Title: Medial occipital cortex participates in a cortical network for transsaccadic feature discrimination: an fMRI paradigm

Abbreviated Title: Dissociating feature-dependent transsaccadic mechanisms

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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.

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; 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). Overall, these studies suggest that a distributed occipital-parietal-frontal network participates in transsaccadic updating of object features.

It has proven more difficult to pinpoint the cortical locations that contribute to transsaccadic feature interactions in human neuroimaging 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., 2021; for temporal considerations, see Fabius et al., 2020). It was speculated that the difference between these last two results (Baltaretu et al., 2020; Baltaretu et al., 2021) 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., 2021). 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.

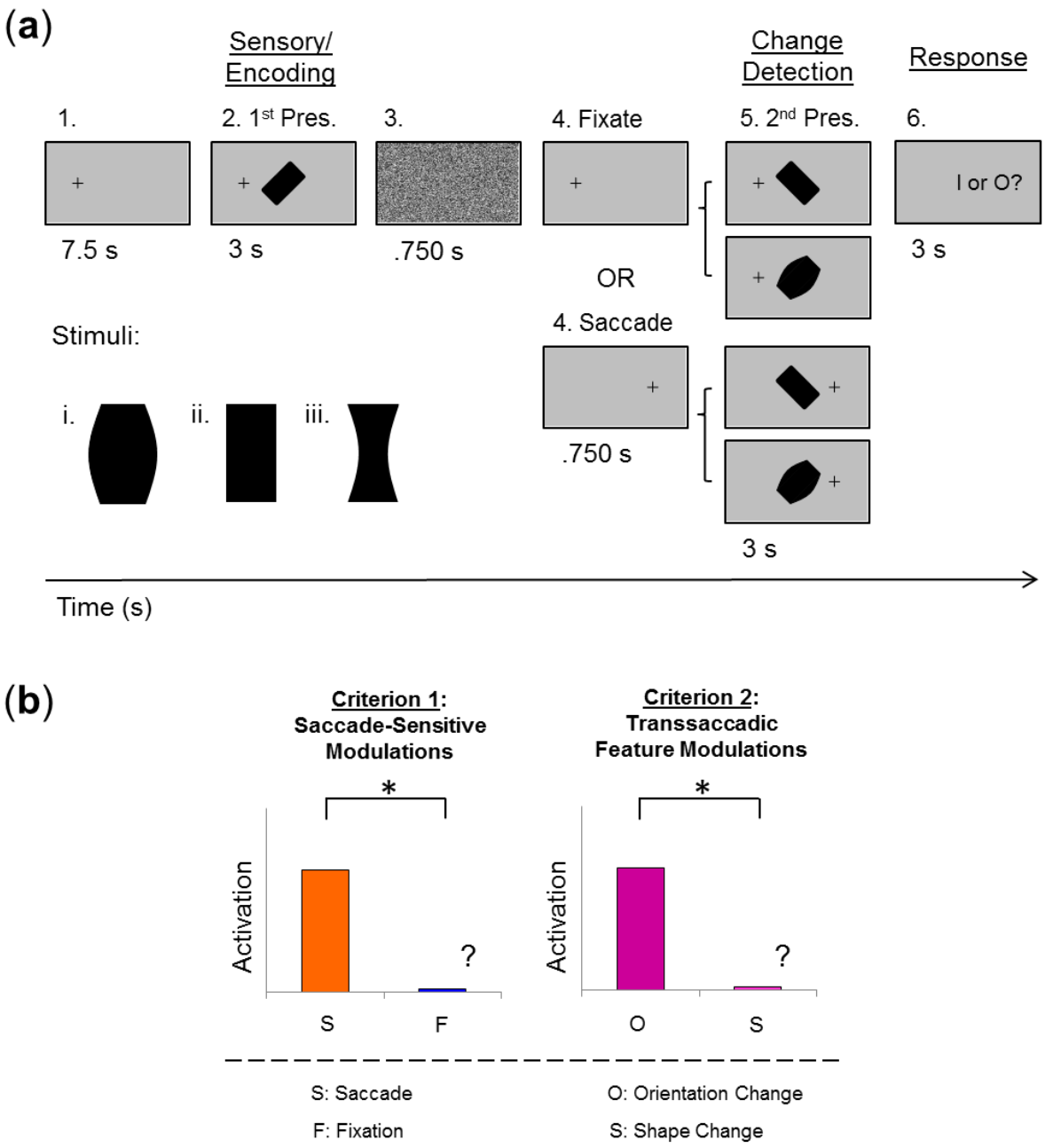

Figure 1. Experimental paradigm and criteria for transsaccadic feature modulation. **(a)** An example trial is presented (initial left fixation, rectangle, 45º) with the four possible main conditions: 1) Fixation, Different Orientation, 2) Fixation, Different Shape, 3) Saccade, Different Orientation, 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.

