & Bruce, 1990; Prime, Vesia, & Crawford, 2010; Baltaretu et al., 2020).

3.3.2.2 Parietal cortex. Figure 3.5 follows the same conventions as Figure 3.4, but shows our parietal data. Again, Figure 3.5a shows the *Saccade* > *Fixation* contrast and peak sites from the experimental transsaccadic task (orange), as well as the saccade

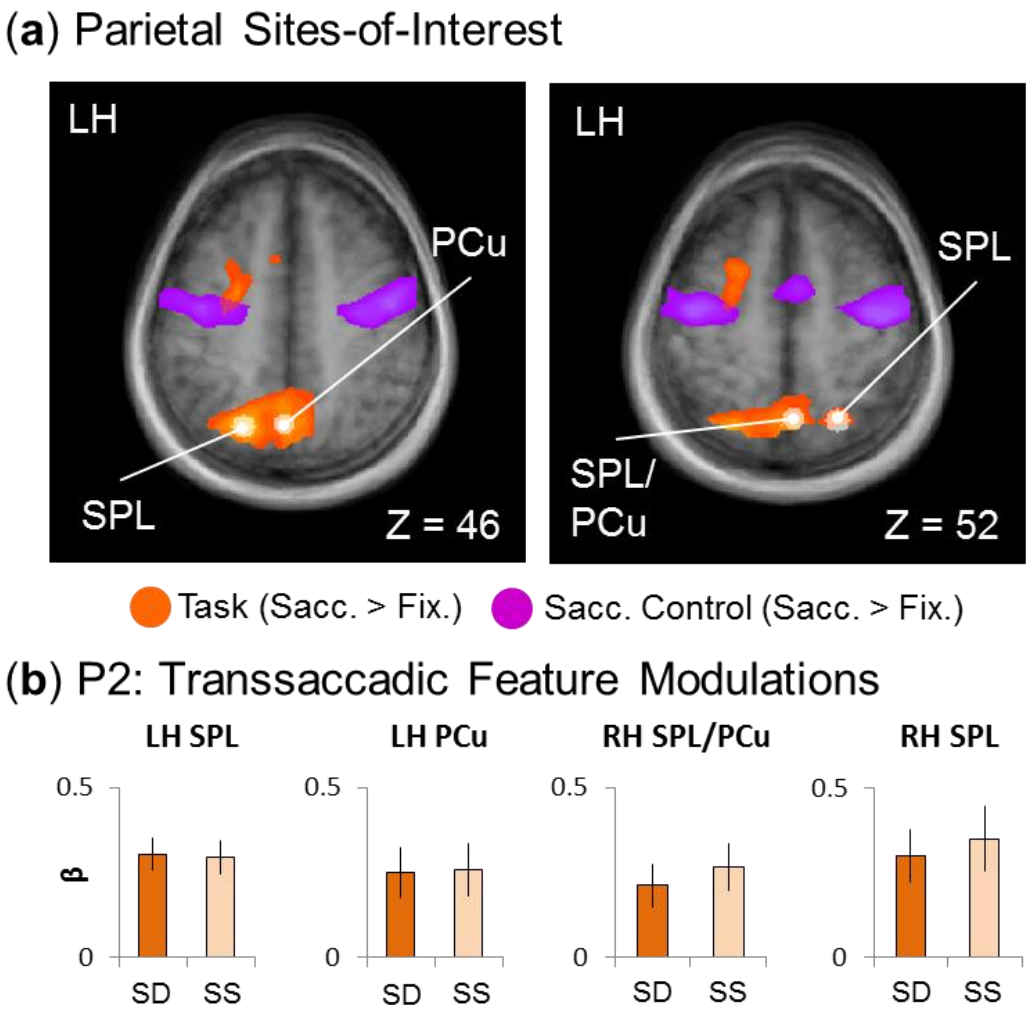


Figure 3.5. Testing feature specificity in parietal sites-of-interest. **a.** The sites-of-interest within the parietal cortex were localized, the peak voxels of which are visualized in the transverse slices through the average brain of all (n=15) participants via the white dots. (These regions are superimposed onto activation maps from an RFX GLM for the experimental transsaccadic data (n=15; orange) and from the separate saccade control task (n=12; fuchsia) (BrainVoyager QX v2.8; www.brainvoyager.com).) Spheres (radius= 5 mm) were created around the peak voxels and β-weights were then extracted and tested. The specific regions were centred on left superior parietal lobule (SPL), left precuneus (PCu), a region in right hemisphere spanning across SPL and PCu (SPL/PCu), and right SPL. **b.** Feature-specificity (Fig. 3.2, prediction 2a) was tested within the parietal sites-of-interest. For these sites to show this type of specificity, there is an expectation that there will be greater β-weights for the *Saccade/Different* than the *Saccade/Same* condition. Of the four regions, none shows this directional *suppression* effect. Bar graphs show mean β-weights ± SEM analyzed using one-tailed repeated measures t-tests.

control contrast (fuchsia). The white arrows/dots indicate the sites of peak activity used for further testing of bilateral SPL and bilateral PCu, with right PCu bordering on SPL (Table 3.1). None of these sites appears to overlap with activation in the control task (Figs. 3.3, 3.5a), suggesting task-specific saccade modulations. Figure 3.5b shows the mean β-weights used for testing prediction 2 (Fig. 3.2; n = 15). Contrary to this prediction, none of these areas showed feature repetition *suppression* (Table 3.1). Overall, our parietal sites were modulated by saccades in a task-specific manner, and did not show transsaccadic feature modulations.

3.3.2.3 Occipital cortex. Figure 6 follows the same conventions and methods as Figures 3.4 and 3.5, except showing our occipital cortex data. Again, Figure 3.6a shows the *Saccade* > *Fixation* contrast and peak sites from the experimental transsaccadic task (orange), as well as the saccade control contrast (fuchsia). The white arrows/dots indicate the sites of peak activity used for further testing (bilateral LG and Cu; Table 3.1; extracted from experimental task data). In this case, all of these sites overlapped with the activation produced by the saccade control task (Figs. 3.3, 3.6a). Figure 3.6b shows the mean β-weights used to test prediction 2 (Fig. 3.2; *Transsaccadic Frequency Modulations (Enhancement)*). Here, we compared *Different* (SD) versus *Same* (SS) spatial frequency in the experimental *Saccade* task (n = 15). Right Cu showed significantly greater modulation in the *Same* condition (Table 3.1), with the other regions showing a similar trend (right LG and left Cu) or no feature-specific effect (left LG). In summary, our occipital sites showed general saccade modulations, and most showed repetition *enhancement*,

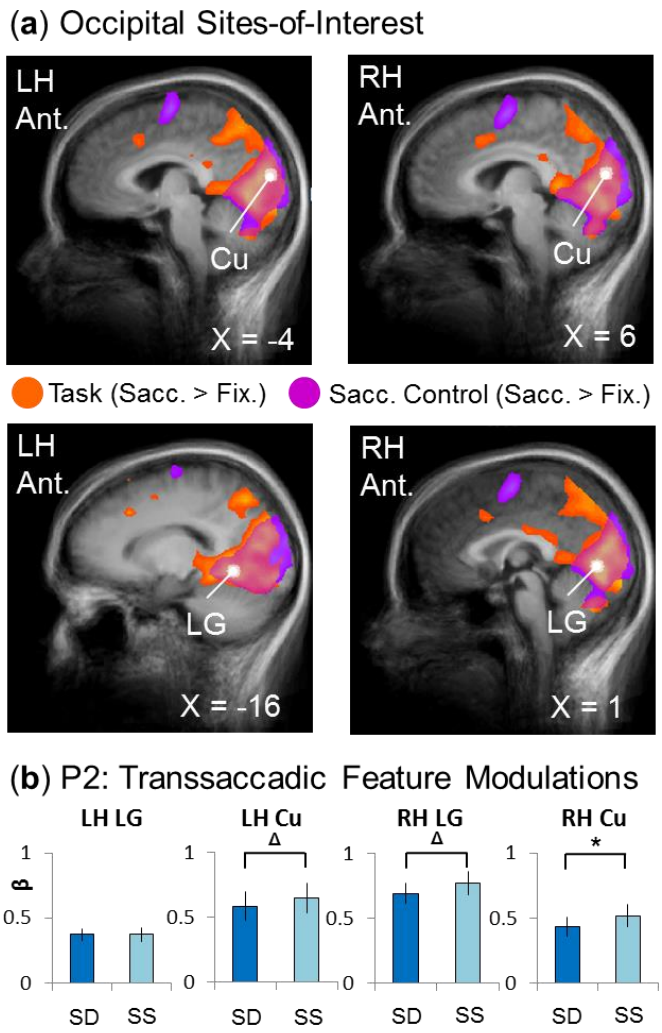


Figure 3.6. Testing feature specificity in occipital sites-of-interest. **a.** The sites-of-interest within the occipital cortex were determined and are visualized on the slices of the averaged brains of all (n=15) participants. (These regions are superimposed onto activation maps from an RFX GLM for the experimental transsaccadic data (n=15; orange) and from the separate saccade control task (n=12; fuchsia) (BrainVoyager QX v2.8; www.brainvoyager.com).) The white dots represent the peak voxels of each site-of-interest. The top two panels show the location of left lingual gyrus (LG) and cuneus (Cu) (left and right, respectively), whereas the bottom two panels show the locations of the right LG and Cu (left and right panels, respectively). **b.** Based on previous findings for enhancement within occipital regions (see main text), we tested prediction 2c (see Fig. 3.2) to determine if these occipital sites-of-interest show a feature-specific effect for spatial frequency. These effects would be consistent with greater β-weights for the *Saccade/Same* condition than for the *Saccade/Different* condition. Bar graphs show the extracted β-weights from each of the four regions, of which right Cu shows a statistically significant effect ($p < 0.05$) and left Cu and left LG show a trend toward significance ($p < 0.10$). Bar graphs show mean β-weights ± SEM analyzed using one-tailed repeated measures t-tests.

i.e., they showed the properties expected for transsaccadic feature interactions (Dunkley et al., 2016; Baltaretu et al., 2020).

3.4 Discussion

The goal of this study was to determine whether the involvement of the cerebral cortex in transsaccadic updating of visual location and orientation generalizes to other object features, such as spatial frequency. Overall, frontoparietal cortex showed saccade modulations that appeared to be largely task-specific, but did not show significant transsaccadic modulation for spatial frequency. In contrast, occipital cortex showed general saccade modulations, and transsaccadic feature modulations (repetition *enhancement*). Of the individual sites tested, only right cuneus passed (with statistical significance) both of our predefined criteria for putative transsaccadic updating (Baltaretu et al., 2020).

3.4.1 Role of frontoparietal and occipital cortex in transsaccadic updating

Previous studies have implicated frontal (Prime, Vesia, & Crawford, 2010), parietal (Morris et al., 2007; Dunkley et al., 2016; Baltaretu et al., 2020), and occipital (Malik et al., 2015; Dunkley et al., 2016) cortex in various aspects of transsaccadic processing for visual location and orientation. The current results extend these findings to spatial frequency processing, and show both similarities and differences. It has been proposed previously that frontal cortex (i.e., frontal eye fields and perhaps supplementary eye fields) are involved in producing a saccade efference copy that projects to the visual system for functions like transsaccadic updating (Goldberg & Bruce, 1990; Prime, Vesia, & Crawford, 2010). We did not find anything inconsistent with that idea. First, the areas we found were

at (or near) those classical oculomotor structures, with mSFG just anterior to the coordinates for supplementary eye fields and PCSd overlapping with the coordinates for the frontal eye fields (Table 3.1). Second, the latter region overlapped partially with activation in our saccade control task (Figs. 3.3, 3.4a). Finally, this region did not show significant transsaccadic feature modulations for either orientation (Baltaretu et al., 2020) or spatial frequency, so it may not be directly involved in those processes.

It has previously been shown that PPC areas, specifically intraparietal sulcus and adjacent portions of inferior PPC, are involved in transsaccadic processing of object location and orientation, respectively (Medendorp et al., 2003; Khan et al., 2005; Morris et al., 2007; Prime et al., 2008; Dunkley et al., 2016; Baltaretu et al., 2020). In some respect, the current results are similar to our previous grasp orientation results (Baltaretu et al., 2020): the PPC saccade modulations identified here did not overlap with classic saccade motor areas (Goldberg & Bruce, 1990; Gaymard & Pierrot-Deseilligny, 1999; Krauzlis, 2005) or the activation observed in our saccade control task (Fig. 3.3, 3.5a). In other words, they appeared to be largely task-specific, as observed in grasp areas in our previous study (Baltaretu et al., 2020). However, instead of the saccade modulations observed in SMG in our previous orientation studies, we found modulations in more dorsomedial superior parietal and precuneus locations. Further, we did not observe significant feature modulations in any of these sites. This suggests that SMG may be specialized for transsaccadic orientation processing, and the other PPC areas are related to other aspects of the task (discussed in more detail below).

Other studies have implicated occipital cortex in gaze-centered remapping (Merriam et al., 2003; Khan et al., 2005; Nakamura & Colby, 2002) and transsaccadic orientation

processing (Malik et al., 2015; Dunkley et al., 2016). Here, all of the occipital sites that we investigated showed saccade modulations in both our experimental and control tasks. Second, occipital cortex showed transsaccadic feature repetition *enhancement*, which reached significance in right cuneus (with trends in left cuneus and right lingual gyrus; Fig. 3.6b). Thus, of all the sites we examined, only cuneus met our full criteria (general saccade modulation and feature modulation) for transsaccadic feature processing. In this respect, cuneus shows similar properties to SMG (Dunkley et al., 2016; Baltaretu et al., 2020), except that it seems to be involved in spatial frequency processing rather than orientation processing.

Finally, the areas that showed transsaccadic feature modulations were predominantly located in the right hemisphere (Fig. 3.6b), consistent with the lateralization observed previously for spatial attention (Stone et al., 1991; Malhotra et al., 2009), spatial updating (Pisella et al., 2011), and transsaccadic orientation processing (Dunkley et al., 2016; Baltaretu et al., 2020). But, again, the specific cortical regions involved were different: in contrast to transsaccadic orientation processing areas (SMG, ‘V4’), the activity described here was located in more dorsomedial sites such as cuneus.

