Title: Dorsomedial occipital cortex participates in a cortical network for transsaccadic feature discrimination

Abbreviated Title: Dissociating feature-dependent transsaccadic mechanisms

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Abstract

To date, the cortical correlates of human transsaccadic vision have only been probed with single object features such as orientation (associated with repetition suppression in the supramarginal gyrus; SMG) and spatial frequency (associated repetition enhancement in dorsomedial occipital cortex; cuneus). Here, we used functional magnetic resonance imaging to identify cortical modulations associated with transsaccadic discrimination 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 bilateral region-of-interest (ROI) analysis was performed, based on the previously identified SMG and Cuneus sites. Of these, only cuneus was modulated here by *both* saccades and feature (i.e., orientation vs. shape) discrimination. A whole-brain voxelwise contrast (Saccade > Fixation; n=17), followed by a search within significant clusters for feature modulation, confirmed peak modulation in left cuneus. Used as a seed region for network analysis, this site 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 discrimination. Together with the previous literature, this suggests that separate mechanisms exist for transsaccadic perception of intrinsic (spatial frequency, shape) versus extrinsic (location, orientation) object features, but these mechanisms may not simply summate to perform more complex multi-feature tasks.

Keywords

Saccades, transsaccadic perception, occipital cortex, fMRI, functional connectivity

Introduction

Our ability to extract pertinent visual information from our surroundings is largely dependent on the brain's ability to aim, and account for, saccades (Javal, 1879; Rayner & Pollatsek, 1992; Wade et al., 2003). Saccades help to gather new visual information by aligning the fovea with objects of interest, but also disrupt 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 real-world need to process multiple features simultaneously. Here, we examined the cortical mechanisms of transsaccadic perception in a task that required discrimination of two different features: object orientation and object shape.

In theory, transsaccadic updating of oculomotor, spatial, and feature information might occur through feedback signals to occipital cortex, parieto-temporal interactions, or convergence of these signals in frontal cortex (Melcher & Colby, 2008; Prime et al., 2008, 2011; Hamker et al., 2011). To this end, 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). 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). Feature remapping has been observed in some monkey LIP neurons (Subramanian & Colby, 2014), and a recent study has shown that stimulus features (specifically, spatial frequency) can be decoded from whole-brain magnetoencephalography signals after an intervening saccade (Fabius et al., 2020). Finally, it has been shown that transsaccadic memory of object orientation can be disrupted by perisaccadic transcranial stimulation (TMS) over occipital, inferior parietal, dorsomedial frontal, and dorsolateral prefrontal cortex (Prime et al., 2008, 2010; Tanaka et al., 2014; Malik et al., 2015). Overall, these studies suggest that a distributed occipital-parietal-frontal network participates in transsaccadic updating.

It has proven difficult to localize the specific cortical locations that contribute to specific 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 differentially 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 feature), whereas occipital cortex showed repetition enhancement (*more* activation for the same feature). Specifically, right inferior parietal cortex (supramarginal gyrus, SMG) was

consistently 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). It was speculated that the difference between these results (Baltaretu et al., 2020, 2021) was due to fundamentally different perceptual processes, i.e., changes of object orientation versus identity (Valyear et al., 2006).

Note that the preceding transsaccadic fMRI experiments (Dunkley et al., 2016; Baltaretu et al., 2020, 2021) only examined transsaccadic changes in one feature at a time. Since participants were only instructed to attend to one feature, it is possible that the specificity of the results was enhanced by top-down attention. 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. This requires distributed attention, and potentially more complex cortical mechanisms.

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). We then searched for regions that met both of two criteria: saccade sensitivity and transsaccadic feature (orientation versus shape) change sensitivity (Fig. 1b). We tested these criteria using a region of interest (ROI) analysis based on our previous studies (Baltaretu et al., 2020, 2021) and whole-brain voxelwise analysis, followed by functional connectivity analysis of the identified site(s). Based on our single-feature 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 dorsomedial occipital cortex (Baltaretu et al., 2021). However, we found that only cuneus was significantly modulated by transsaccadic judgements *between* shape *and* orientation change, and show that this area participates in a saccade-dependent network involving the dorsal and ventral visual streams.