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, criterion1), 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.

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. 1b, criterion 1). Significant saccade sensitivity ($p < 0.001$) was found in left parietal and bilateral occipital cortex, predominantly in the medial aspects (Fig. 2). A large swath of bilateral occipital activation

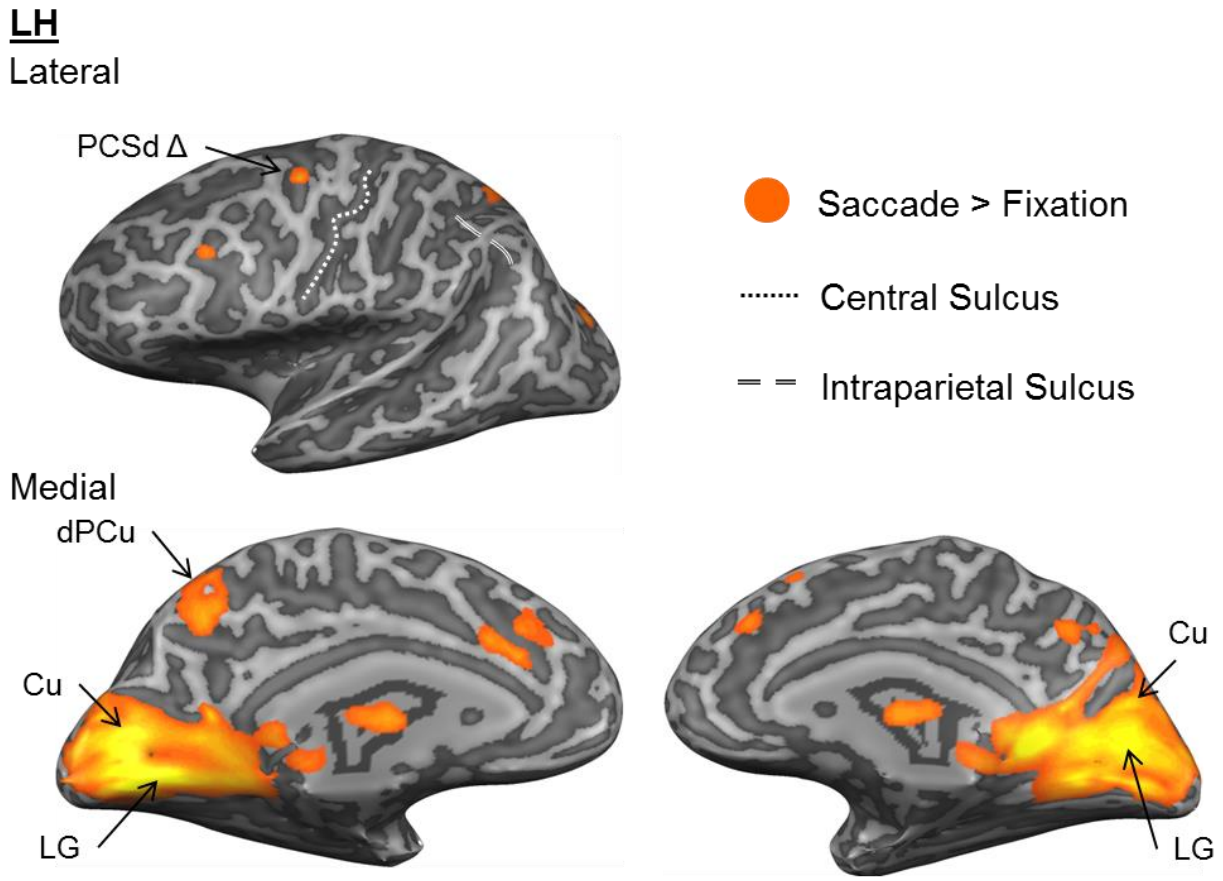

Figure 2. Saccade-sensitive effects. A voxelwise map from an RFX GLM (n=17; $p < 0.001$; cluster threshold correction; orange) is presented on an inflated brain rendering of an example participant. The upper left panel shows a lateral view of the left hemisphere, with activation in dorsal precentral 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).

Region	Talairach coordinates						Active Voxels	References
	x	y	z	Std x	Std y	Std z		
Parietal Areas								
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
Occipital Areas								
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 1. Regions and Talairach coordinates for saccade-sensitive parietal and occipital regions-of-interest.

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. 2; Table 1).

Cortical modulations for transsaccadic perception of object orientation versus shape.

In order to test our second criterion (Fig. 1b, criterion 2), we performed an Orientation > Shape change contrast, only within the voxels activated in the first saccade contrast (Fig. 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 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 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 1). In short, because this region of feature-selective activity was identified within the areas that showed significant saccade modulations (Fig. 2), it satisfied both of our criteria (Fig. 1b).