3.4.2 Relation to other parietal and occipital functions

Clearly, the cortical regions identified here are not only involved in transsaccadic visual processing, but their other roles seem complementary. Ventral cuneus and lingual gyrus collectively contain extrastriate cortex (Wen et al., 2018), which receives visual input from further upstream, subcortical thalamus and is involved in virtually visual functions, including spatial frequency processing (Bellebaum et al., 2008). Our specific cuneus site

appears to be dorsal to V1, likely in human V3 (Table 3.1). V3 receives input from V1, projects to both the dorsal and ventral stream areas (Felleman et al., 1997) and is responsive to processing global features such as motion and patterns (Felleman & Van Essen, 1987; Gegenfurtner et al., 1997; Braddick et al., 2001). Given its involvement in transsaccadic location remapping (Nakamura & Colby, 2002; Merriam et al., 2003), V3 seems to be an ideal candidate for transsaccadic processing of complex visual features.

In general, precuneus is associated with complex visuospatial transformations (Gorbet et al., 2004; Fernandez-Ruiz et al., 2007; Chen et al., 2018). Dorsal precuneus is associated with reaching (Galletti, Fattori, Battaglini, et al., 1996; Galletti, Fattori, Kutz, et al., 1999; Pitzalis et al., 2015), saccades (Schraa-Tam et al., 2009; Tosoni et al., 2014), and visual memory (Schott et al., 2018), whereas SPL is associated with grasp formation. These areas may have been activated for the manual response (Zysset et al., 2002). Whereas SPL showed transsaccadic feature modulations in our previous grasp orientation study (Baltaretu et al., 2020), they did not show feature modulations in the current study. This makes sense in light of the details of the task. First, spatial frequency is less relevant for grasp formation than object orientation. Second, in the current study, feature-related grasp shaping was not required, only a button press.

3.4.3 Why is transsaccadic perception feature- and task-dependent?

As noted above, our previous experiments showed transsaccadic modulations for object orientation in inferior parietal cortex (specifically SMG) along with some task-dependent extrastriate (Dunkley et al., 2016) and superior parietal areas (Baltaretu et al., 2020). Why would the sites and networks observed for transsaccadic spatial frequency processing in

the current study be so different? In part, it is likely that transsaccadic perception builds on computations already used during fixation, which are themselves feature- and task-dependent (Duhamel, Colby, & Goldberg, 1992; Oliva & Torralba, 2006; Melcher, 2007; Subramanian & Colby, 2014), especially in the higher-level visual areas activated in our tasks (Cavanna & Trimble, 2006; Treserras et al., 2009). At early levels like V1, there is clear multiplexing of orientation and spatial frequency (Tootell et al., 1988; Nauhaus et al., 2012), but at higher levels these features may tap into entirely different processes. As noted above, a change in orientation is relevant for spatial processing and actions like grasping (Monaco et al., 2011; Baltaretu et al., 2020), whereas a change in spatial frequency can denote, for example, changes in higher level cognitive processes such as perceived identity and affordance, evoking very different cortical mechanisms (Valyear et al., 2006). Conversely, it is likely that more automatic bottom-up aspects of transsaccadic integration (such as the automatic integration of motion signals across saccades) (Melcher & Morrone, 2003) involve different mechanisms again, perhaps primary visual cortex (Nakamura & Colby, 2002; Merriam et al., 2003). Thus, the notion of a dedicated 'transsaccadic perception centre' is likely naïve: transsaccadic vision, not prolonged fixation, is normal vision, and has likely developed different and nuanced mechanisms, depending on feature and task details.

3.4.4 Conclusion

In this fMRI study, we set out to explore the cortical mechanism for transsaccadic processing of spatial frequency, with emphasis on the role of PPC and occipital cortex. It has been shown previously that PPC and occipital cortex show both saccade and feature modulations during transsaccadic processing of object orientation. The modulations

found here showed several similar properties, in terms of saccade specificity, laterality, and occipital repetition enhancement. However, whereas SMG and putative V4 were implicated in orientation processing (Dunkley et al., 2016; Baltaretu et al., 2020), we found activation for different (more dorsomedial) areas for spatial frequency processing, perhaps with a special role for right cuneus. It remains to be seen how these functions extend to other object properties, such as shape, and how they are combined for more real-world tasks. Overall, these findings support the role of parietal and occipital cortex in transsaccadic vision, but suggest that different cortical networks are recruited for transsaccadic processing of different features.

3.5 Materials and methods

3.5.1 Participants

We tested 21 (human) participants from York University (Toronto, Canada) of whom 15 met our inclusion criteria for analyses (see Behavioural analysis and exclusion criteria), thus exceeding the requirement for sufficient statistical power (see Power analysis) (Ten Brink et al., 2019). These 15 individuals (average age: 26.6 +/- 4.3 years; age range: 21-37; 11 females and 4 males; all right-handed) had no neurological disorders and normal or corrected-to-normal vision. Informed consent was obtained from each participant; all participants were remunerated for their time. We confirm that the experimental protocol involving human participants was approved by and in accordance with guidelines of the York University Human Participants Review Subcommittee.

3.5.2 Experimental set-up

Participants passed initial MRI safety screening and were then instructed on the experimental task. Participants practiced before taking part in the experiment. Once they felt comfortable with the task, they assumed a supine position on the MRI table, with their head resting flat within a 32-channel head coil. An apparatus, holding a mirror to reflect images from the screen in the MRI bore, was attached to the head coil. An MRI-compatible eye-tracker (iViewX, SensoMotoric Instruments) was also attached to the apparatus in order to record the position of the right eye. Participants held an MRI-compatible button box in their right hand. Their right index and middle fingers rested on two buttons, used to provide the task responses when presented with the 'go' cue (see General paradigm).

3.5.3 Stimuli

During the experiment, participants were presented with an 18° stimulus that contained a vertical sine-wave grating pattern, averaged to the mean luminance of the screen. Stimuli were presented in the centre of the screen on a light gray background (MATLAB; Mathworks, Inc.). The two spatial frequencies that were tested were 0.7 or 1.1 cycles/degree (cpd) (see Fig. 3.1a).

3.5.4 General paradigm

In order to identify the cortical activity correlates of transsaccadic perception of spatial frequency, we used a modified 2 (Gaze: Fixate or Saccade) x 2 (Spatial Frequency: 0.7 or 1.1 cpd) slow event-related fMRI design (Dunkley et al., 2016). Here, we modulated the spatial frequency (repeated or changed within the same trial; *'Same'* and *'Different'*

conditions, respectively) and/or position of the eyes (continued fixation of gaze or a saccade was produced; *'Fixation'* and *'Saccade'* conditions). This resulted in four main conditions: 1) Fixation/Same, 2) Fixation/Different, 3) Saccade/Same, and 4) Saccade/Different. These were randomly intermingled and repeated four times within each run; there were six runs in total for each participant.

3.5.5 Trial sequence

Each trial was composed of three main phases: 1) an initial presentation of the stimulus, which requires sensory processing and working memory storage ('*Sensory/Memory'* phase); 2) a second presentation of the stimulus, which requires sensory processing and (oculomotor) updating (for saccades) ('*Visual/Oculomotor Updating'* phase); and 3) a response period, where a button press was made to indicate if the spatial frequency of the stimulus presentations was the same or different (*'Response'* phase). The sequence of events in each trial (Fig. 3.1a) began with a 2 s fixation period, with the fixation cross presented at one of two possible positions (13.5° to the left or right of centre, or 4.5° to the left or right of the central stimulus). The stimulus was then presented in the centre for 5.8 s, followed by a 200 ms static noise mask. Once the mask disappeared, a fixation cross appeared for 200 ms at the same position (*Fixation* condition) or the other fixation position (*Saccade* condition) (see Fig. 3.1b for eye position trace). The central stimulus was presented a second time for 5.8 s at the same spatial frequency (*Same* condition) as in the *Sensory/Memory* phase or at the other spatial frequency (*Different* condition). Finally, after the fixation cross and stimulus disappeared, a written prompt ('R or N?') appeared for 8 s in the same location as the fixation cross, prompting participants to

indicate via button press whether the spatial frequency of the two stimulus presentations was the same (R) or different (N).

Each trial sequence lasted 22 s in total. The four main conditions were repeated four times per run, resulting in 16 trials per run. Each run started and ended with a 16 s period of central fixation, serving as a baseline. Overall, each run lasted 6 min 24 s.

3.5.6 Saccade control task

We ran a separate saccade control task in order to identify regions of the brain that respond to saccade production (over those that respond to fixations only). The sequence of events began with an 8 s fixation period of a central white cross on a black background. This was followed by a period of directed saccadic eye movements between two fixation crosses, randomly from left to right across trials, for 8 s. The pattern of fixation followed by saccades was repeated 16 times per control run, lasting ~4 min 16 s for each of two runs.

3.5.7 MRI parameters

A 3T Siemens Magnetom TIM Trio MRI scanner at the York MRI Facility was used to acquire fMRI data. An echo-planar imaging (EPI) sequence (repetition time [TR] = 2000 ms; echo time [TE] = 30 ms; flip angle [FA] = 90°; field of view [FOV] = 240 x 240 mm, matrix size = 80 x 80, in-plane resolution = 3 mm × 3 mm; slice thickness = 3 mm) was acquired in ascending, interleaved order for each of the six functional runs and for the two separate saccade localizer runs. Thirty-three contiguous slices were acquired per volume

for a total of 192 volumes of functional data in each experimental run, and 128 volumes of data for each saccade control run. A T1-weighted anatomical reference volume was obtained for each participant using an MPRAGE sequence (TR= 1900 ms; FA= 256 mm x 256 mm; voxel size= 1 x 1 x 1 mm^3). 192 slices were acquired per volume of anatomical data.

3.5.8 Analysis

3.5.8.1 Power analysis

To determine the appropriate number of participants to provide a sufficient effect size and level of power, we used results from the most recent, relevant findings (Baltaretu et al., 2020). Specifically, we used the effect size (0.887, Cohen's d) from the most relevant region of activation in parietal cortex (i.e., SMG) and applied the following properties: 1) two-tailed t-test option, 2) an α value of 0.05, and 3) a power value of 0.85. Using G*Power 3.1 (Faul et al., 2009), we determined that a minimum of 14 participants would be required to achieve an actual power value of 0.866. As noted above, we tested a total of 21 participants in order to exceed this minimal number, after application of exclusion criteria in the next section.

3.5.8.2 Behavioural data and exclusion criteria

In our previous studies (Dunkley et al., 2016; Baltaretu et al., 2020), we found that experiments such as this are highly sensitive to head motion. Due to excessive head motion, data were excluded from analyses on the basis of two criteria: 1) presence of head motion over 1 mm/degree and/or 2) any abrupt motion of the head over 0.5

mm/degrees. If more than 50% of all data (i.e., at least 3 runs out of the total 6 runs for a given participant) were removed from analysis, the entire data set from that participant was removed. On this basis, data from six participants were removed. From the remaining 15 participants, one run was removed from data analysis for each of two participants, and two runs were removed for each of another two participants, for a total of six runs (6.7%).

Eye tracking and button-press data were analyzed post-image acquisition in order to determine whether the task was completed correctly or not. Eye position data (e.g., Fig. 3.1b) were inspected visually to confirm that the eye fixated on the fixation crosses (within a region of 2º of fixation) and/or moved to the correct saccade location when prompted to do so in all trials. Button press responses were also inspected offline to ensure that participants responded correctly to the *Same*/*Different* condition trials. On these bases, 41 trials were excluded from further analysis (across all participants, a maximum of four trials were removed for any given participant, with a mode of one; 3.1% of the remaining data). Overall, accuracy of the 15 participants included in the final data analysis was 97.4% ± 3.1%. Separated by condition type, accuracy was 1) 95.3% ± 5.4% for the Fixation/Same condition, 2) 98.1% ± 3.1% for the Fixation/Different condition, 3) 96.9% ± 3.7% for the Saccade/Same condition, and 4) 97.8% ± 2.7% for the Saccade/Different condition. A repeated-measures ANOVA showed no main effect of eye movement ($F_{1,14}$=0.485, p= 0.489), no main effect of feature ($F_{1,14}$=3.278, p= 0.076), nor interaction ($F_{1,14}$=0.950, p= 0.334). Only data for correct trials were included in all further analyses.

3.5.8.3 Functional imaging data: experimental

To model the fMRI BOLD response, we used a general linear model (GLM) analysis. In this model, a standard two-gamma haemodynamic response function (BrainVoyager QX 2.8, Brain Innovation) was convolved with predictor variables (Dunkley et al., 2016). We had five major classes of predictors for each trial: 1) a baseline predictor ("Baseline"), corresponding to the first and last 16 s of each run; 2) "Fixate", which represented initial trial fixation (either left or right); 3) "Adapt", which modeled the activity in response to the first stimulus presentation; 4) "Fixate/Same", "Fixate/Different", "Saccade/Same", or "Saccade/Different" to model activity in response to the second stimulus presentation in one of the four main conditions; and 5) "Response", which modeled the activity for the button press response period. GLMs were generated using the eight predictors per run for each participant (BrainVoyager QX 2.8, Brain Innovation).

Preprocessing of functional data from each run for all participants included slice scan-time correction (cubic spline), temporal filtering (for removal of frequencies < 2 cycles/run), and 3D motion correction (trilinear/sinc). Anatomical data were transformed to Talairach space (Talairach & Tournoux, 1988). Functional data were coregistered using gradient-based affine alignment (translation, rotation, scale affine transformation). Lastly, the functional data were spatially smoothed using a Gaussian kernel with a full width at half maximum of 8 mm.

Using the random-effects (RFX) GLM with all of the runs of all of the remaining 15 participants, we performed two major types of analyses: 1) site-of-interest prediction testing and 2) voxelwise contrasts (see *Hypothesis testing: Analysis and statistical considerations* and *Voxelwise map contrasts: Analysis* and statistical considerations for details).

3.5.8.4 Functional imaging data: saccade control task

Each run of the saccade task had 16 repetitions of the fixation trials (8 s of central fixation) and saccade trials (8 s of directed saccades). Each trial type was coded by an 8 s predictor ("Fixation" for the fixation trials, and "Saccade" for the saccade trials). These predictors were convolved with the standard two-gamma haemodynamic response function (BrainVoyager QX 2.8, Brain Innovation). Preprocessing of functional and anatomical data occurred as for experimental data (see previous).