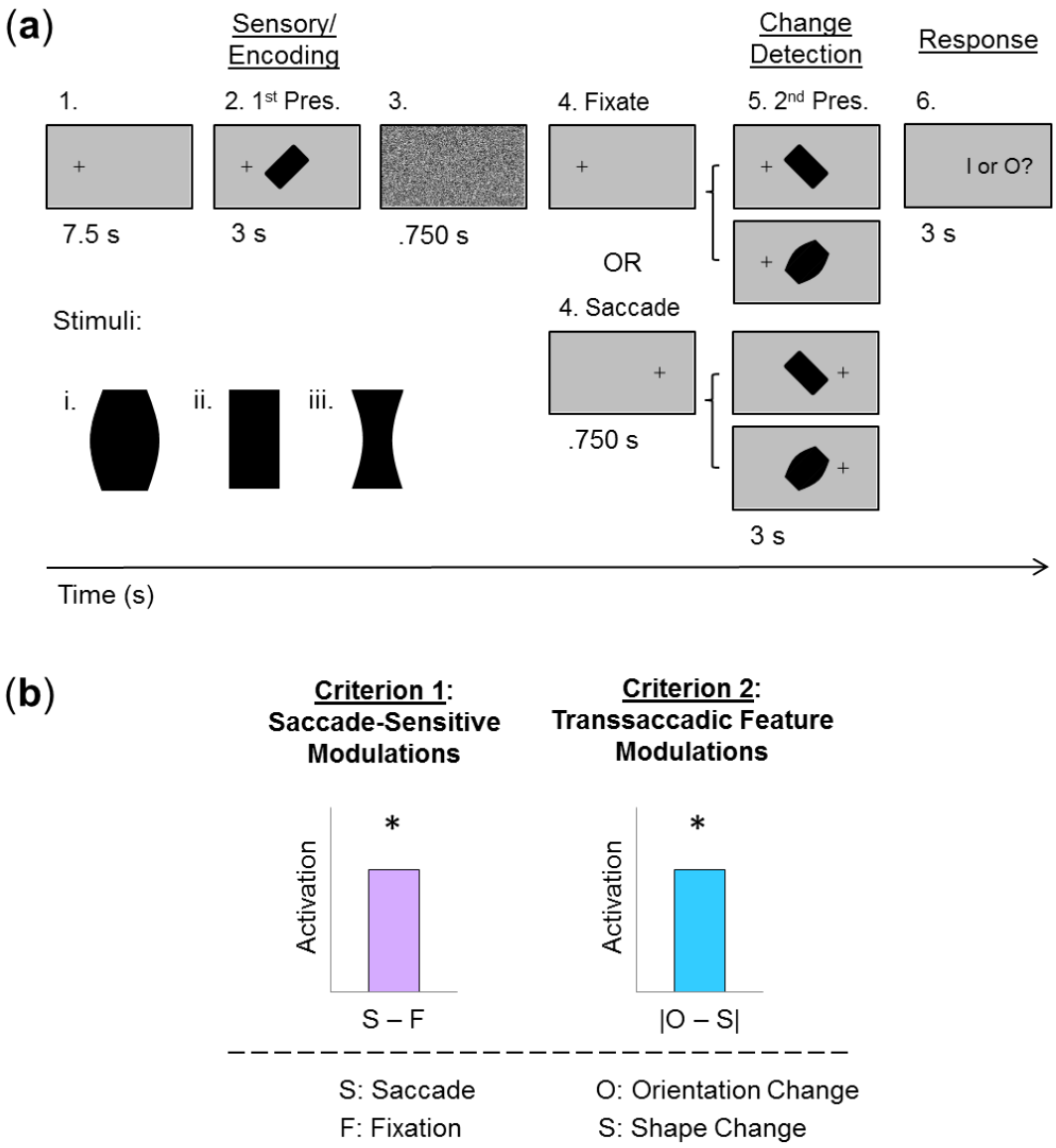

Figure 1. Experimental paradigm and criteria for transsaccadic feature modulation. **(a)** An example trial is presented (initial left fixation, rectangle, 45º) with the four possible main conditions: 1) Fixation, Different Orientation, 2) Fixation, Different Shape, 3)

Saccade, Different Orientation, or 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, or hourglass) was first presented at 45º to the left or right of vertical, while the participant was looking to the left or right of centre; 2) *Change Detection*, wherein the same object was presented at the orthogonal orientation (*Different Orientation* condition) or a different object at the same initial orientation (*Different Shape* condition) while participants fixated on the initial fixation cross (*Fixation* condition) or after they made a saccade (*Saccade* condition); and 3) *Response*, where participants made 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 identify transsaccadic feature regions. Such regions should meet *both* of the following criteria. Criterion 1: Saccade modulations. Areas that integrate saccade and feature information should show a significantly higher 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 a significant absolute difference in activity in response to one object feature change over another (stated in absolute terms: |Orientation - Shape change|, O, S, respectively). See Results for detailed predictions.

Materials and Methods

Participants.

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 perception studies (Baltaretu et al., 2020). We performed a power analysis (G*Power) using this effect size (0.887), with the following parameters: 1) two-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 participant's data were excluded, as this person did not complete the experiment, and three participants' data were excluded due to poor behavioural performance (i.e., less than 80% behavioural 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 informed 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 always visible (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 (Fig. 1a). The dimensions of the rectangle were 12° x 6°; the other two objects had the same area as the rectangle.

General paradigm/procedure.

Experiment.

To determine the cortical correlates of transsaccadic perception of object orientation versus shape, we used an event-related fMRI design (Fig. 1a). Each trial commenced with a fixation 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 in a different orientation (*Orientation change* condition) or one of the other two different objects presented in the same orientation (*Shape change* condition) appeared in the 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. 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 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 the 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 Gaussian kernel of 8 mm full width at half maximum. 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) “FixOC”, for an entire trial during which participants maintained fixation throughout while only the orientation of the same object changed; 2) “FixSC”, for a trial during which participants maintained fixation while only the shape of the object changed; 3) “SaccOC” for a trial during which participants had to make a saccade while only the orientation of

the object changed; and 4) “SaccSC” for a trial where participants made a saccade while only the shape of the object 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.

Region-of-interest (ROI) analysis.