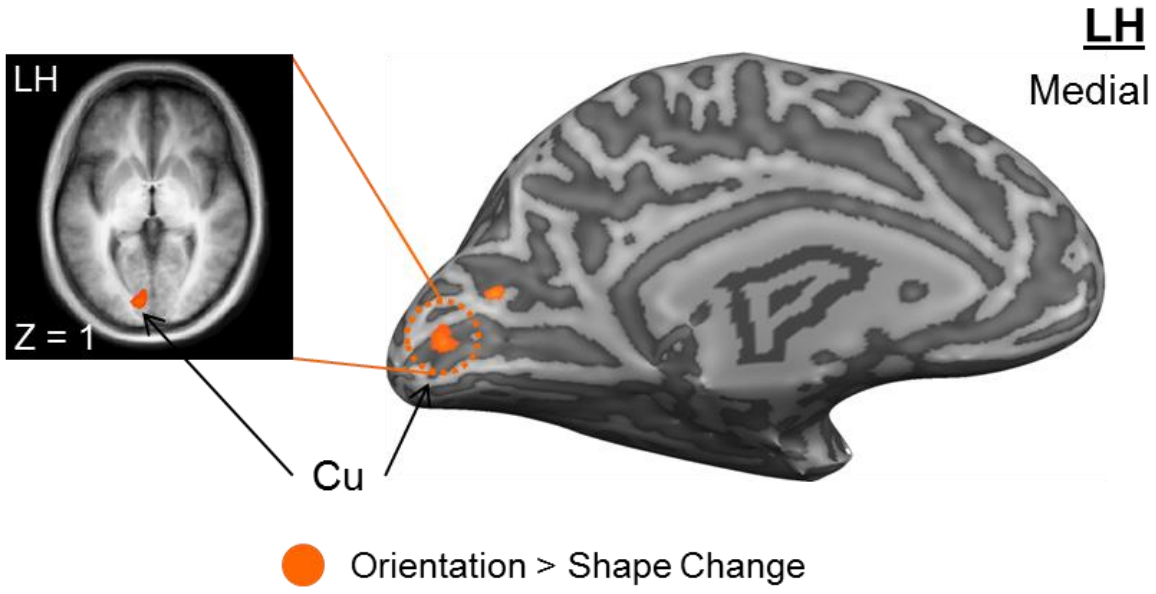

Figure 3. Direct comparison of saccade-related cortical modulations for changes in orientation vs. shape. Within cortex that showed saccade-sensitivity (Fig. 2), we then applied an Orientation > Shape change contrast (RFX GLM; n=17; $p < 0.001$; cluster threshold correction) in order to identify feature-sensitive 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.