On the basis of behavioural data analysis (i.e., excessive motion > 1 mm), data from three participants were removed, leaving saccade control task data for 12 participants. These data were used in the prediction testing in order to identify regions related to the production of saccades.

3.5.8.5 Voxelwise map contrasts: analysis and statistical considerations

We conducted voxelwise contrasts on data from the 15 participants included in the analysis for experimental task, and separately on the remaining 12 participants for the saccade control task. For analysis purposes, we divided the experimental task data into the *Sensory/Memory* phase (when participants saw and initially remembered the stimulus) and *Visual/Oculomotor Updating* phase (when saccades occurred and the stimulus reappeared). For all (voxelwise) contrasts, we first applied a False Discovery Rate (FDR) of $q < 0.05$, followed by cluster threshold correction (BrainVoyager QX v2.8, Brain Innovation) to our contrasts. This included the *Saccade* > *Fixation* contrast shown in Figs. 3.3, 3.4a, 3.5a, and 3.6a (orange), and the contrasts shown in supplementary

figures (*Sensory/Memory* phase activity > Baseline, Fig. 3.S1; *Visual/Oculomotor Updating* > *Sensory/Memory* contrast, Fig. 3.S2).

3.5.8.6 Hypothesis testing: analysis and statistical considerations

In order to localize our site-of-interest testing, we used a similar approach to site localization as in Song and Jiang (2006); Baltaretu et al. (2020); and Tsushima et al. (2020) by first applying a whole-brain contrast of interest to only our experimental task data (n=15): Saccade – Fixation (FDR with $q < 0.05$, followed by cluster threshold correction) (Fig. 3.3a). We then localized the peaks of our *a priori* predicted frontal, parietal and occipital activations and then used BrainVoyager (BrainVoyager QX v2.8, Brain Innovation) to create 5 mm-radius spheres surrounding the peak voxels (Table 3.1). Finally, we extracted the mean β-weights across voxels within each sphere for the experimental data (n=15) in order to test our hypotheses within the identified parietal and occipital regions (i.e., to identify the presence of a transsaccadic feature-specific effect). For our first prediction (Fig. 3.2), these analyses were carried out for 15 participants who met our behavioural criteria (see *Methods: Behavioural data and exclusion criteria*; Fig. 3.3, orange) and the 12 participants who met our behavioural criteria for the saccade control task (see *Methods: Functional imaging data: saccade control task.*; Fig. 3.3, fuchsia). For our second prediction (Fig. 3.2), these analyses were carried out for the 15 participants who met our behavioural criteria.

Using the β-weights, we looked for specific directionality in the second prediction that we tested (Fig. 3.2), so we used one-tailed repeated measures t-tests (to identify feature-related specificity). For the frontal regions, where did not have a direction

hypothesis, we tested feature sensitivity using two-tailed repeated measures t-tests. For the results of these analyses, we provided all relevant t-values, p-values and effect sizes (Cohen's d, determined using G*Power; Table 3.1) (Faul et al., 2009).

Table 3.1 Regions, Talairach coordinates, and statistical results for tests of Prediction 2 (t-value, p-value, and effect size) for parietal and occipital sites-of-interest from the Visual/Oculomotor Updating phase.

Site-of-Interest	**Talairach Coordinates**			**Testing Prediction 2**			**Ref's**
	x	y	z	T-value	P-value	Effect Size	
Frontal Areas							
LH dorsal Precentral Sulcus	-24	-3	46	2.145	0.097	0.46	[23]
RH medial Superior Frontal Gyrus	6	14	40	2.145	0.363	0.24	[71]
Parietal Areas							
LH Superior Parietal Lobule	-21	-64	46	0.384	0.35	0.099	[25]
LH Precuneus	-3	-63	47	-0.190	0.57	0.049	[53]
RH Superior Parietal Lobule/Precuneus	2	-60	54	-1.098	0.86	0.28	[53]
RH Superior Parietal Lobule	21	-61	52	-1.599	0.93	0.41	[25]
Occipital Areas							
LH Lingual Gyrus	-16	-55	-6	0.0731	0.53	0.019	[72]
LH Cuneus	-4	-85	14	-1.443	0.085	0.37	[73]
RH Lingual Gyrus	1	-71	1	-1.663	0.059	0.43	[72]
RH Cuneus	6	-79	15	-1.960	0.035	0.51	[73]

CHAPTER 4

MEDIAL OCCIPITAL CORTEX PARTICIPATES IN A CORTICAL NETWORK FOR TRANSSACCADIC PERCEPTION OF OBJECT SHAPE VERSUS ORIENTATION: AN FMRI PARADIGM

Baltaretu, B.R., Stevens, W.D., Freud, E., & Crawford, J.D. (submitted). Medial occipital cortex participates in a cortical network for transsaccadic perception of object shape versus orientation: An fMRI paradigm.

4.1 Abstract

To date, the cortical correlates for human transsaccadic vision have been probed for single object features such as orientation (associated with parietal repetition suppression) and spatial frequency (associated with occipital repetition enhancement). Here, we used functional magnetic resonance imaging to distinguish cortical modulations associated with transsaccadic perception of multiple object features. Participants (n=21) viewed a 2D object and then, after sustained fixation or a saccade, judged whether the shape *or* orientation of the re-presented object had changed. Since feature change was randomized, participants had to remember both features across saccades to perform the task. A whole-brain voxelwise contrast (Saccade > Fixation; n=17) uncovered areas that might be specialized for transsaccadic memory, updating and/or perception, including medial occipital, dorsomedial posterior parietal, and dorsal frontal cortex. Searching within these regions, we then employed a feature contrast (Orientation vs. Shape change). This contrast revealed feature-specific modulations (consistent with shape change enhancement) in left medial occipital cortex. The peak site (left cuneus) showed (contralateral) functional connectivity with early visual cortex (lingual gyrus), object-processing areas (occipitotemporal cortex) and saccade / motor areas in parietal cortex. These observations show that medial occipital cortex participates in a cortical network involved in transsaccadic feature perception. Together with the previous literature, this suggests separate mechanisms for transsaccadic perception of intrinsic object features (spatial frequency, shape) versus object location and orientation.

4.2 Introduction

Our ability to extract pertinent visual information from our surroundings is largely dependent on the brain's ability to aim and account for rapid eye movements, i.e., saccades (Javal, 1879; Wade et al., 2003; Rayner & Pollatsek, 1992). Saccades help gather new visual information by aligning the fovea with objects of interest, but also disrupts visual stability and memory by displacing the retinal image relative to other objects (Irwin, 1996; Melcher & Colby, 2008). It is thought that during saccades, oculomotor signals are used to remap / update retinal location (Duhamel et al., 1992; Merriam et al. 2003; Klier & Angelaki, 2008; Mathôt & Theeuwes, 2010; Burr & Morrone, 2011; Rao et al., 2016; Bisley et al., 2020) and features such as orientation (Melcher & Colby, 2008; Prime et al., 2011). Recently, it has been shown that parietal and occipital cortex are involved in transsaccadic memory of spatial orientation and frequency (Dunkley et al., 2016; Baltaretu et al., 2020; 2021). However, these studies did not account for the need to process multiple features in real world vision and did not discriminate transsaccadic memory vs. perception (see below for details). Here, we investigated both these factors, in a task that involved memory of multiple stimulus features but focused on their interactions with a post-saccadic stimulus.

Single unit recordings and neuroimaging studies have shown that the cortical regions involved in saccade production, such as lateral intraparietal cortex (LIP) and the frontal eye fields (FEF), are also involved in transsaccadic updating/remapping of object location (Duhamel et al., 1992; Umeno & Goldberg, 1997; Medendorp et al. 2004; Merriam et al. 2003; Zirnsak et al., 2014). Feature remapping has been observed in some monkey LIP neurons (Subramanian & Colby, 2014), and transcranial stimulation (TMS) over the

human occipital, parietal, and frontal and parietal eye fields interrupts transsaccadic memory of multiple object orientations (Prime et al., 2008, 2011). Location remapping has also been observed in monkey and human occipital cortex (Nakamura & Colby, 2000, 2002; Merriam et al., 2007; Neupane et al., 2016; Hartmann et al., 2017), whereby TMS applied thereto disrupts feature remapping into the perturbed visual field (Malik et al., 2015). Finally, a recent study has shown that stimulus features (specifically spatial frequency) can be still be decoded from whole brain MEG signals after an intervening saccade (Fabius et al., 2020) Overall, these studies suggest that a distributed occipital-parietal-frontal network participates in transsaccadic updating of object features.

It has proven more difficult to localize the cortical locations that contribute to specific transsaccadic feature interactions in human fMRI studies (Lescroart et al., 2016). However, through the use of repetition enhancement / suppression (Grill-Spector & Malach, 2001; Segaert et al., 2013), it has been shown that some cortical areas are modulated when a stimulus object is presented both before and then after a saccade with either the same or different features. In these experiments, parietal cortex tended to show repetition suppression (less activation for the same stimulus), whereas occipital cortex showed repetition enhancement (more activation for the same feature). Specifically, right inferior parietal cortex (supramarginal gyrus; SMG) and sometimes right ventrolateral occipital cortex (‘putative V4’) were modulated by transsaccadic changes in object orientation (Dunkley et al., 2016; Baltaretu et al., 2020). In contrast, right dorsomedial occipital cortex (cuneus) was modulated by transsaccadic changes in spatial frequency (Baltaretu et al., 2021a). It was speculated that the difference between these last two

results (Baltaretu et al., 2020; Baltaretu et al., 2021a) was to related changes of orientation versus identity, as observed during gaze fixation (Valyear et al., 2006).

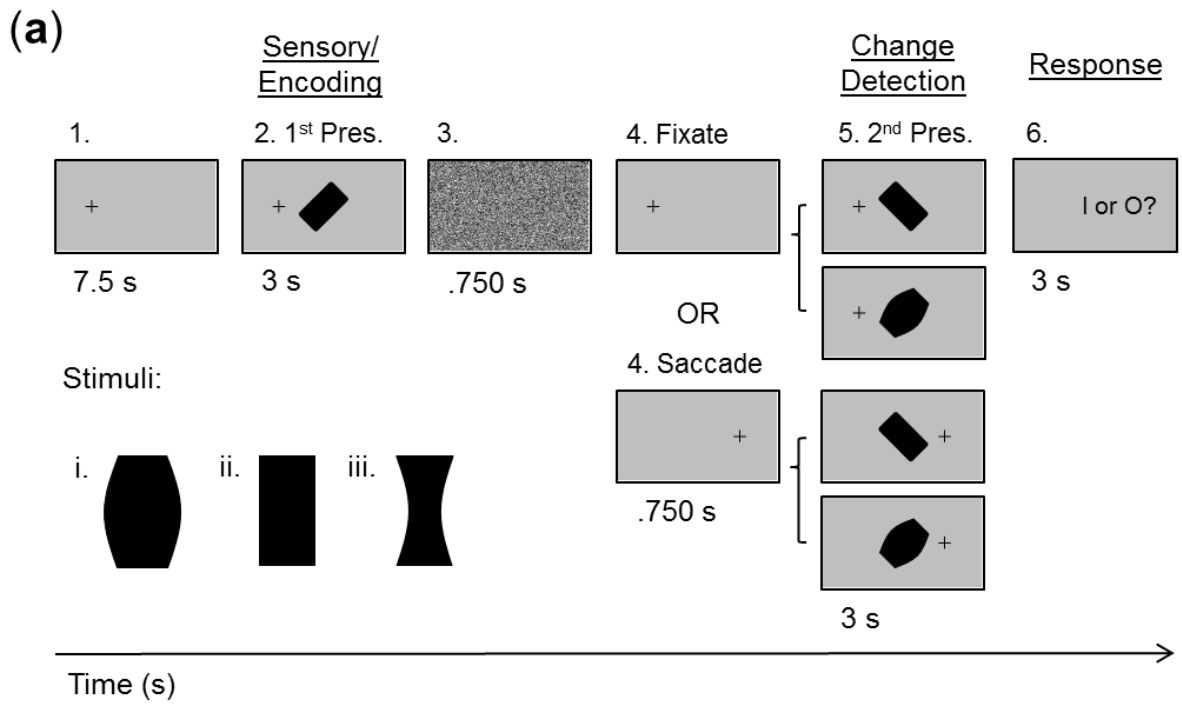
The preceding transsaccadic fMRI experiments (Dunkley et al., 2016; Baltaretu et al., 2020) had two important limitations. First, they only examined transsaccadic changes in one feature at a time. In real world conditions, the brain must bind multiple features together to represent an object (Treisman, 1998; Colzato et al., 2006; Utochkin & Brady, 2020), and presumably retain this binding across saccades. Second, because these studies only examined one feature at a time, it was not possible to disentangle if the effects were driven by the influence of instructions on pre- and perisaccadic signals versus the influence of postsaccadic stimulus changes on these signals.

Here, our aim was to test the cortical underpinnings of transsaccadic perception of multiple object features, using a functional magnetic resonance imaging (fMRI) paradigm that required participants to remember both object shape and orientation across a saccade and then discriminate which one of these had changed (Fig. 1a). Since this task required participants to retain both features until the post-saccadic stimulus appeared, it was now possible to analyze the data such that feature-specific memory signals would cancel up until they interact with the new stimulus to perceive the change. Based on our previous findings, we expected transsaccadic changes in object orientation to modulate SMG (Dunkley et al., 2016; Baltaretu et al., 2020), whereas changes in shape (an intrinsic object property like spatial frequency) were expected to modulate occipitotemporal cortex (Grill Spector et al., 1999; Koutstaal et al., 2001; Valyear et al., 2006; Baltaretu et al., 2021a). We did not find orientation modulations in SMG (perhaps due to the experimental design noted above). Instead, we found that medial occipital cortex (cuneus) is 1)

associated with discrimination of postsaccadic changes in object shape versus orientation, and 2) participates in a functional network ideally suited for transsaccadic perception of object features.