A hypothesis-driven region-of-interest (ROI) analysis was performed based on Talairach coordinates obtained our previous studies (Baltaretu et al., 2020, 2021). Specifically, we used the previously identified coordinates of peak modulation for transsaccadic orientation changes (right SMG) and spatial frequency changes (right cuneus), which we hypothesized would generalize to transsaccadic shape detection if cuneus plays a more general role in object *identity*. We then mirrored these coordinates laterally to obtain four ROIs (i.e., bilateral SMG and cuneus; Fig. 2a, Table 1). Spheres were created around these coordinates with a 5-mm radius were created using BrainVoyager QX v2.8 (Brain Innovation). β-weights were then extracted and inspected for hemispheric differences with a two-tailed repeated-measures t-test. If a significant result was obtained, the β-weights from the left and right hemispheres were analyzed separately for each of the two

criteria (Fig. 1b; see Results for details). On this basis, we pooled data only for cuneus. Within each of the ROIs, two two-tailed repeated-measures t-tests were applied to test for each of our two criteria (Figs. 1b, 2b; i.e., for saccade (criterion 1) and feature (criterion 2) sensitivity). As such, the p-values were False Discovery Rate (FDR) adjusted for the tests applied to three ROIs. See Results and Table 1 for further information.

Whole-brain univariate analysis for saccade and feature sensitivity.

We performed a whole-brain analysis to 1) confirm the results of our ROI analysis, and 2) identify the optimal seed site for functional connectivity analysis. For these univariate analyses, we applied two contrasts to test for two effects. First, we performed a whole-brain voxelwise Saccade > Fixation contrast to identify cortical regions that were modulated by saccades in this task (Fig. 3). Second, we applied an Orientation > Shape change contrast within those saccade-sensitive regions to identify regions that were also feature sensitive (Fig. 3). To each of the resulting volumetric maps, we applied a threshold of $p < 0.001$, followed by cluster correction (minimum cluster threshold for Saccade > Fixation contrast = 35 voxels; minimum cluster threshold for the second contrast, Orientation > Shape contrast = 16 voxels; BrainVoyager QX v2.8, Brain Innovation). Regions that are labeled (Fig. 3) passed both the statistical p-value threshold and cluster correction.

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 peak site of saccade / feature modulation identified in our whole-brain analysis (Talairach coordinates: -10, -85, 3). For optimal signal processing, we used a sphere of radius = 4 mm around this site. 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 constitute the functional network that shows 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.

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 among 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. Based on our previous experiments (Baltaretu et al., 2020, 2021), we expected two 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 modulated by judgement of a shape versus orientation change following the saccade (Fig. 1b, criterion 2). We applied these criteria first for a region-of-interest analysis based on sites identified in previous studies, and then verified these results in a whole-brain analysis to identify the optimal seed site for functional network analysis.

Region-of-interest analysis of saccade and feature modulations.

We performed a hypothesis-driven region-of-interest analysis based on Talairach coordinates (Table 1) of two sites obtained from previous fMRI studies. In these studies, the supramarginal gyrus (SMG) showed repetition suppression during transsaccadic

changes in object orientation whereas cuneus (Cu) showed repetition enhancement during transsaccadic changes in spatial frequency (Baltaretu et al., 2020, 2021). In each case, we tested both the peak site of modulation reported in the literature and the mirror site in the opposite hemisphere, forming bilateral pairs (Fig. 2b).

To qualify as sites for transsaccadic perception, we required each region to pass two criteria (Fig. 1b). First, they must show saccade modulations, because saccade signals would be required to spatially update the signals (Melcher & Colby, 2008; Prime et al., 2011; Baltaretu et al., 2020, 2021). For this prediction, both sites would be expected to show greater activity in the saccade versus fixation task. The second criterion was that (to be involved in transsaccadic feature retention and feature discrimination) these sites should be differentially modulated by changes in shape *versus* orientation following the saccade. To generate specific predictions, we initially assumed that SMG and cuneus would contribute independently, and in a summative manner, to shape-orientation discrimination. Here, the prediction depends on both feature sensitivity and hemodynamics (repetition suppression versus enhancement). In the case of SMG, we expected transsaccadic repetition *suppression* for orientation change (Baltaretu et al., 2020), which should yield a positive O-S modulation (Fig. 1b, criterion 2). If cuneus is involved in the transsaccadic perception of object identity (Baltaretu et al., 2021), it should be modulated by changes in shape. However, cuneus shows repetition *enhancement*, which should also yield a positive O-S modulation. All these predictions were one-tailed, but we performed two-tailed statistical tests to be conservative.

To test our SMG and cuneus sites, we created spheres (radius = 5 mm) around the site of peak modulation and mirrored Talairach coordinate, and then extracted β-weights for

these sites. Cuneus did not show significant hemispheric differences ($p > 0.05$), so data from these bilateral pair were pooled. SMG showed a significant hemispheric difference ($p = 7.9 \times 10^{-22}$), so these ROIs were analyzed separately. Repeated-measures t-tests were then used to test our specific criteria in each of the ROIs, using an FDR-corrected p-value. SMG did not show significant saccade or feature modulations. Cuneus was the only site to pass our saccade modulation criterion (Fig. 2b, S-F) and our second feature criterion (Fig. 2b, O-S). This confirms that bilateral cuneus was involved in transsaccadic discrimination of multiple object features in this task, but also suggests that our initial assumption (that single-feature functions would summate to solve this task) was false.