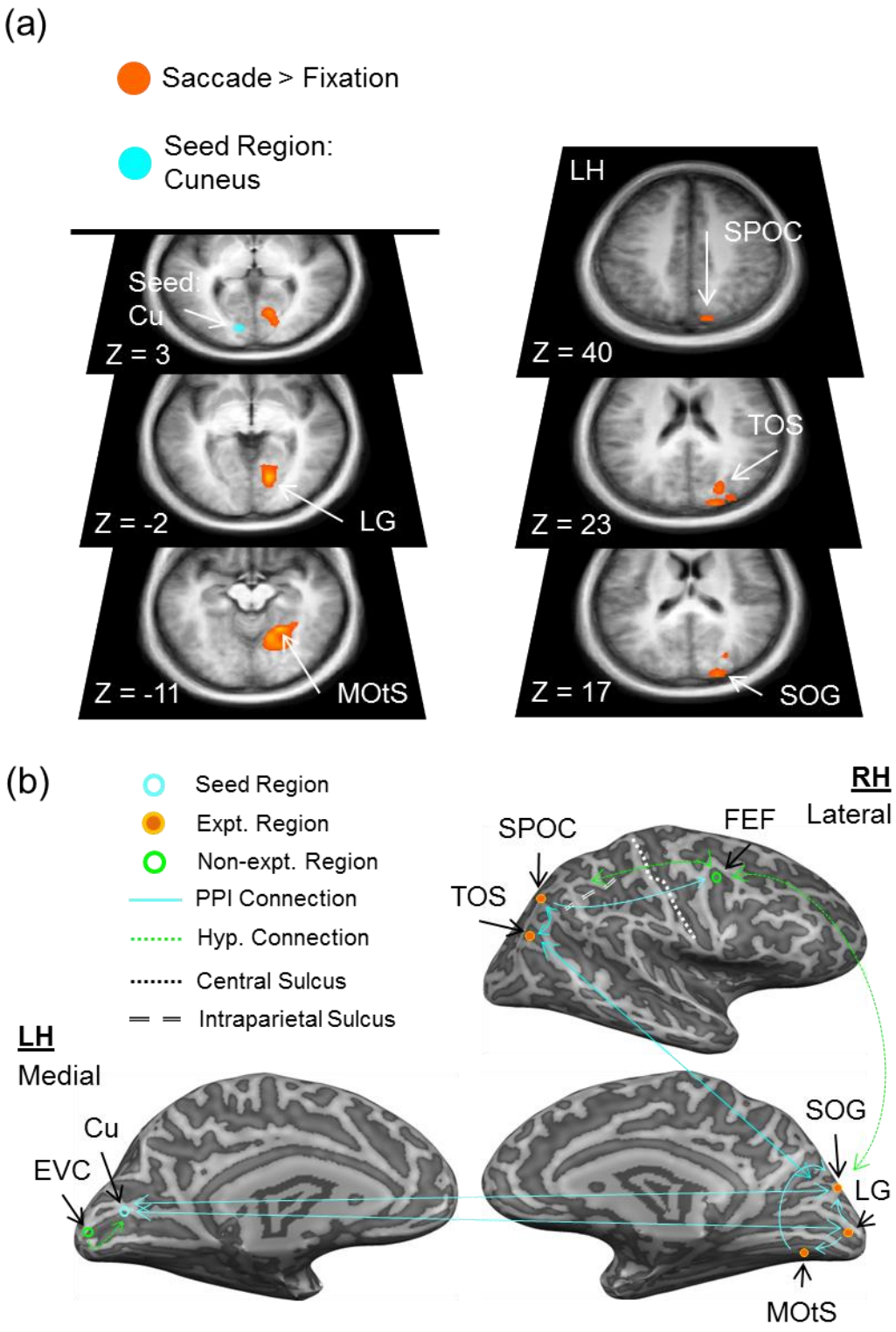

Figure 4. Functional connectivity network involved in transsaccadic updating of object features (orientation, shape). **(a)** Transverse slices through the average brain of all

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.

Region	Talairach coordinates						Active Voxels	References
	x	y	z	Std x	Std y	Std z		
Frontal Areas								
RH ventral Precentral Sulcus	45	-1	34	2.7	2.4	2.8	779	Grafton et al., 1997
Parietal Areas								
RH Superior Parietal Lobule	21	-65	51	2.8	2.8	2.7	863	Lambert et al., 2002
RH Mid-Intraparietal Sulcus	30	-57	43	2.7	2.8	2.5	772	Pertzov et al., 2011
Occipital Areas								
RH Superior Occipital Gyrus	10	-91	15	2.8	2.1	2.8	632	Salmon et al., 1996
RH Lingual Gyrus	10	-89	-6	2.9	2.9	2.9	1000	Decety et al., 1994
LH Lingual Gyrus	-12	-73	-5	2.8	2.8	2.9	963	Decety et al., 1994
Occipitotemporal Areas								
RH Medial Occipito-temporal Gyrus	32	-47	-13	2.9	2.9	2.9	996	ten Donkelaar et al., 2018
RH Medial Occipito-temporal Sulcus	14	-68	-14	2.9	2.9	2.9	999	Podrebarac et al., 2014
LH Medial Occipito-temporal Sulcus	-26	-58	-10	2.4	2.4	2.2	489	Podrebarac et al., 2014

Table 2. Functional connectivity network regions and Talairach coordinates resulting from psychophysiological interaction (PPI) analysis with left cuneus as the seed region.

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., 2021). 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.

Discussion

Our aim here was to investigate whether transsaccadic perception of object features engages a general, feature-insensitive cortical mechanism or if it recruits cortical regions in a feature-specific manner. 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.

Possible roles of medial occipital cortex in transsaccadic integration.

In this and our previous study on spatial frequency (Baltaretu et al., 2021), 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 re-entrant 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.

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., 2021).

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., 2021).

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.

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.

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.

Materials and Methods

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.

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.

General paradigm/procedure.

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.

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.

Analysis.

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.

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. 2). Second, we applied an Orientation > Shape change contrast to only the previous saccade-sensitive regions (Fig. 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. 2, 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. 2).

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) passed both p-value and cluster correction criteria.

CRediT author statement:

Bianca R. Baltaretu: Conceptualization, Methodology, Investigation, Formal analysis, Writing – Original Draft, Writing – Review & Editing, Visualization **W. Dale Stevens**: Formal analysis, Writing – Review & Editing **Erez Freud**: Formal analysis, Writing – Review & Editing **J. Douglas Crawford**: Conceptualization, Methodology, Formal analysis, Writing – Review & Editing, Project administration, Funding acquisition

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