4.3 Results

To identify areas involved in transsaccadic discrimination of object orientation versus shape, we employed a task (Fig. 1a) where 21 participants briefly viewed an object with one of three shapes (a rectangle, a convex 'barrel', or a concave 'hourglass') at one of two orientations (45° clockwise or counterclockwise). They either maintained fixation to the left or right of this object or made a saccade to the opposite side. Then, they re-viewed an object with either a different shape or different orientation from the same options, and then indicated which feature had changed. 17 participants met our behavioural inclusion criteria for analysis of fMRI data collected during this task. fMRI analysis was done on the change detection portion of the task. Based on our previous experiments (Baltaretu et al., 2020, 2021), we expected areas involved in transsaccadic shape / orientation discrimination to show *both* of the following two properties: they should be modulated by saccades (Fig. 1b, criterion 1), and they should be differentially modulated by shape versus orientation change (Fig. 1b, criterion 2). To test this, we first performed a whole-brain Saccade > Fixation contrast, and then looked within resulting voxels for feature-specific modulations. Finally, we tested the functional connectivity of the site that showed peak modulations in the latter contrast, as described below.



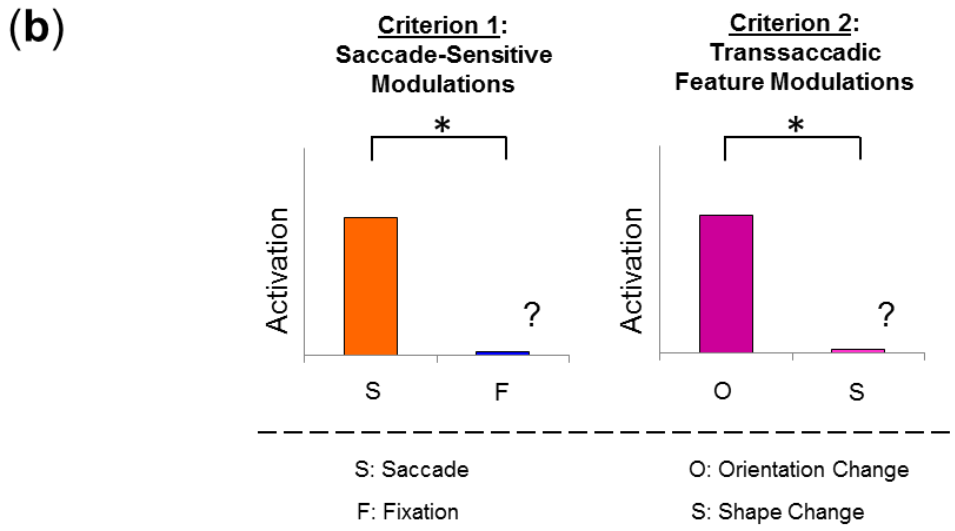


Figure 4.1. Experimental paradigm and criteria for transsaccadic feature modulation. **(a)** An example trial is presented (initial left fixation, rectangle, 45º) with the four possible main conditions: 1) Fixation, Different Orientation, 2) Fixation, Different Shape, 3) Saccade, Different Orientation, and 4) Saccade, Different Shape. Each of the 19.5 s trials had three main phases: 1) *Sensory/Encoding*, during which the stimulus (one of the three possible objects: rectangle, barrel-shaped, or hourglass-shaped) was first presented at 45º to the left or right of vertical, while looking to the left or right of centre; 2) *Change Detection*, wherein the same object is presented at the orthogonal orientation (*Different*

Orientation condition) or a different object at the same initial orientation (*Different Shape* condition) while fixating on the initial fixation cross (*Fixation* condition) or after making a saccade (*Saccade* condition); and 3) *Response*, where participants use a button press response to make a judgment about whether the shape ('I') or the orientation ('O') of the object has changed across the two stimulus presentations. **(b)** Criteria used to test saccade and feature modulations in order to identify transsaccadic feature regions. Criterion 1: The saccade-related modulations in such a region would be expected to show greater activity in response to the Saccade condition as compared with the Fixation condition (i.e., Saccade > Fixation, S, F, respectively). Criterion 2: A transsaccadic feature integrator should also show feature modulations. This would be observed through greater activity in response to one object feature change over another (e.g., Orientation > Shape change, O, S, respectively). These feature modulations would be expected in regions that first show saccade-related effects. Here, we anticipate a *nondirectional* difference between the two object feature changes.

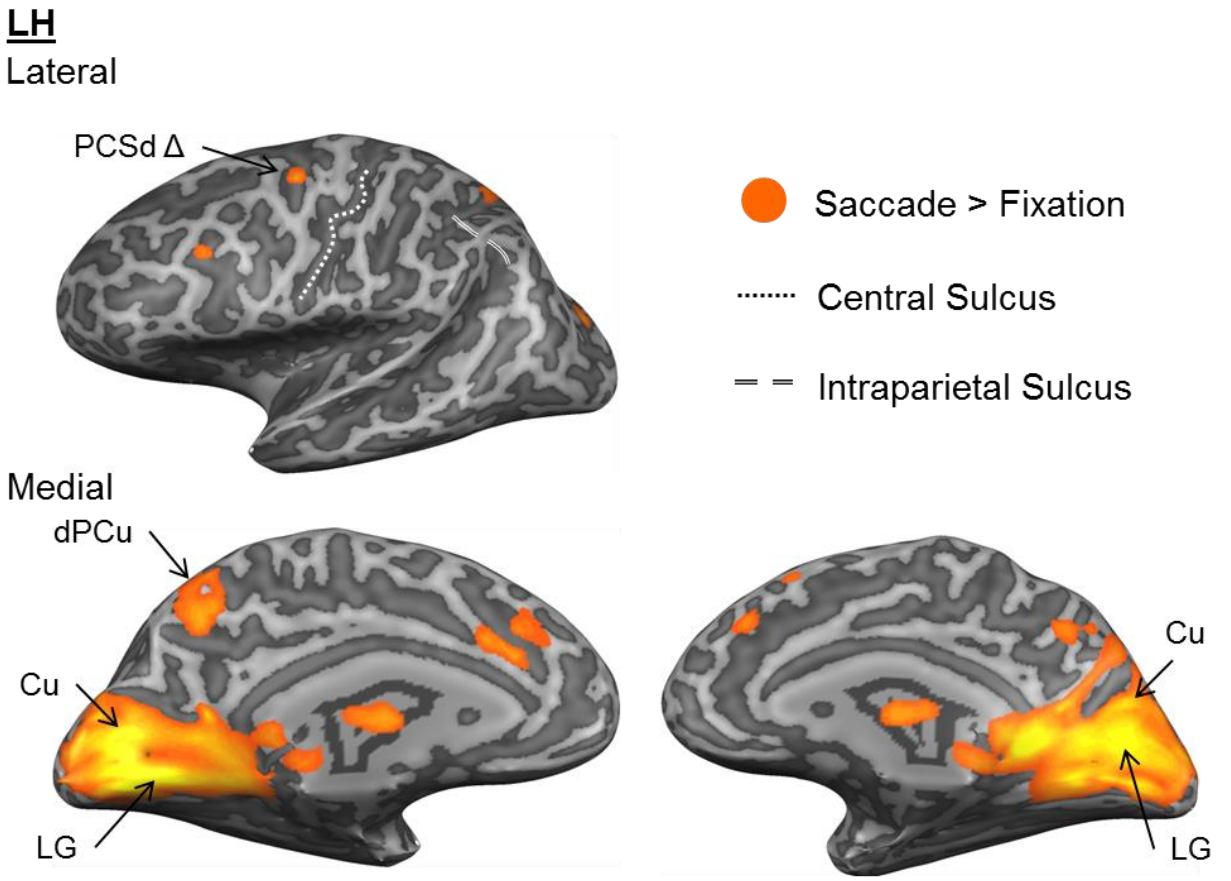


Figure 4.2. Saccade-sensitive effects. A voxelwise map from an RFX GLM (n=17; p < 0.001; cluster threshold correction; orange) is presented on an inflated brain rendering of an example participant. The upper left panel shows a lateral view of the left hemisphere, with activation in dorsal precentral sulcus (Δ indicates that this region passed only p-value correction). The lower panels present the medial views of the left and right hemispheres, respectively, which show activation in occipital and parietal cortex. Occipital regions include bilateral lingual gyrus (LG) and cuneus (Cu), whereas parietal activation is found in left dorsal precuneus (dPCu).

4.3.1 Saccade-specific cortical modulations

As in Baltaretu et al. (2021), we first isolated regions that were sensitive to saccades by applying a whole-brain Saccade > Fixation contrast (Fig. 4.1b, criterion 1). Significant saccade sensitivity ($p < 0.001$) was found in left parietal and bilateral occipital cortex, predominantly in the medial aspects (Fig. 4.2). A large swath of bilateral occipital activation included bilateral lingual gyrus (LG) and cuneus (Cu). There was also activation in medial parietal cortex, specifically left dorsal precuneus (dPCu). Finally, there was also a trend in activation in dorsal precentral sulcus (PCSd), likely the frontal eye field (Fig. 4.2; Table 4.1).

4.3.2 Cortical modulations for transsaccadic perception of object orientation versus shape

In order to test our second criterion (Fig. 4.1b, criterion 2), we performed an Orientation > Shape change contrast, only within the voxels activated in the first saccade contrast (Fig. 4.2). Note that when orientation changed shape stayed constant, and when shape changed orientation stayed constant, so this can be viewed as a repetition-dissociation task. The predictions here are more complex than the case with single feature repetition because they depend on whether one expects 1) orientation or shape change to dominate, 2) repetition suppression or enhancement, and how these interact. Based on previous results (Dunkley et al., 2016; Baltaretu et al., 2020, 2021), we expected higher positive modulation for Orientation change (repetition suppression) in parietal cortex, so the parietal prediction is a positive contrast. In the case of occipital cortex, the expectation

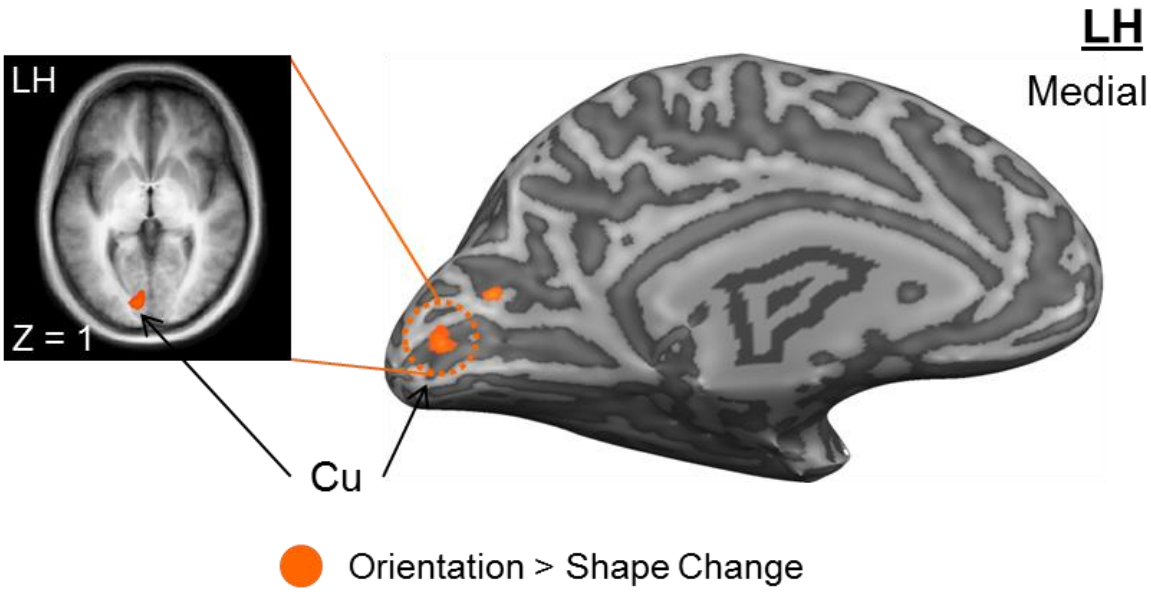


Figure 4.3. Direct comparison of saccade-related cortical modulations for changes in orientation vs. shape. Within cortex that showed saccade-sensitivity (Fig. 4.2), we then applied an Orientation > Shape change contrast (RFX GLM; n=17; $p < 0.001$; cluster threshold correction) in order to identify feature-sensitive regions. The results of these orthogonal contrasts are presented as the voxelwise map overlaid onto the inflated brain rendering of an example participant. From the medial view of the left hemisphere on the righthand side, it can be seen that activation showing feature-sensitivity is located in the left occipital lobe. More specifically, this is within the cuneus (Cu), which can be seen to a greater extent on the slice through an average brain of all participants on the lefthand side. These findings suggest that perception of transsaccadic changes in multiple object features engages medial occipital (cuneus) cortex.

is higher but negative modulation for shape change (repetition suppression), so the signs cancel and the Orientation > Shape change prediction is again positive.

The results are shown in Figure 4.3. We did not find significant feature modulations in parietal cortex, but instead found activation in left medial occipital cortex, specifically within the cuneus (dorsal to calcarine fissure) (see Table 4.1). In short, because this region of feature-selective activity was identified within the areas that showed significant saccade modulations (Fig. 4.2), it satisfied both of our criteria (Fig. 4.1b).

4.3.3 Functional connectivity of cuneus with visual and sensorimotor regions

Thus far, our results support the idea that medial occipital cortex is involved in the discrimination of intrinsic object features (Baltaretu et al., 2021a). To understand how the left medial occipital cortex (Fig. 3) interacts with other saccade-modulated areas during our task, we performed a psychophysiological interaction (PPI) analysis. We used a seed region localized to the left cuneus and then, identified regions that showed significant functional connectivity with left cuneus for saccade-related modulations, using a Saccade > Fixation contrast (Baltaretu et al., 2020). This analysis resulted in significant activation, contralateral (right), in occipital, occipitotemporal, and parietal cortex (Fig. 4, Table 2). Specifically, we observed significant functional connectivity with early-to-intermediate visual occipital (right lingual gyrus, LG, superior occipital gyrus, SOG, and transverse occipital sulcus, TOS), object-processing areas of occipitotemporal (right medial occipitotemporal sulcus, MOtS), and sensorimotor parietal (right superior parieto-occipital cortex, SPOC) cortex.