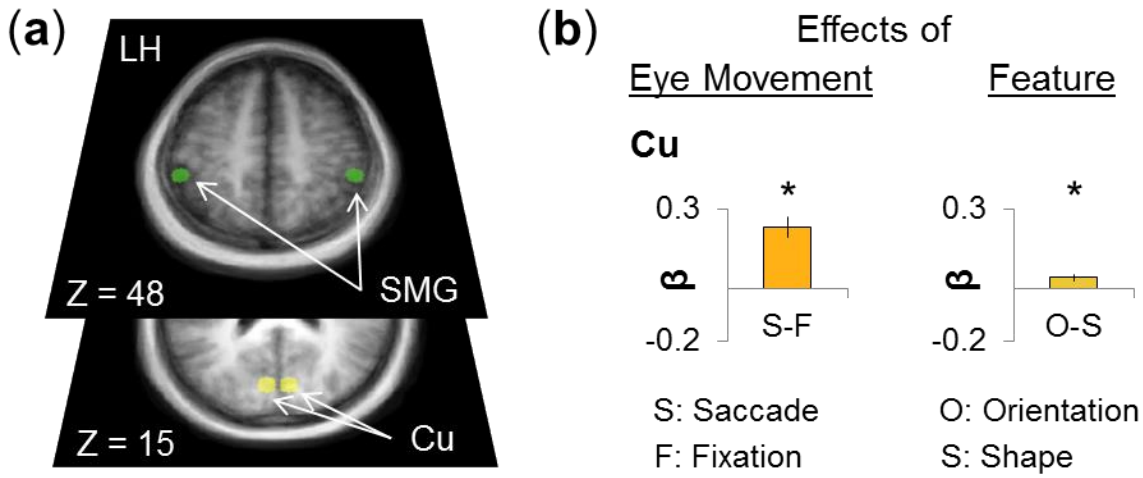

Figure 2. Region-of-interest (ROI) analysis results for tests of eye movement and/or feature effects. (**a**) Transverse slices (Talairach z-coordinate provided) through the average brain of all participants (n = 17) are shown for two sets of ROIs on the left (top: SMG, bottom: cuneus). (**b**) Bar graphs plotting the difference in β-weights (with SEMs as error bars) for eye movement (leftmost; Saccade – Fixation, S – F) and feature (rightmost; Orientation – Shape change, O – S). Of the two sets of ROIs tested, only cuneus showed both eye movement and feature effects, as was expected from similar results in another transsaccadic perception study (Baltaretu et al., 2021). SMG (not shown) did not show significant influence of either eye movements or feature change.

Region	Talairach coordinates			Criterion 1		Criterion 2		Ref's
	x	Y	z	T	P	T	P	
Occipital Cortex								
Cuneus	±6	-79	15	5.8	0.00028	2.9	0.0085	Baltaretu et al., 2021
Parietal Cortex								
LH Supramargi-nal Gyrus	-49	-40	48	-0.6	0.87	0.2	0.93	Baltaretu et al., 2020
RH Supramargi-nal Gyrus	49	-40	48	-0.2	0.93	0.1	0.93	Baltaretu et al., 2020

Table 1. Regions-of-interest, Talairach coordinates, t-statistic (T), and p-values (P) for *a priori* selected areas tested for saccade and feature modulations.

Whole-brain analysis and identification of a seed region for network analysis.

The second step in our analysis was to test our predictions (Fig. 1b) at the whole-brain level. This served two functions: to test the possibility that some other area (besides cuneus) is actually the peak site for saccade/feature modulations in this task, and to determine the optimal seed region for functional network analysis (see next section). To do this, we applied the same basic criteria used in our ROI analysis (Fig. 1b) to a voxelwise analysis. First, we applied a whole-brain Saccade > Fixation contrast (Fig. 1b, criterion 1). Significant saccade sensitivity ($p < 0.001$, uncorrected) was found in left parietal and bilateral occipital cortex, predominantly in the medial aspects (Fig. 3, mauve). Activation peaks (Table 2) occurred in bilateral lingual gyrus (LG) and cuneus (Cu), left dorsal precuneus (dPCu), and a trend in dorsal precentral sulcus (likely FEF, not shown).

We then applied our second criterion (Fig. 1b, criterion 2) by using an Orientation > Shape change contrast within the voxels activated in the first saccade contrast. This resulted in a small but significant area within left Cu (Fig. 3, sky blue). In short, this region satisfied both of our criteria (Fig. 1b). The site of peak feature modulation (Talairach coordinates: -10, -85, 3) is indicated by the white dot in Figure 3. This site was located within the region of saccade modulation spanning Cu (Fig. 3, Table 2) and was inferior and caudal to the specific left Cu site used in our ROI analysis above (Table 1), and was in the opposite hemisphere to the peak site for transsaccadic spatial frequency perception (Baltaretu et al., 2021). This site was then used as the seed region for our subsequent network analysis.