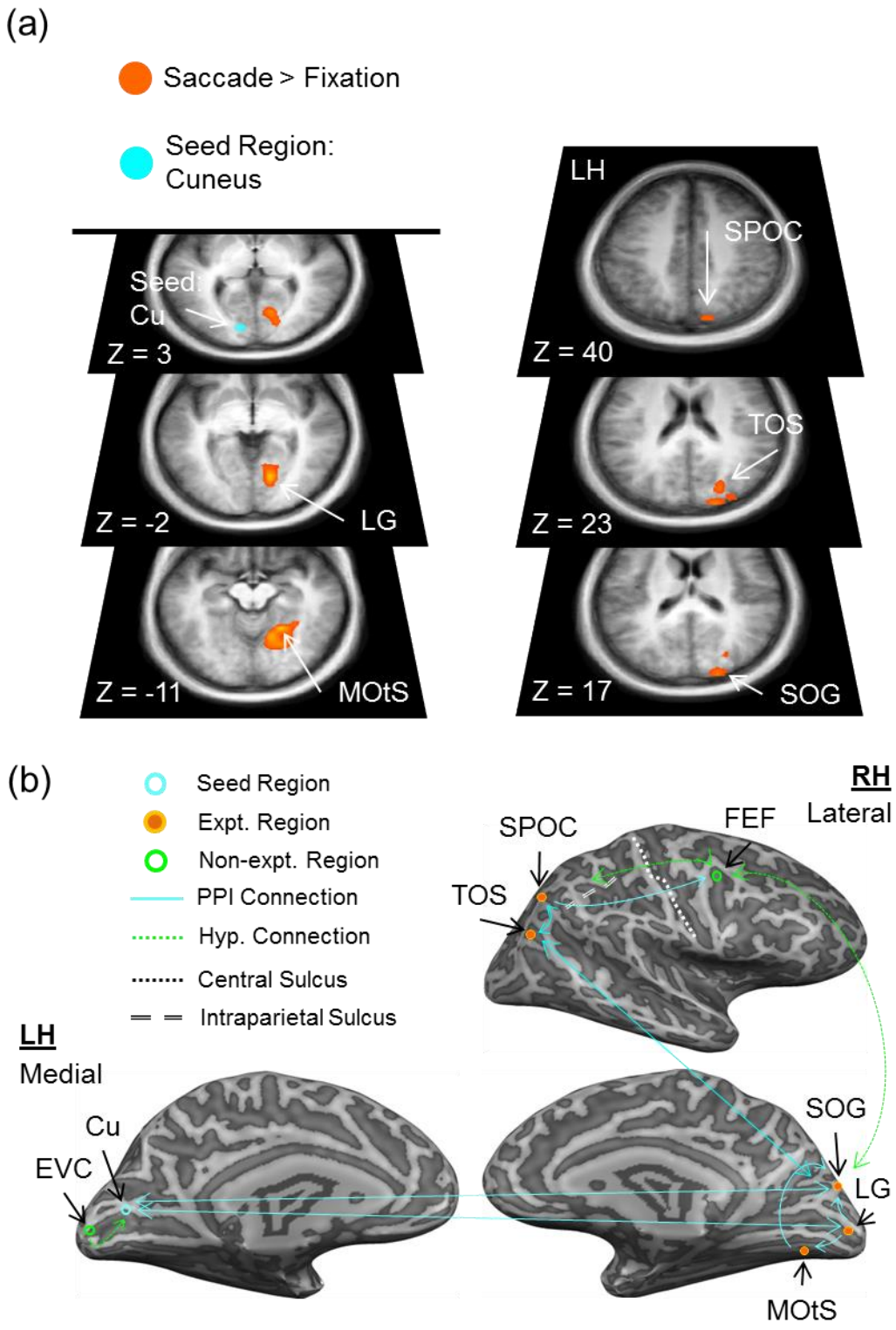


Figure 4.4. Functional connectivity network involved in transsaccadic updating of object features (orientation, shape). **(a)** Transverse slices through the average brain of all participants (n=17) are shown from most superior to inferior along the vertical axis. 'Z' components of the regions' Talairach coordinates are reported for reference. Shown in

cyan is the seed region, left cuneus (Cu). Using a Saccade > Fixation contrast, a psychophysiological interaction (PPI) contrast revealed statistically significant (RFX GLM; $p < 0.001$; cluster threshold correction) between left cuneus and parietal (right superior parieto-occipital cortex, SPOC), occipital (right transverse occipital sulcus, TOS, superior occipital gyrus, SOG, and lingual gyrus, LG), and occipitotemporal (right medial occipitotemporal sulcus, MOtS) regions. This suggests that extrastriate left cuneus is engaged in communication with early visual occipital, object centric occipitotemporal, sensorimotor parietal cortex in order to update object orientation and shape information across saccades. **(b)** A functional network model proposed to highlight the possible interactions between left cuneus and a two-stream progressing from early visual occipital (lingual gyrus, LG; superior occipital gyrus, SOG) to 1) object-processing occipitotemporal (medial occipitotemporal sulcus, MOtS) and 2) saccade / motor parietal (superior parieto-occipital cortex, SPOC) regions. It is possible that the right frontal eye field (FEF) is able to account for saccade production signals and communicate with relevant occipital (e.g., SOG) and parietal (i.e., SPOC) regions to ensure saccadic updating. Expt. Region refers to a region that showed activation in our task; Non-expt. Region refers to a region that we did not directly find to be active in our task (e.g., early visual cortex, EVC; FEF); PPI connection refers to a connection derived from our PPI results; and Hyp. Connection refers to a hypothesized connection between regions in our model.

4.4 Discussion

Our aim here was to investigate the mechanism(s) for transsaccadic perception of object features. First, we identified the cortical correlates that were saccade-sensitive (i.e., greater cortical engagement for saccades versus fixation), which were concentrated in parietal and occipital cortex. Testing within these regions, we found feature sensitivity in left medial occipital cortex (peaking in cuneus). Finally, our functional connectivity analysis, showed that left cuneus communicates with a widespread network that spans visual / object processing areas and saccade / sensorimotor regions.

4.4.1 Possible roles of medial occipital cortex in transsaccadic integration

In this and our previous study on spatial frequency (Baltaretu et al., 2021a), medial occipital cortex (likely comprising visual areas V2, V3; McKeefry et al., 1997) appears to play an important role in the postsaccadic integration of old and new information. These areas are ideally suited to provide the rudimentary machinery for transsaccadic feature analysis (Nakamura & Colby, 2000, 2002). First, they are well-positioned to provide rapid, bottom-up operations on their anatomic inputs from V1 (Livingstone & Hubel, 1988; Sincich & Horton, 2002, 2005). Second, they include the requisite machinery for orientation, spatial frequency, and early shape processing (Tootell et al., 1988; Gegenfurtner et al., 1996; Fang et al., 2005). Third, there are indications even these areas are able to store information in some sense (Tong, 2003). Fourth, these areas V1, V2, and V3 are known to show saccade modulations consistent with remapping signals (Nakamura & Colby, 2000, 2002; Merriam et al., 2007; Malik et al., 2015). Finally, these areas have reciprocal connections with both ‘ventral stream’ object recognition areas

(Salin & Bullier, 1995; Lamme & Roelfsema, 2000; Tong, 2003), and dorsal stream saccade and attention areas (Corbetta et al., 1998; Yantis et al., 2002; Behrmann et al., 2004). This feedback, in combination with V1/V2/V3 retinotopic topography (absent at higher levels), makes this area ideally suited for integrating location and identity information across saccades (Prime et al., 2005, 2008, 2011). Thus, situated at both early and intermediate stages of object feature processing, with abilities to monitor several object feature changes and receive feedback signals for attention and saccades, medial occipital cortex is an excellent candidate for transsaccadic feature perception.

4.4.2 Feature-specific transsaccadic mechanisms

Although theoretical discussions of transsaccadic feature integration suggested a role for occipital cortex (Prime et al. 2006, 2008, 2011; Hamker & Zirnsak, 2006), initial experiments sought a 'transsaccadic integration centre' with considerable emphasis on parietal cortex as a general hub (Prime et al., 2008; Subramanian & Colby, 2014; Dunkley et al., 2016; Baltaretu et al., 2020). However, considering the diversity and regionalization of visual functions (Grill-Spector et al., 2001; James et al., 2003; for review, see Grill-Spector & Sayres, 2006), and the prevalence of saccades in normal vision (Land & Hayhoe, 2001; Land, 2006), the notion that this would all be handled in one cortical 'bottleneck' is likely naïve. As noted in the introduction, transsaccadic updating of object location is found throughout visual and visuomotor cortex (Irwin, 1991; Duhamel et al., 1992; Melcher & Colby, 2008; Ten Brink et al., 2019). Our previous neuroimaging experiments showed that transsaccadic changes in object orientation modulate human SMG, and possibly V4 in some tasks (Dunkley et al., 2016; Baltaretu et al., 2020),

whereas transsaccadic changes in spatial frequency modulated the cuneus (Baltaretu et al., 2021a).

Based on the common role of spatial frequency and shape (as intrinsic object features related to *identity),* versus object *orientation* (which can be manipulated without changing identity), we speculated that cuneus would be modulated by transsaccadic shape changes, whereas SMG would be modulated by orientation changes. In the experiment, cuneus was modulated by both saccades and feature discrimination as predicted, and in the correct directions (assuming transsaccadic repetition enhancement in occipital cortex; Dunkley et al., 2016; Baltaretu et al., 2020). It is noteworthy that transsaccadic modulations primarily occurred in the right hemisphere in our previous studies, whereas left cuneus was modulated in the current study (although, it communicated with right hemisphere sites; see below). This might indicate left cuneus showed more specialization for shape versus orientation, although this runs contrary to neuropsychological and imaging findings (Davidoff & Warrington, 1999; Koutstaal et al., 2001). Alternatively, this could indicate hemispheric specialization or shape versus orientation *discrimination* (Baltaretu et al., 2021b).

It is also noteworthy that here, unlike our previous experiments (Dunkley et al., 2016; Baltaretu et al., 2020), we did not observe SMG modulations in the presence of transsaccadic orientation changes. This might be because medial occipital cortex was sufficient for the feature discrimination task used here, i.e., as noted above it already has the necessary signals to construct both orientation and shape in a discrimination task such as this. Likewise, it may be that SMG activity was engaged more in our previous tasks because object identity was fixed, and participants were only focused on orientation

changes. However, it could also be that SMG activity was statistically masked, either due to divided attention (with shape) or because our feature contrast was designed to negate top-down influences during the pre- and perisaccadic intervals.

Conversely, our design allows us to claim that medial occipital cortex is specifically sensitive to transsaccadic interactions, i.e., between stored presaccadic information and bottom-up sensory influences during the postsaccadic interval. This could still be attention-dependent (i.e., participants were instructed to detect the change), but could produce detectible feature-specific modulations until the actual change occurred.

4.4.3 Transsaccadic networks: task-specificity and lateralization

In our previous study, where participants were required to update grasp orientation across saccades (Baltaretu et al., 2020), they recruited a cortical network that included each element required for the task, including a transsaccadic orientation updater (SMG), saccade signals (FEF), and grasp motor areas (anterior intraparietal and superior parietal cortex). Likewise, in the current study, we identified a network that seems eminently suitable for our feature discrimination task (Fig. 4b): cuneus/lingual gyrus for early feature processing (McKeefry et al., 1997; Fang et al., 2005; Cavina-Pratesi et al., 2010), scene-relevant object processing in intermediate transverse occipital cortex (Bettencourt & Xu, 2013), occipitotemporal cortex for higher order shape recognition (Lerner et al., 2001; Ben-Shachar et al., 2007), and posterior parietal cortex for saccade / reach updating signals (Duhamel et al., 1992; Medendorp et al., 2003; Merriam et al., 2003; Rossit et al., 2013). We did not find FEF in our connectivity analysis here, but given its known projections to parietal and occipital cortex (and tend toward saccade modulation in Figure

2), it may still have contributed. The fact that one study used real 3D stimuli, whereas this one used 2D stimuli can also make a difference (Snow et al., 2011; Freud et al., 2018). Considering 1) the distributed nature of these functional connections and 2) their predominance in right cortex, it stands to reason that brain damage therein and TMS applied to a number of these areas can interrupt transsaccadic processing, and that the right hemisphere appears to be most sensitive to these effects (Sapir et al., 2004; Ten Brink et al., 2019). This has implications for visual health that have not been fully explored.

4.5 Conclusion

Here, we used fMRI to dissociate the transsaccadic mechanisms for two different object features, in a task where participants could only discriminate these features after the saccade. Our current findings support a specific role of medial occipital cortex in transsaccadic feature discrimination, specifically for shape versus orientation changes, and implicate this area in a distributed cortical network for transsaccadic perception. Taken together with the previous literature, these results suggest that the cortical mechanisms for transsaccadic perception are both feature- and task-dependent. Specifically, signals related to location updating have been observed throughout visual and visuomotor systems (Duhamel et al., 1992; Nakamura & Colby, 2000, 2002), but there appears to be localization of updating signals related to object orientation in SMG (Dunkley et al., 2016; Baltaretu et al., 2020, 2021) and transsaccadic integration of object features in medial occipital cortex (here and Baltaretu et al. (2021)). These areas apparently form functional connectivity with saccade centers (presumably providing the

updating signal) and higher order object recognition and/or motor areas, as required for the task. Together, this model provides a putative neuroanatomy for transsaccadic vision.

4.6 Materials and Methods

4.6.1 Participants

In order to determine the appropriate number of participants required to run in this study, we used the effect size from right SMG, which is closest to predicted SMG here, found in the most recent of a series of transsaccadic integration studies (Baltaretu et al., 2020). We then performed a power analysis (G*Power) using this effect size (0.887), with the following parameters: 1) one-tailed t-tests for the difference of matched pair means, 2) a desired power value of 0.90, and 3) an alpha-value of 0.05. On this basis, the suggested number of participants was 13, though we wanted to ensure full desired power, so we analyzed data from 17 participants. The expected power was 0.914.