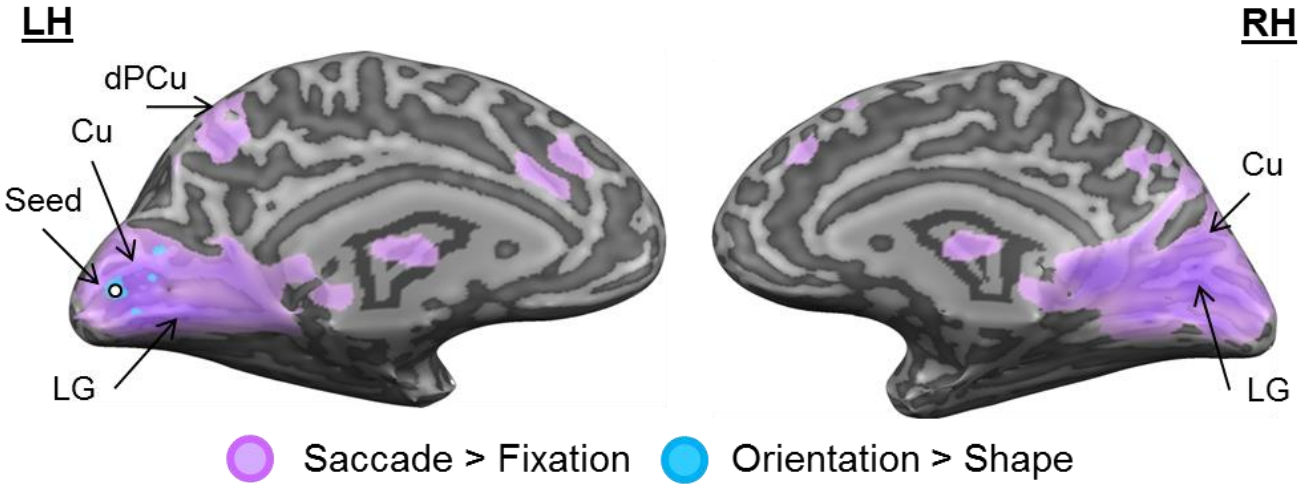

Figure 3. Localization of saccade and feature effects. Two voxelwise maps from an RFX GLM (n=17; p < 0.001; cluster threshold correction) are presented on an inflated brain rendering of an example participant (medial views of left and right hemispheres, respectively). First, saccade effects were localized using a whole-brain Saccade > Fixation contrast (mauve). This contrast revealed extensive medial activation in occipital and posterior parietal cortex, with peaks (Table 2) in bilateral cuneus (Cu) and lingual gyrus (LG) and left dorsal precuneus (dPCu). Left dorsal precentral sulcus (likely the frontal eye field, not shown) also showed activation, but only the p-value correction criterion was met). Second, within saccade-sensitive regions (mauve), feature effects were found using an Orientation > Shape change contrast in left Cu (sky blue). The region

(Talairach coordinates: -10, -85, 3; peak shown via white dot) was used as a seed region for subsequent functional connectivity analysis (see Fig. 4).

Region	**Talairach coordinates**						**Active Voxels**	**References**
	x	Y	z	Std x	Std y	Std z		
<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
<u>Parietal Areas</u>								
LH dorsal Precuneus	-6	-57	41	2.3	2.3	2.2	526	Fletcher et al., 1995

Table 2. Regions and Talairach coordinates for saccade-sensitive parietal and occipital regions-of-interest.

Functional connectivity of cuneus with visual and sensorimotor regions.

In the final step of our analysis, we defined a sphere (radius = 4 mm) around the left Cu site defined in the previous section as a seed region for psychophysiological interaction (PPI) analysis. This analysis provides a network of cortical regions that show temporally correlated activation with a specific seed region in a particular task context. Specifically, we identified regions that showed significant functional connectivity with this region based on a Saccade > Fixation contrast (Baltaretu et al., 2021). This analysis resulted in significant contralateral connectivity with (right) occipital, occipitotemporal, and parietal cortex (Fig. 4a, Table 3). 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.

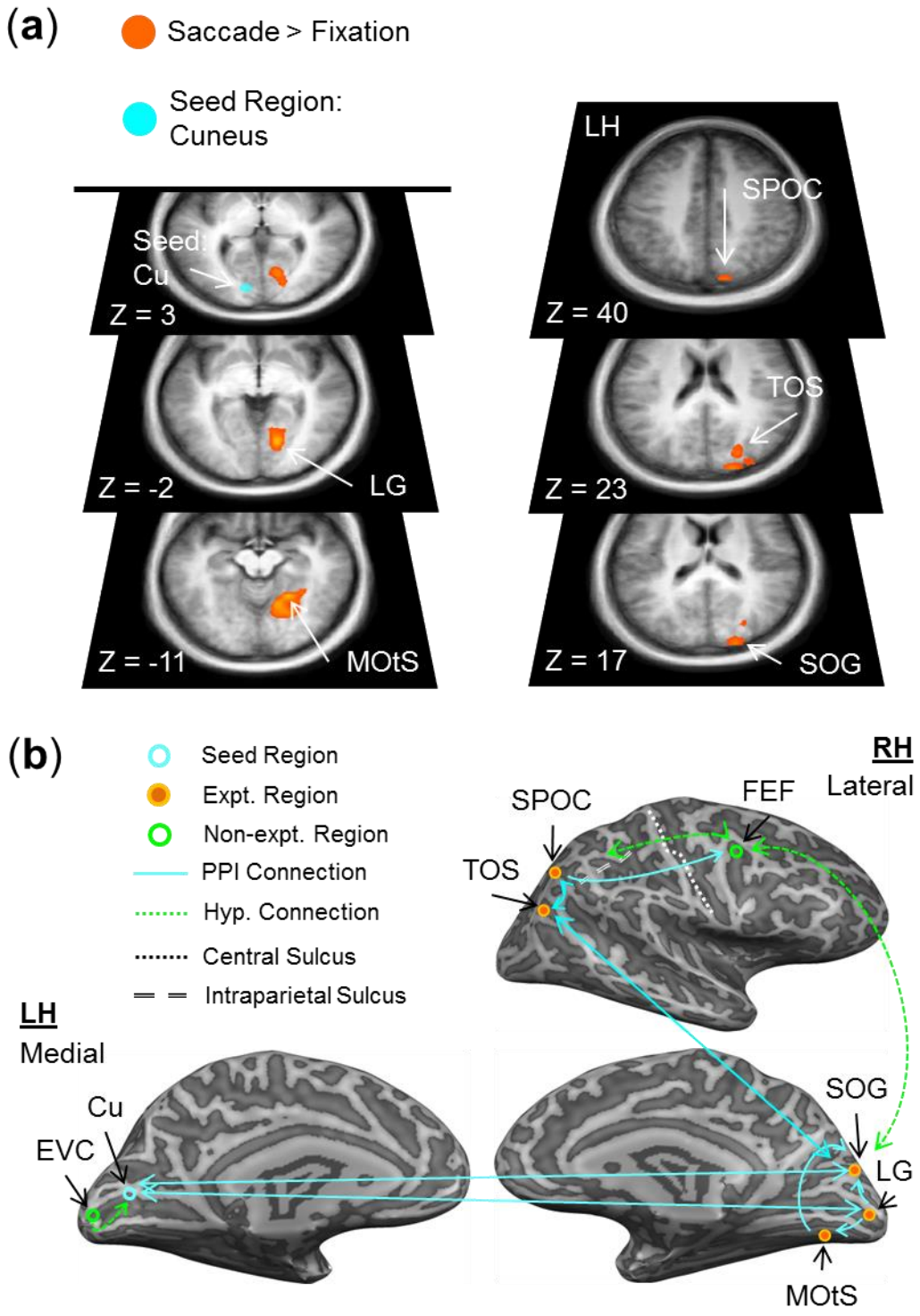

Figure 4. Functional connectivity network involved in transsaccadic updating of object features (orientation, shape). **(a)** Transverse slices through the average brain of all participants (n=17) are shown from most superior to inferior along the vertical axis. 'Z' components of the regions' Talairach 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) functional connectivity 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. (Note that these correlations do not necessarily imply direct anatomical connections.) **(b)** A hypothetical 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		
Seed Region								
LH Cuneus	-10	-85	3					
Occipital Areas								
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
Occipitotemporal Areas								
RH Medial Occipito-temporal Sulcus	20	-53	-11	2.7	2.5	2.2	616	Podrebarac et al., 2014
Parietal Areas								
RH Superior Parieto-occipital Cortex	12	-82	40	2.2	1.9	2.5	287	Rossit et al., 2013

Table 3. Functional connectivity network regions and Talairach coordinates resulting from psychophysiological interaction (PPI) analysis with left cuneus as the seed region.

Discussion

Our aim here was to investigate whether transsaccadic discrimination of multiple features relies on the same or different mechanisms, as those for single features. First, we tested for saccade and feature sensitivity in four regions that either showed both these properties in previous transsaccadic tasks involving single features (SMG, Cu; Baltaretu et al., 2020,

2021) or showed shape-orientation discrimination (Valyear et al., 2006). Of these regions, only Cu showed both saccade and feature sensitivity in the current task. We, then, used voxelwise subtractions to identify regions that showed both saccade and feature sensitivity in the current task. This identified a small cluster of activity in medial occipital cortex, with a peak in left Cu (i.e., dorsal to the calcarine fissure). Using this site for functional connectivity analysis, we found that left cuneus communicates with a widespread network that spans visual/object processing areas and saccade/sensorimotor regions. Overall, each of these analyses support the notion that the cuneus participated in a network for transsaccadic feature discrimination in our task.

Possible roles of medial occipital cortex in transsaccadic perception.

In this and our previous study on spatial frequency (Baltaretu et al., 2021), dorsomedial occipital cortex plays an important role in the postsaccadic integration of old and new information. Based on their Talairach coordinates, the cuneus sites described here likely fall within a region spanning visual areas V2 and V3 (McKeefry et al., 1997). These areas are ideally suited to provide the rudimentary machinery for transsaccadic feature analysis (Nakamura & Colby, 2000, 2002; Prime et al. 2008, 2011). 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 that 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 the capability 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 some theoretical discussions of transsaccadic feature perception have suggested a role for occipital cortex (Prime et al. 2006, 2008, 2011; Hamker & Zirnsak, 2006), initial experimental studies emphasized the parietal cortex as the key 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 the combination of saccades and vision would be handled by one specialized mechanism seems unlikely. 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; Fabius et al., 2020), whereas

transsaccadic perception of object orientation, spatial frequency, and shape appears to involve parietal, medial occipital, and, in some cases, lateral occipital cortex (Dunkley et al., 2016; Baltaretu et al., 2020; Baltaretu et al., 2021).

Based on the common properties of spatial frequency and shape (as intrinsic object features related to object *identity)*, we speculated that cuneus would be modulated by transsaccadic shape changes. In the experiment, cuneus was modulated by both saccades and feature discrimination as predicted, and in the predicted 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 that 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. It is also possible (although, perhaps unlikely) that our participants only focused on shape change in this task, and treated orientation change as a repetition condition. Conversely, it may be that SMG activity was more engaged in our previous

tasks because participants were entirely focused on orientation changes, whereas here, SMG activity may have been statistically masked by other activity. Finally, one of our previous orientation studies employed real 3D stimuli (Baltaretu et al., 2020) which can change fMRI results (Snow et al., 2011; Freud et al., 2018). However, there is evidence that comparison between features evokes different mechanisms than the sum of the parts (Valyear et al., 2006). Likewise, our results were not simply the sum of predictions based on single features, perhaps suggesting additional complexity in the transsaccadic system.

Transsaccadic networks: Task-specificity and lateralization.

Considering the complexity of transsaccadic signals discussed above, it seems likely that these mechanisms can be better understood at a network level. 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 it trended toward saccade modulation, and is known to project to parietal and occipital visual areas.