Twenty-one participants with normal or corrected-to-normal vision from York University, Toronto, Canada took part in this study. One participants' data were excluded, as this person did not complete the experiment, and two participants' data were excluded for decreased (less than 80% behavioural performance) accuracy across all runs, which left 17 participants' data for all further analyses. Participants were compensated monetarily for their time. All participants were right-handed (mean age: 28.7 +/- 5.2, 12 females). All participants provided written consent and did not have any neurological disorders. This experiment was approved by the York University Human Participants Review Subcommittee.

4.6.2 Experimental set-up and stimuli

Participants were first required to pass MRI screening. Upon successful completion of this step, participants were introduced to the task. Once they felt comfortable with the requirements of the task, they were asked to assume a supine position on the MRI table. Their head lay in a 64-channel head coil. A mount on the head coil was used to support an infrared eye-tracker (for the right eye) to ensure appropriate fixation/eye movements, as well as a mirror that reflected the image of the screen from inside the MRI bore. iViewX software (SensoMotoric Instruments) was used to record eye movements for offline verification of correct behavior (see exclusion criteria above). Participants were provided with a button box that was held with the right hand (index and middle fingers positioned over the first and second buttons, respectively). Button-press responses were analyzed offline.

The experiment was conducted under conditions of complete darkness. A fixation cross was used and always present (except during the presentation of the mask) to direct participants' gaze as required by the task. The fixation cross could appear approximately 7° from either the left or right edge of the gray screen (45.1° x 25.1°) along the horizontal meridian. The black stimulus always appeared in the center of the screen and was either a: 1) rectangle, 2) barrel-shaped object, or 3) an hourglass-shaped object. The dimensions of the rectangle were 12° x 6°; the other two objects had the same area as the rectangle.

4.6.3 General paradigm/procedure

4.6.3.1 Experiment

In order to determine the cortical correlates of transsaccadic integration for object orientation versus shape, we used an event-related fMRI design (Fig. 1). Each trial commenced with a fixation of a cross, presented either to the left or right center, for 7.5 s. Then, the central object (rectangle, barrel-shaped, or hourglass-shaped object) appeared for 3 s at +/- 45° from vertical. This was followed by a static noise mask for 0.75 s to avoid an afterimage. The fixation cross would then appear either at the same position as before the mask (*Fixation* condition) or at the other location (*Saccade* condition) for 0.75 s. The same object presented at the other possible orientation (*Orientation change* condition) or one of the remaining two objects presented in the same orientation (*Shape change* condition) appeared in center for 3 s. The object disappeared and the fixation cross was replaced by an instruction ('I or O?') for 3 s, indicating that participants should indicate if the two objects presented in the trial changed in shape (first button, 'I') or in orientation (second button, 'O'). Thus, there were four main conditions: 1) Fixation, Orientation change, 2) Fixation, Shape change, 3) Saccade, Orientation change, or 4) Saccade, Shape change. (There was never an instance of both or neither orientation and shape changing within a trial.) These trial types were randomly intermingled within a run (24 trials); there were eight runs in total. Each run began and ended with central fixation for 18 s (i.e., between trials) to establish baseline measures.

4.6.3.2 Imaging parameters

We used a 3T Siemens Magnetom Prisma Fit magnetic resonance imaging (MRI) scanner. Functional experimental data were acquired with an echo-planar imaging (EPI)

sequence (repetition time [TR]= 1500 ms; echo time [TE]= 30 ms; flip angle [FA]= 78 degrees; field of view [FOV]= 220 mm x 220 mm, matrix size= 110 x 110 with an in-slice resolution of 2 mm x 2 mm; slice thickness= 2 mm, no gap) for each of the eight runs in an ascending, interleaved manner. A total of 312 volumes of functional data (72 slices) was acquired. In addition to the functional scans, a T1-weighted anatomical reference volume was obtained using an MPRAGE sequence (TR= 2300 ms, TE= 2.26 ms; FA= 8 degrees; FOV= 256 mm x 256 mm; matrix size= 256 x 256; voxel size= 1 x 1 x 1 mm^3). 192 slices were acquired per volume of anatomical data.

4.6.4 Analysis

4.6.4.1 Behavioural data

Eye movements and button presses were recorded throughout the experiment; the former were monitored during the experiment and analyzed offline to ensure appropriate fixation and saccade production. If participants made eye movements when not required to, the data associated with those trials were excluded from further analysis. In addition, data for trials where incorrect button presses were made were excluded from any additional analysis. On these bases, 148 trials were removed (out of 3264 trials; 4.5%) for all 17 participants.

4.6.4.2 Functional imaging data

Functional data from each run for each participant were preprocessed (slice time correction: cubic spline, temporal filtering: <2 cycles/run, and 3D motion correction: trilinear/sinc). Raw anatomical data were transformed to a Talairach template (Talairach

& Tournoux, 1988). Functional data were coregistered via gradient-based affine alignment (translation, rotation, scale affine transformation). A last step of preprocessing involved applying smoothing using a FWHM of 8 mm. On the basis of missing predictors (due to modeling by Error predictor, more than 50% of trials with incorrect behavioral response), nine runs across all participants were removed from the overall random effects general linear model (RFX GLM; i.e., 216 trials out of 3116 trials; 6.9%).

A GLM was generated for each participant for every run. The GLM contained 4 predictors: 1) “FixOR”, for an entire trial during which participants maintained fixation throughout that was accompanied by only a change in the orientation of the same object; 2) “FixID”, for a trial during which participants maintained fixation while only the shape of the objects changed; 3) “SaccOR” for a trial during which participants had to make a saccade while only the orientation of the object changed; and 4) “SaccID” for a trial where participants made a saccade while only the shape of the objects changed. The first presentation of the stimulus was referred to as the *Sensory/Encoding* phase and the second presentation period was referred to as the *Change Detection* phase. These GLMs were created in BrainVoyager QX 20.6 (Brain Innovation), where each of the predictors was convolved with a haemodynamic response function (standard two-gamma function model) (Friston et al., 1997). GLMs were additionally adjusted via the addition of a last, confound predictor (“Error”) to account for any errors made during trials due to unwanted eye movements or incorrect button responses.

For these univariate analyses, we applied three sets of contrast to test for three effects. First, we investigated saccade-related effects only by applying a Saccade > Fixation contrast to the data (Fig. 4.2). Second, we applied an Orientation > Shape change

contrast to only the previous saccade-sensitive regions (Fig. 4.3). To each of the resulting volumetric maps, we applied $p < 0.001$, followed by cluster correction (minimum cluster threshold for Saccade > Fixation contrast = 35 voxels; minimum cluster threshold for second Orientation > Shape contrast = 16 voxels; BrainVoyager QX v2.8, Brain Innovation). Regions that are labeled (Figs. 4.2, 4.3) passed both statistical p-value threshold and cluster correction, whereas regions denoted with a triangle passed only p-value correction (i.e., PCSd, Fig. 4.2).

4.6.4.3 Psychophysiological interaction

Our last goal was to uncover the functional network for saccade-related updating during transsaccadic perception. In order to do this, we conducted psychophysiological interaction (PPI) analysis (Friston et al., 1997; McLaren et al., 2012; O'Reilly et al., 2012; Baltaretu et al., 2020) on data extracted from the key medial occipital region, i.e., left cuneus (radius = 4 mm; Talairach coordinates: -10, -85, 3). To perform this analysis, we used three predictors: 1) a physiological component (which is accounted for by z-normalized time courses obtained from the seed region for each participant for each run); 2) a psychological component (task predictors, i.e. for the Saccade and Fixation conditions, were convolved with a hemodynamic response function), and 3) a psychophysiological interaction component (multiplication of seed region z-normalized time courses with task model in a volume-by-volume manner). For the psychological component, the *Saccade* predictors were set to a value of '+1', whereas the Fixation predictors were set to a value of '-1'; all other predictors were set to a value of '0' in order to determine the responses to Saccades as compared to Fixation. (For greater

detail, please see O'Reilly et al. (2012) and Baltaretu et al. (2020).) We created single design matrices for each run for each of the 17 participants, which were ultimately included in an RFX GLM. Then, we used the third, psychophysiological interaction predictor to determine the regions that comprise the functional network that show saccade-related modulations for feature updating. To the resulting volumetric map, we applied a $p < 0.001$, followed by cluster threshold correction. Regions that are labeled (Fig. 4.4) passed both p-value and cluster correction criteria.

Table 4.1 Regions and Talairach coordinates for saccade-sensitive parietal and occipital regions-of-interest.

Region	**Talairach coordinates**						**Active Voxels**	**References**
	x	y	z	Std x	Std y	Std z		
<u>Parietal Areas</u>								
LH dorsal Precuneus	-6	-57	41	2.3	2.3	2.2	526	Fletcher et al., 1995
RH Superior Parietal Lobule	2	-61	57	2.2	2.3	2.2	525	Lambert et al., 2002
<u>Occipital Areas</u>								
LH Cuneus	-12	-70	9	2.2	2.2	2.2	522	Lambert et al., 2002
LH Lingual Gyrus	-6	-62	-2	2.3	2.3	2.3	552	Decety et al., 1994
RH Lingual Gyrus	12	-45	-2	2.3	2.2	2.2	526	Decety et al., 1994

Table 4.2 Functional connectivity network regions and Talairach coordinates resulting from psychophysiological interaction (PPI) analysis with left cuneus as the seed region.

Region	**Talairach coordinates**						**Active Voxels**	**References**
	x	y	z	Std x	Std y	Std z		
<u>Parietal Areas</u>								
RH Superior Parieto-occipital Cortex	12	-82	40	2.2	1.9	2.5	287	Rossit et al., 2013
<u>Occipital Areas</u>								
RH Transverse Occipital Sulcus	20	-80	23	2.1	2.7	2.5	540	Bettencourt & Xu, 2013
RH Superior Occipital Gyrus	19	-92	19	2.4	2.0	2.6	454	Salmon et al., 1996
RH Lingual Gyrus	13	-70	-5	2.8	2.7	2.8	898	Decety et al., 1994
<u>Occipitotemporal Areas</u>								
RH Medial Occipito-temporal Sulcus	20	-53	-11	2.7	2.5	2.2	616	Podrebarac et al., 2014

CHAPTER 5

GENERAL DISCUSSION

5.1 Overview

This chapter will start off by summarizing the results of the experiments contained herein and the implications they have, as they relate to the updating of different object features across saccades, within the larger context of the field of transsaccadic perception. This will be followed by an assessment of the questions that remain unanswered, a discussion of the possible, related applications and future directions of the field.

5.2 Advancing the field of transsaccadic perception

Assessments of the type of information that can be retained across saccades have focused on four main topics: 1) bottom-up feature processing, 2) visual working memory, 3) top-down influences, and 4) underlying mechanisms. To date, attempts to determine (single) object feature processing across saccades in a bottom-up manner have demonstrated that orientation (Melcher, 2007; Dunkley et al., 2016; Fornaciai et al., 2018; Stewart & Schütz, 2018a,b; Baltaretu et al., 2020), spatial frequency (Fabius et al., 2020), contrast (Prime et al., 2006), colour (Wittenberg et al., 2008; Stewart & Schütz, 2018b), motion (Melcher & Morrone, 2003; Fracasso et al., 2010; Fabius et al., 2016), and form (Melcher, 2005; Demeyer et al., 2010; Paeye et al., 2017) can be retained and updated. This has also been extended to more complex stimuli like faces (Wolfe & Whitney, 2015). In terms of visual working memory, approximately three-to-four object features can be retained (Prime, Tsotsos, Keith et al., 2007; Prime, Vesia, & Crawford, 2008, 2010; Tanaka et al., 2014). Whether an object (feature) is updated across saccades can also be influenced by top-down signals related to salience (Gottlieb et al., 1998) for example. Attention for relevant objects has been demonstrated for a future saccade endpoint (Rolfs

et al., 2011), an idea that has recently pointed to the importance of task locations (Arkesteijn et al., 2019; for further exploration of endogenously or exogenously driven attentional effects on vision, see review by Failing & Theeuwes, 2018; Dugué et al., 2020). Although the agreed-upon mechanism that underlies transsaccadic perception as it relates to visual stability remains to be determined (Vuong et al., 2019; see Melcher & Colby, 2008), there is growing evidence for remapping as a major component (e.g., Duhamel, Colby, & Goldberg, 1992; Umeno & Goldberg, 1997; Nakamura & Colby, 2000, 2002; Melcher, 2007; Merriam et al., 2007; Cavanagh et al., 2010; Mathôt & Theeuwes, 2010; He et al., 2018; for review, see Klier & Angelaki, 2008; Higgins & Rayner, 2015; although, see Fabius et al., 2020).

The neural correlates of remapping have been found in several regions across the cortex; though, neurophysiological investigations have focused on one region at a time. In particular, remapping has been observed in occipital cortex, extending from early visual processing regions (V1) to more intermediate occipital regions (V2, V3, V3A, V4) in a gradient effect (where early processing V1 neurons show a more modest effect than higher-order areas like V4; Nakamura & Colby, 2000, 2002; Merriam et al., 2007). Remapping has also been shown for shape and object location in parietal LIP (Duhamel, Colby, & Goldberg, 1992; Subramanian & Colby, 2014) and more frontally, in FEF (Umeno & Goldberg, 1997). However, there has been little exploration of a more whole-brain level of the cortical regions that are involved in updating object location / features across saccades (Medendorp et al., 2003; Dunkley et al., 2016).

The first study here was conducted to determine if the cortical regions engaged in the transsaccadic updating of object orientation (Dunkley et al., 2016) would also be active when this process was extended to a different modality (i.e., motor – grasping). The results indicate that parietal cortex is more extensively involved in updating saccade signals for object orientation changes for grasping (Baltaretu et al., 2020). In contrast to activation in a single parietal region (SMG) for changes in a 2D oriented stimulus, traditional grasp-related regions (Culham et al., 2003; Filimon et al., 2009; Filimon, 2010) were recruited in addition to SMG. These findings highlight two points: 1) for object orientation changes, transsaccadic perception is consistent in its recruitment of the inferior parietal SMG region, suggesting it may be a transsaccadic region that responds in a feature-specific and task-irrelevant manner and 2) parietal cortex might serve a more general role in transsaccadic perception, showing recruitment of additional task-relevant regions (i.e., regions involved in processing saccade-related signals in reach / grasp areas). Additional functional connectivity analysis showed a tight network of communication between right SMG and reach / grasp parietal and saccade-related frontal regions. These findings strengthen our understanding of the visuospatial role of parietal cortex (e.g., SMG in response to changes in object orientation across saccades), show how cortex is engaged for an additional modality, and establish the feature-related functional network.

In the second experiment, the cortical correlates for spatial frequency changes across saccades were investigated in order to further determine if a different object feature would engage similar inferior parietal regions, and parietal cortex more generally. Saccades were found to engage an extensive swath of cortex, as compared with a separate

saccade-only control task (Fig. 3.3), where the experimental task engaged particular extrastriate occipital, superior parietal, and likely saccade frontal regions in contrast to predominantly medial occipital and frontal areas. Of the saccade-related cortical recruitment in the experimental task, further tests showed additional feature sensitivity in one area in medial occipital cortex (i.e., right cuneus) (Fig. 3.6) with trends in additional occipital regions (i.e., left cuneus and lingual gyrus) and frontal dorsal precentral sulcus (likely FEF). Compared with the cortical recruitment for object orientation of either 2D or 3D objects (Snow et al., 2011; Dunkley et al., 2016; Baltaretu et al., 2020), saccade-specific feature effects were found in an extrastriate occipital region with task (saccade) sensitive recruitment in parietal cortex. This indirect comparison points to the idea of feature-sensitive transsaccadic mechanisms, instead of a singular feature-independent mechanism.

In order to provide a more direct test for transsaccadic perception of object features, I compared orientation and shape change across saccades in the third study. Out of the occipital and parietal regions that showed saccade sensitivity, left posteromedial occipital cortex (located in cuneus) showed additional feature effects. One feature / limitation of this study is that the study was based on traditional fMRIa paradigms, though there were no additional conditions where a feature was repeated (e.g., in a Saccade trial, the same object could have been presented at the same initial orientation). This would have allowed adaptation-like subtractions to determine the effects of one feature at a time, despite having to pay attention to two features simultaneously. Given the absence of these conditions, it is difficult to make strong conclusions about which of the features (shape or orientation) is driving feature modulation effects in extrastriate cortex. Depending on

whether the feature effects in the third study were driven by suppression for orientation changes or enhancement for shape changes, it may suggest that one of the higher-level object properties that spatial frequency communicates is related to object identity (Bar, 2004; Bar et al., 2006) and that this portion of occipital cortex is sensitive to low- and high-levels of information. Further, functional connectivity analysis showed a network between left cuneus and early visual occipital, object-sensitive occipitotemporal, and oculomotor / sensorimotor parietal regions. In contrast to the first study, wherein only one feature was tested, the functional network in the final study showed a more extensive network, possibly responding to the additional cognitive load of the task.

It is important to acknowledge that, as alluded to in this section, although these three studies have in common the shared goal of identifying the cortical correlates for transsaccadic perception, they differ in two major ways: 1) stimulus complexity and 2) task / cognitive effort. In terms of stimulus complexity, the 2D sine-wave grating in Experiment 2 would be considered the least complex in terms of perception, followed by the 2D shapes (rectangle, barrel, and hourglass) of Experiment 3, and finally, the 3D rotatable and graspable oblong object of Experiment 1. In theory, visual cortex processes the sine-wave grating frequencies (Schiller et al., 1976b; Tootell et al., 1988) in Experiment 2 which would then be combined with top-down (corticocortical and/or corticosubcortical) mediated signals (Tong, 2003; Saalmann et al., 2007; Gilbert et al., 2013; Nurminen et al., 2018), in addition to the remapping signals that account for saccade production (Nakamura & Colby, 2002; Merriam et al., 2007). Given the role of ventral regions in the processing of objects, in particular the lateral occipitotemporal complex (LOC; this comprises a caudal-dorsal portion, LO, and an anterior-ventral region

within posterior fusiform, PF/LOa; Grill-Spector, Kushnir, Edelamn, et al., 1999), one might have expected this component of the ventral stream to be involved in the third experiment here (Valyear et al., 2006). LO would be a viable candidate, given its preference for objects (Grill-Spector, Kushnir, Edelman, et al., 1999); however, the results did not indicate activation within this region (Fig. 4.3). This suggests that transsaccadic perception requirements may extend beyond those for specialized object recognition (Grill-Spector, Kushnir, Edelman, et al., 1999; Grill-Spector, Kourtzi, & Kanwisher, 2001); though, these regions may still be involved (perhaps, at earlier processing stages), given the communication observed between extrastriate cuneus and ventral, object-centric regions in occipital and occipitotemporal cortex (Fig. 4.4; Konkle & Oliva, 2012). Curiously, extrastriate cortex was involved in transsaccadic effects in Experiments 2 and 3, despite increased stimulus complexity (sine-wave grating versus three differently shaped objects) and number of features probed (spatial frequency vsersus shape / orientation, respectively). When object orientation was probed, on the other hand, a new set of regions was involved, including SMG (Dunkley et al., 2016). Early orientation processing occurs in striate (Schiller et al., 1976a; Blasdel & Fitzpatrick, 1984) and extrastriate (Vanduffel et al., 2002) cortex, so it would be conceivable that these same regions might also be involved not just in processing spatial frequency and shape information across saccades, but also orientation. One may ascribe these differences to the three-dimensional nature of the stimulus in Experiment 1; however, orientation was also probed by Dunkley et al. (2016) using a sine-wave grating whose orientation was probed and also found that parietal cortex (specifically, SMG) is involved in transsaccadic feature interactions for this feature. Thus, stimulus complexity may not be sufficient to

explain the differences observed in the subsets of cortex for the transsaccadic tasks used here, wherein different features were tested.

The difference in stimulus complexity was also intertwined with different levels of cognitive effort across the three tasks. In Experiment 2, participants were responsible for making judgments about the change in spatial frequency of the stimulus (which was indicated via button press). Experiments 1 and 3 were more similar, in terms of cognitive effort, which was greater than for Experiment 2. Similar to Experiment 2, the first experiment required that object orientation be remembered; however, this information then had to be additionally transformed into the appropriate coordinate system for motor planning and accurate execution (Lacquaniti & Caminiti, 1998; Batista et al., 1999; Crawford et al., 2004; Olivier et al., 2007). Although Experiment 3 probed transsaccadic perception using 2D objects, participants were required to remember not just a single feature each trial, but a conjunction of object shape and orientation (Luck & Vogel, 1997). Capacity for multiple object features has been shown for three to four items (Prime, Tsotsos, Keith, et al., 2007; Prime, Vesia, & Crawford, 2008, 2010, 2011); though, remembering both features required a greater cognitive demand than for a single feature. Despite greater cognitive effort for Experiments 1 and 3 where orientation versus shape / orientation were tested, respectively, cortical recruitment was similar between (the cognitively easier) second and third experiments (though, this difference might be reflected in the laterality of the results; Tomasi et al., 2007; Bartolomeo & Malkinson, 2019; Figs. 3.6 and 4.3). Although the cognitive component of the three experiments may not explain the differences in cortical recruitment for the features tested here, the interaction effort associated with the stimulus type is a related component to consider. Due to the two-

dimensional nature of the stimuli in Experiments 2 and 3 versus the 3D stimuli used in Experiment 1, the effort associated with perception / action could have resulted in different cortical activation. Cortex has been shown to process object images differently than real objects (Snow et al., 2011). Not only is this difference present for passive viewing, but also for real actions to real versus imagined objects (Króliczak et al., 2007; Freud et al., 2018). At first glance, the results from the three studies here would support this idea. Extrastriate cortex was associated with processing of both the sine-wave grating (Expt. 1) and the 2D objects (Expt. 2), whereas different, parietal regions were recruited for the processing of a 3D object (Expt. 3). (One related caveat is that, although Experiment 1 involved a real action (grasping) toward a real object, Experiments 2 and 3 required participants to make judgments about stimulus changes within a trial via button press. However, button presses were used to ensure that participants were paying attention to the task, they served as a measure of behavioural performance, and have been associated with different cortical regions than the ones observed here (Windischberger et al., 2003). Also, they occurred after the processing of the second stimulus presentation and were not as related for the task, as is the case for processing of object features for grasping (Taira et al., 1990; Ganel & Goodale, 2003).) However, evidence for parietal (i.e., SMG) recruitment in a transsaccadic task where a 2D stimulus, similar to the one used in Experiment 2, whose orientation was changed (Dunkley et al., 2016) argues against the idea that the results strictly reflect the 2D / 3D distinction of the stimuli.

Based upon the initial findings of Dunkley et al. (2016), I hypothesized that transsaccadic perception may involve a single mechanism for multiple object features, with particular emphasis on the role of parietal cortex. Given this hypothesis, similar cortical regions

should have been active across all three experiments discussed here. However, different cortical regions recruited for when spatial frequency and shape were modulated (i.e., extrastriate cortex) versus object orientation (i.e., parietal cortex). Thus, I must fail to reject the alternative hypothesis – that transsaccadic perception does not rely upon a singular, special cortical mechanism. The results from the three studies point to the underlying nature of the object feature as the factor that separates transsaccadic mechanisms: largely qualitative object features (i.e., object identity, perhaps communicated through a low-level object feature, such as spatial frequency, or through more complex features, such as object shape) seem to engage visual regions (that can tap into more ventral / object-related regions; Fig. 4.4), whereas more quantitative features (e.g., orientation) engage dorsal, parietal regions (regardless of whether the stimulus is low-level (Dunkley et al., 2016) or 3D (Baltaretu et al., 2020), or whether motor output will occur; Króliczak et al., 2007). This distinction may be contributed to by the 'separation' of the two visual streams (Ungerleider & Mishkin, 1982; Goodale & Milner, 1992; although Goodale & Westwood, 2004), which serve different perception / action purposes. The functional networks that were determined in Experiments 1 and 3 also reflect this idea. When intrinsic object properties, such as shape, were tested, extrastriate cortex was shown to communicate with largely visual and object-related cortical regions (Fig. 4.4). For (3D) object orientation changes, SMG was shown to communicate with other sensorimotor parietal and putative frontal saccade-related regions (Fig. 2.5). Ultimately, the mediation of which transsaccadic mechanisms will be tapped into may be governed / assisted by the saccade system – communication between frontal eye regions (e.g., FEF) with medial occipital cortex can help with assessments about object identity,

whereas interactions with inferior parietal cortex can assist with judgments about object orientation. Previous investigations into bottom-up versus top-down processing in areas, including FEF and LIP (PEF), suggest that LIP shows a rapid bottom-up response for targets (and their location), whereas frontal cortex takes on top-down attentional control role for target selection (Buschman & Miller, 2007). These top-down signals, after selecting the particular target, could be passed along to ventral, visual regions to communicate particular features, such as shape (Hamker, 2003; McCarthy, Kohler, Tse, et al., 2015). Hamker (2003) suggests that FEF neurons associated with saccade production could communicate with extrastriate (V4) and inferior temporal cortex to further refine object perception. Overall, these findings suggest that transsaccadic perception may: 1) involve not just a single mechanism, 2) show feature dependence, 3) reflect qualitative versus quantitative object properties, 4) recruit additional, specialized modality-related cortex, and 5) engage existing and supporting functional networks. The control over the engagement of particular transsaccadic mechanisms may depend on the saccade system, with communication to medial occipital cortex assisting object identification versus interactions with inferior parietal cortex aiding in judgements about object orientation.

5. 3 Outstanding questions

One of the first conclusions to draw from the comparison of the largely perceptual orientation study (Dunkley et al., 2016) and the first experiment here (Baltaretu et al., 2020) is that there seem to be task- / modality- dependent cortical modulations. What is

the relationship like between vision and other modalities, such as audition and touch? For example, it is likely that a link exists between two senses that are associated with spatial encoding, such as vision and audition (O'Leary & Rhodes, 1984; Rolfs et al., 2005; Sosa et al., 2010; Godfroy-Cooper et al., 2015; Daemi et al., 2016; for review, see Bulkin & Groh, 2006). Arguably, one might expect to observe regions that show eye- and head-centered encoding, such as within intraparietal cortex, given evidence of activation from visually responsive neurons that was correlated with that of auditorily responsive neurons (Mullette-Gillman et al., 2005; Mohl et al., 2019). In addition to the mapping feature is the aspect of timing in crossmodal relationships. For example, both vision and haptic exploration are associated with an intermingling of exploration (saccades for vision, haptically for touch) and fixation (Grunwald et al., 2014). Would the temporal dynamics of the production of saccades enhance or impair the ability to recognize or interact with an object (Göttker et al., 2020)? What are the behavioural and cortical consequences of the difference in timescales for visual versus haptic perception (James et al., 2007)? Although haptic exploration has largely been associated with activation in somatosensory cortex (e.g., Bonda et al., 1996; Reed et al., 2004; for review, see James et al., 2007), further investigations are needed to provide a comprehensive understanding of the influence of vision (i.e., saccade production) on haptic object perception (Klatzky et al., 1993; Norman et al., 2004; Gepshtein et al., 2005; Reuschel et al., 2010) at the cortical level.

Although I tested the cortical correlates for transsaccadic perception of orientation, spatial frequency, and then compared orientation with shape, this is not a complete survey of the cortical mechanisms for transsaccadic perception. Given the results for the three experiments, I would expect to observe different transsaccadic cortical mechanisms for

other features, such as colour and motion. Bottom-up colour processing has been shown in visual area V4 (Zeki, 1973; Lueck et al., 1989; Bartels & Zeki, 2000), an area that has also been associated with remapping properties (Merriam et al., 2007). Psychophysical studies show that colour can be updated across saccades (Wittenberg et al., 2008; Tas et al., 2021). Thus, it is plausible that transsaccadic mechanisms for an object feature such as colour may also engage extrastriate cortex (i.e., V4) and perhaps, more ventral object-centric regions (Grill-Spector, Kushnir, Edelman, et al., 1999; Grill-Spector, Kourtzi, & Kanwisher, 2001) in a functional network. Similarly, motion is another feature that was shown to be updated across changes in eye position (Melcher & Morrone, 2003; Fracasso et al., 2010; Fabius et al., 2016). Although motion processing occurs in the middle temporal (MT; V5) (Maunsell & Van Essen, 1983; Van Essen & Maunsell, 1983) area, evidence from recent neurophysiological recordings by Yao et al. (2016) points to remapping abilities in MT. Spatial encoding of these features would be expected to also recruit posterior parietal regions, especially if there is interaction with an object in order to explore multiple object features (Grefkes et al., 2002; Gardner, Babu, Ghosh et al., 2007; Gardner, Babu, Reitzen, et al., 2007; Schaffelhofer et al., 2015; Marangon et al., 2016). On the other hand, ventral regions may also be more engaged for object recognition perception (Grill-Spector & Malach, 2001; Lerner et al., 2001; Grill-Spector, 2003; Freud & Behrmann, 2020; for review, see Goddard, 2017) for various objects or tools (Valyear & Culham, 2006).