Finally, although we used left cuneus as a seed region here, it is noteworthy that its activity predominantly correlated with activity in right occipital and parietal cortex. Right cortex also predominated in our previous regional and network analyses (Dunkley et al., 2016; Baltaretu et al., 2020, 2021). Consistent with this, transsaccadic memory is most sensitive to right parietal stimulation and brain damage (Sapir et al., 2004; Prime et al., 2008, Ten Brink et al., 2019). This is generally consistent with the role of parietal cortex in spatial attention and cognition, and suggests that impaired transsaccadic perception might play a role in better-known disorders like hemispatial neglect (Ptak & Müri, 2013).

Conclusion

Here, we used fMRI to test the cortical correlates of transsaccadic perception in a task where participants had to remember and discriminate changes in object shape versus orientation after the saccade. Our current findings support a specific role of medial occipital cortex in transsaccadic feature discrimination, specifically for differentiating 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

perception of object features in medial occipital cortex (here and Baltaretu et al. (2021)). These areas may not simply 'sum' to perform more complex tasks, but apparently form ad-hoc 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 provides a putative functional anatomy for transsaccadic vision.

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References

Baltaretu, B.R., Monaco, S., Velji-Ibrahim, J., Luabeya, G.N., Crawford, J.D., 2020. Parietal cortex integrates saccade and object orientation signals to update grasp plans. J. Neurosci. 40(23), 4525-4535.

Baltaretu, B.R., Dunkley, B.T., Stevens, W.D., Crawford, J.D., 2021. Occipital cortex is modulated by transsaccadic changes in spatial frequency: an fMRI study. Sci. Rep. 11, 8611.

Ben-Shachar, M., Dougherty, R.F., Deutsch, G.K., Wandell, B.A., 2007. Differential sensitivity to words and shapes in ventral occipito-temporal cortex. Cereb. Cortex 17(7), 1604-1611.

Berhmann, M., Geng, J.J., Shomstein, S., 2004. Parietal cortex and attention. Curr. Opin. Neurobiol. 14(2), 212-217.

Bettencourt, K.C., Xu, Y., 2013. The role of transverse occipital sulcus in scene perception and its relationship to object individuation in inferior intraparietal sulcus. J. Cogn. Neurosci. 25(10), 1711-1722.

Bisley, J.W., Mirpour, K., Alkan, Y., 2020. The functional roles of neural remapping in cortex. J. Vis. 20(6), 1-15.

Burr, D. C., & Morrone, M. C. (2011). Spatiotopic coding and remapping in humans. Philos. Trans. R. Soc. Lond. B, Biol. Sci. 366(1564), 504-515.

Cavina-Pratesi, C., Kentridge, R.W., Heywood, C.A., Milner, A.D., 2010. Separate channels for processing form, texture, and color: Evidence from fMRI adaptation and visual object agnosia. Cereb. Cortex 20(10), 2319-2332.

Chen, X., Wang, F., Fernandez, E., Roeflsema, P.R., 2020. Shape perception via a high-channel-count neuroprosthesis in monkey visual cortex. Science 370(6521), 1191-1196.
Colzato, L.S., Raffone, A., Hommel, B., 2006. What do we learn from binding features? Evidence from multilevel feature integration. J. Exp. Psychol. Hum. Percept. Perform. 32(3), 705-716.
Corbetta, M., Akbudak, E., Conturo, T.E., Snyder, A.Z., Ollinger, J.M., Drury, H.A., …, Shulman, G.L., 1998. A common network of functional areas for attention and eye movements. Neuron 21(4), 761-773.
Costello, M.C., Madden, D.J., Mitroff, S.R., Whiting, W.L., 2010. Age-related decline of visual processing components in change detection. Psychol. Aging 25(2), 356-368.
Culham, J.C., Valyear, K.F., 2006. Human parietal cortex in action. Curr. Opin. Neurobiol. 16(2), 205-212.
Currie, C.B., McConkie, G.W., Carlson-Radvansky, L.A., Irwin, D.E., 2000. The role of the saccade target object in the perception of a visually stable world. Percept. Psychophys. 62(4), 673-683.
Davidoff, J., Warrington, E.K., 1999. The bare bones of object recognition: implications from a case of object recognition impairment. Neuropsychologia 37(3), 279-292.
De Valois, R.L., Yung, E.W., Hepler, N., 1982. The orientation and direction selectivity of cells in macaque visual cortex. Vis. Res. 22(5), 531-544.
De Valois, R.L., Karen, K., Tootell, R.B., 1983. Spatial-frequency-specific inhibition in cat striate cortex cells. J. Physiol. 336(1), 359-376.
Decety, J., Perani, D., Jeannerod, M., Bettinardi, V., Tadary, B., Woods, R., …, Fazio, F., 1994. Mapping motor representations with positron emission tomography. Nature 371, 600-602.
Duhamel, J.R., Colby, C.L., Goldberg, M.E., 1992. The updating of the representation of visual space in parietal cortex neurons. Science 255(5040), 90-92.
Dunkley, B.T., Baltaretu, B., Crawford, J.D., 2016. Trans-saccadic interactions in human parietal and occipital cortex during the retention and comparison of object orientation. Cortex 82, 263-276.
Fabius, J. H., Fracasso, A., Acunzo, D. J., Van der Stigchel, S., & Melcher, D. (2020). Low-level visual information is maintained across saccades, allowing for a postsaccadic handoff between visual areas. J. Neurosci. 40(49), 9476-9486.
Fang, F., Murray, S.O., Kersten, D., He, S., 2005. Orientation-tuned fMRI adaptation in human visual cortex. J. Neurophysiol. 94(6), 4188-4195.
Fink, G.R., Halligan, P.W., Marshall, J.C., Frith, C.D., Frackowiak, R.S., Dolan, R.J., 1997. Neural mechanisms involved in the processing of global and local aspects of hierarchically organized visual stimuli. Brain 120(10), 1779-1791.
Fletcher, P.C., Frith, C.D., Baker, S.C., Shallice, T., Frackowiak, R.S.J., Dolan, R.J., 1995. The mind's eye – precuneus activation in memory-related imagery. NeuroImage 2, 195-200.
Freud, E., Macdonald, S.N., Chen, J., Quinlan, D.J., Goodale, M.A., …, 2018. Getting a grip on reality: Grasping movements directed to real objects and images rely on dissociable neural representations. Cortex, 98, 34-48.
Freud, E., Behrmann, M., Snow, J.C., 2020. What does dorsal cortex contribute to