Despite being an important instrument for the exploration of cortical processes for transsaccadic perception, one limitation of neuroimaging studies is the reduced temporal resolution. Determining the evolution of cortical recruitment in time across eye

movements would assist in clarifying our understanding of the underlying processes that lead to transsaccadic perception, such as remapping (Klier & Angelaki, 2008; Higgins & Rayner, 2015). Electroencephalography (EEG) recordings (and further decoding) during a transsaccadic task with spatial frequency as the stimulus in question were able to provide a closer look at the temporal dynamics of updating feature information across saccades (Fabius et al., 2020). In particular, their results point to the idea that remapping may not be the underlying process, as presaccadic feature information lingered postsaccadically for approximately 200 ms. Additional EEG and concurrent EEG-fMRI studies are critical for our appreciation of the dynamic nature of transsaccadic perception.

These are just a few of the remaining aspects of transsaccadic perception left to consider. Gaining additional knowledge about the modality-specific and feature-sensitive nature of transsaccadic perception, how cortical processes progress through time, as well as developing a testable computational model (Mohsenzadeh et al., 2016) will be of considerable importance when applying this to potential industry enterprises for example.

5.4 Applications and future directions

Several directions remain in the pursuit of gaining a complete understanding of transsaccadic perception. By expanding our knowledge about how the brain is able to process these individual object features for transsaccadic perception, it would begin to address the first potential question: where does the parsing of transsaccadic cortical mechanisms end? Are these mechanisms completely sensitive to particular object features (as the findings in this dissertation would suggest)? In other words, is there a

cortical network for each unique object feature? When comparing among these features, could analysis of the cortical mechanisms show feature hierarchy? Relationships to saliency / attention would also have to be explored (e.g., Itti & Koch, 2000, 2001). The activation of one transsaccadic feature mechanism at the cortical level may show signs of context-dependence (Dyckman et al., 2007) or sensitivity to other underlying object properties, such as identity (Drissi-Daoudi et al., 2020). Having this knowledge would also help in building a computational model in order to explain how transsaccadic perception for features occurs (Mohsenzadeh et al., 2016). This would provide a first step in creating testable hypotheses about how single features or multiple feature combinations are updated across saccades. These models may also help to shift the debate about the overarching components of transsaccadic perception as a 'single' mechanism (see Melcher & Colby, 2008). For example, determining the temporal evolution of cortical engagement in transsaccadic tasks (Fabius et al., 2020) may sway perspectives on will possible contributing processes, such as remapping.

Identifying these single- and multiple-feature transsaccadic mechanisms will help to establish a fundamental understanding of vision in healthy individuals. Although the explicit investigations related to transsaccadic interactions for single features, such as colour or motion, have not yet been tested at the whole-brain level, having this knowledge would also help to understand how these systems may be affected in particular clinical populations. Colour, for example, was shown to be a source of confidence when tasked with distinguishing objects with a similar shape in a patient with visual agnosia (impaired object perception) (Mapelli & Behrmann, 1997). Object motion has been used to probe updating of object location abilities across saccades in healthy adults (Dessing et al.,

2011), and as a way of creating a diagnostic tool to assess altered perception in older adults (de Dieuleveult et al., 2019). Thus, knowledge about the related cortical mechanisms may help to create treatment programmes for clinical populations, using established and non-invasive tools like TMS in stroke patients for example (Rafique & Steeves, 2020).

Knowledge about the transsaccadic cortical mechanisms for single or multiple features may help with the creation of clinical diagnostic tools and potential industry applications. Clinicians might be faced with identifying the presence and / or extent of visuomotor impairment (Heitger et al., 2004) in an athlete. This may be accomplished by comparing the cortical activation in potentially concussed athletes with that of healthy individuals for instance. Clinicians might also combine neuroimaging assessments with computer-based visuomotor tasks (Hurtubise et al., 2016) in the hopes of acquiring a complete evaluation of impairment that will ultimately guide their recommendation for continued play. Knowing how and which oculomotor regions and additional functional networks may be engaged can assist clinicians in assessing the full extent of cortical damage, as well as potential alternative cortical mechanisms or strategies to utilize in creating treatment plans. For clinical populations that have irreparable damage, clinicians and industry partners may team up to create devices that can restore or enhance diminishing sensory information. A possible application of this information is the production of neuroprosthetic devices, which make use of stimulation of particular regions of visual cortex to aid in ‘seeing’ shapes and motion for example (Chen et al., 2020). Prosthetic device optimization could be achieved by incorporating saccade-related signals through feedback from regions involved in spatial and feature updating, so as to further refine the signal-to-output

process (Patil & Turner, 2008). These regions and their relationship to regions associated with other modalities may also provide (additional) input sources for signal tuning in prosthetic devices for improved audition in people with diminished hearing for example (for review, see Leuthardt et al., 2006; Mullette-Gillman et al., 2005; Mohl et al., 2019). In all of these and related scenarios, it is important to acknowledge that eye movements, like saccades, are likely to impact the efficacy of diagnostic tools and proposed treatments. Thus, our pursuit to identify and understand the underlying cortical mechanisms for transsaccadic perception of object features will help to 1) establish the mechanism(s) involved in healthy individuals, 2) create testable computational models, 3) contribute to the discussion on visual stability, and 4) develop diagnostic tools and refine prosthetic devices for clinical populations.

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APPENDIX I: AUTHOR CONTRIBUTIONS

The doctoral candidate (Bianca-Ruxandra Baltaretu) was involved in experimental design (except for Experiment 2), data acquisition, data analysis, and writing of the manuscripts.

Gaelle N. Luabeya and Jena Velji-Ibrahim were involved in data acquisition and preprocessing for Experiment 1.

Drs. Simona Monaco and Ying Chen were involved in experimental design and manuscript editing for Experiment 1.

Drs. Benjamin T. Dunkley was involved in experimental design and manuscript editing for Experiment 2.

Dr. W. Dale Stevens was involved in experimental design, data analysis, and manuscript editing for Experiments 2 and 3. Dr. Erez Freud was involved in data analysis and manuscript editing for Experiment 3.

APPENDIX II: SUPPLEMENTARY FIGURES

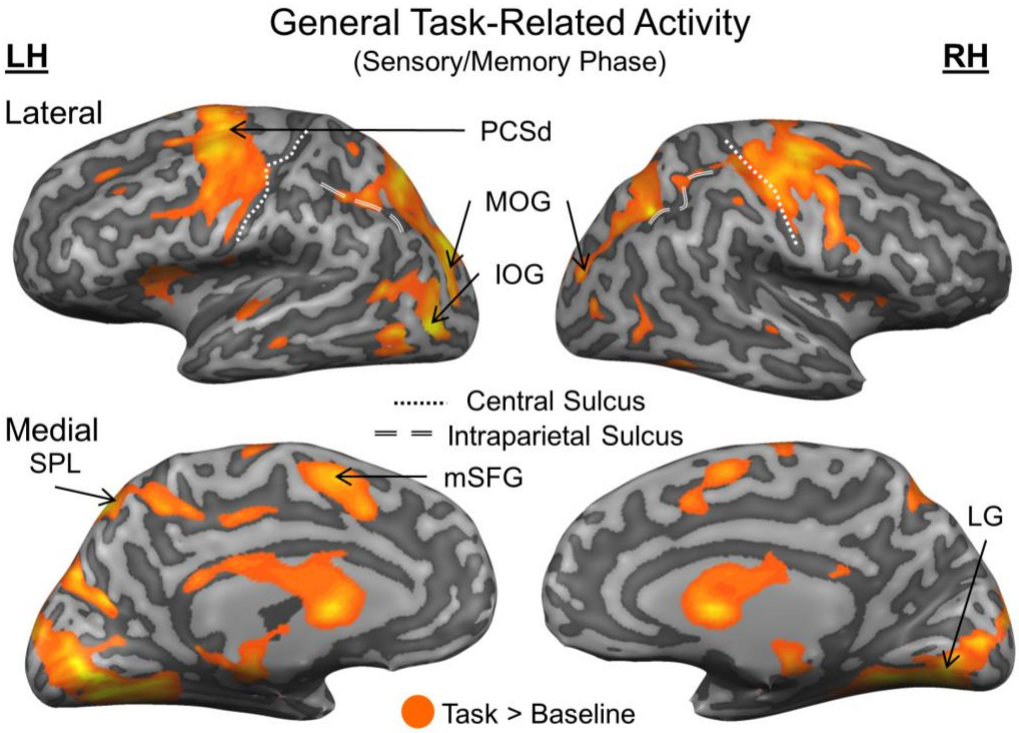

Fig. S1. General task-related activity derived from the *Sensory/Memory* phase. On the inflated brain renderings of an example participant (lateral views shown in the top panels, medial views shown in the bottom panels) in the left and right hemispheres (shown on the left and right, LH, RH, respectively) is overlaid activity (n=15) for the first stimulus presentation (contrast: Task > Baseline) (BrainVoyager QX v2.8; www.brainvoyager.com). As anticipated, early visual (inferior occipital gyrus, middle occipital gyrus, and lingual gyrus), spatial-encoding parietal (superior parietal lobule), and eye-movement frontal (dorsal precentral sulcus (likely frontal eye field) and superior frontal gyrus (likely pre-/supplementary eye field)) showed activation in response to the initial stimulus presentation. *Abbreviations*: IOG, inferior occipital gyrus; MOG, middle occipital gyrus; LG, lingual gyrus; SPL, superior parietal lobe; PCSd, dorsal precentral sulcus; mSFG, medial superior frontal gyrus.

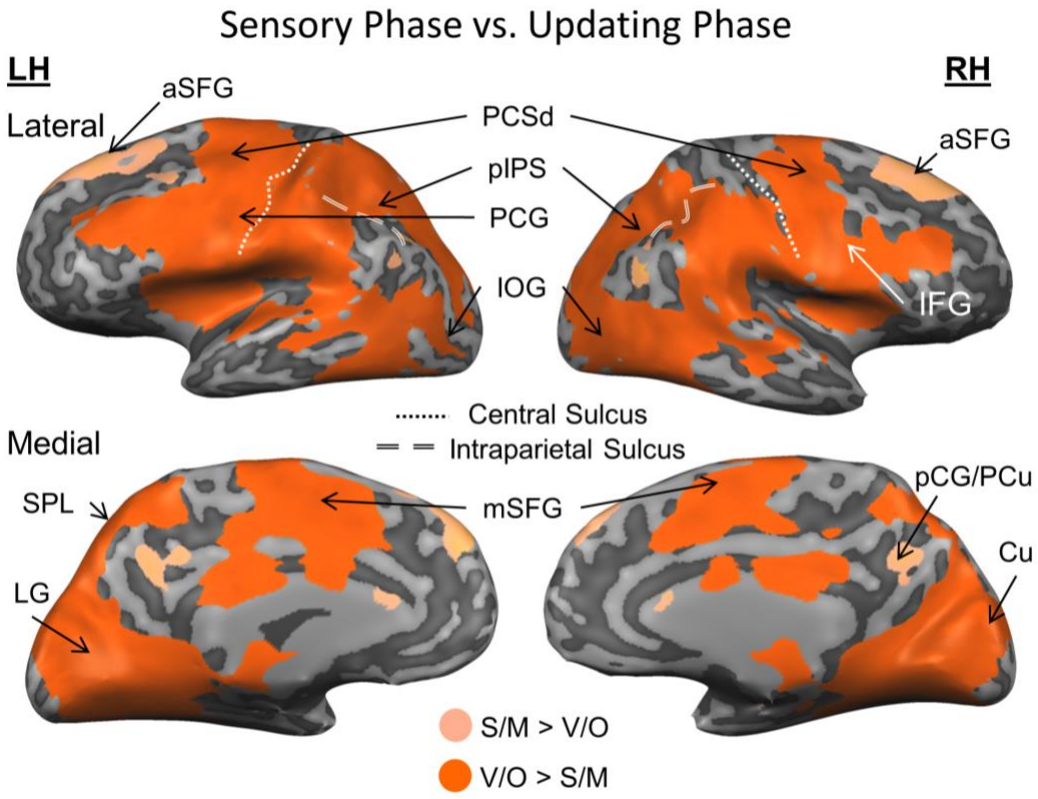

Fig. S2. Phase-specific cortical activation differences for the *Sensory/Memory* and *Visual/Oculomotor Updating* phases. On the inflated brain rendering of an example participant (left panels represent left hemisphere, right panels represent right hemisphere; upper panels show lateral views, lower panels show medial views) are the voxelwise statistical maps of the Sensory/Memory (S/M) > Visual/Oculomotor Updating (V/O) contrast (BrainVoyager QX v2.8; www.brainvoyager.com). Regions that show greater sensitivity during the *Sensory/Memory* phase over the *Visual/Oculomotor Updating* phase are shown in light peach; this activation is observed in medial parieto-limbic cortex (PCu/pCG) and in anterior frontal regions (aSFG). In contrast, regions in burnt orange show greater sensitivity for the change occurring in the *Visual/Oculomotor Updating* phase than in the *Sensory/Motor* phase. This activation spans occipital, parietal, and saccade-related frontal cortex. This suggests a difference in cortical activation across the two stimulus presentation phases. *Abbreviations*: LG, lingual gyrus; Cu: cuneus; IOG, inferior occipital gyrus; PCu/pCG, precuneus/posterior cingulate gyrus; pIPS, posterior intraparietal sulcus; SPL, superior parietal lobule; PCG, precentral gyrus; PCSd, dorsal precentral sulcus; mSFG, medial superior frontal gyrus; aSFG, anterior superior frontal gyrus.