perception? Open Mind 4, 40-56.
Friston, K.J., Buechel, C., Fink, G.R., Morris, J., Rolls, E., Dolan, R.J., 1997. Psychophysiological and modulatory interactions in neuroimaging. NeuroImage 6(3), 218–229.
Gegenfurtner, K.R., Kiper, D.C., Fenstemaker, S.B., 1996. Processing of color, form, and motion in macaque area V2. Vis. Neurosci. 13, 161-172.
Goodale, M.A., Milner, D., 1992. Separate visual pathways for perception and action. Trends Neurosci. 15, 20-25.
Grill-Spector, K. Kourtzi, Z., Kanwisher, N., 2001. The lateral occipital comlex and its role in object recognition. Vis. Res. 41(10-11), 1409-1422.
Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzchak, Y., …, 1999. Differential processing of objects under various viewing conditions in the human lateral occipital complex. Neuron 24(1), 187-203.
Grill-Spector, K., Malach, R., 2001. fMR-adaptation: a tool for studying the functional properties of human cortical neurons. Acta Psychol. 107(1-3), 293-321.
Grill-Spector, K., 2003. The neural basis of object perception. Curr. Opin. Neurobiol. 13(2), 159-166.
Grill-Spector, K., Sayres, R., 2006. Object recognition: Insights from advances in fMRI Methods. Curr. Dir. Psychol. Sci. 17(2), 73-79.
Hamker, F.H., Zirnsak, M., 2006. V4 receptive field dynamics as predicted by a systems-level model of visual attention using feedback from the frontal eye field. Neural Netw. 19, 1371-1382.
Hamker, F. H., Zirnsak, M., Ziesche, A., Lappe, M., 2011. Computational models of spatial updating in peri-saccadic perception. Philos. Trans. R. Soc. B. Biol. Sci. 366(1564), 554-571.
Hartmann, T.S., Zirnsak, M., Marquis, M., Hamker, F.H., Moore, T., 2017. Two types of receptive field dynamics in area V4 at the time of eye movements? Front. Syst. Neurosci. 11, 1-7.
Hubel, D.H., Wiesel, T.N., 1968. Receptive fields and functional architecture of monkey striate cortex. J. Physiol. 195(1), 215-243.
Iacoboni, M., Zaidel, E., 2004. Interhemispheric visuo-motor integration in humans: the r ole of the superior parietal cortex. Neuropsychologia 42(4), 419-425.
Irwin, D.E., 1996. Integrating information across saccadic eye movements. Curr. Dir. Psychol. Sci. 5(3), 94–100.
James, T.W., Culham, J., Humphrey, G.K., Milner, A.D., Goodale, M.A., 2003. Ventral occipital lesions impair object recognition but not object-directed grasping: an fMRI study. Brain 126(11), 2463-2475.
Javal, E., 1879. Essai sur la physiologie de la lecture. Ann. Ocul. (Paris). 82, 242-253.
Karnath, H.-O., Perenin, M.-T., 2005. Cortical control of visually guided reaching: Evidence from patients with optic ataxia. Cereb. Cortex 15(10), 1561-1569.
Klier, E.M., Angelaki, D.E., 2008. Spatial updating and the maintenance of visual constancy. Neuroscience 156(4), 801–818.
Kourtzi, Z., Erb, M., Grodd, W., Bülthoff, H.H., 2003. Representation of the perceived 3-D object shape in the human lateral occipital complex. Cereb. Cortex 13(9), 911-920.

Koutstaal, W., Wagner, A.D., Rotte, M., Maril, A., Bucker, R.L., …, 2001. Perceptual specificity in visual object priming: functional magnetic resonance imaging evidence for a laterality difference in fusiform cortex. Neuropsychologia 39(2), 184-199.
Lambert, S., Sampaio, E., Scheiber, C., Mauss, Y., 2002. Neural substrates of animal mental imagery: calcarine sulcus and dorsal pathway involvement – an fMRI study. Brain Res. 924(2), 176-183.
Lamme, V.A.F., Roelfsema, P.R., 2000. The distinct modes of vision offered by feedforward and recurrent processing. Trends Neurosci. 23(11), 571-579.
Land, M.F., Hayhoe, M., 2001. In what ways do eye movements contribute to everyday activities? Vis. Res. 41(25-26), 3559-3565.
Land, M.F., 2006. Eye movements and the control of actions in everyday life. Prog. Retin. Eye Res. 25(3), 296-234.
Lerner, Y., Hendler, T., Ben-Bashat, D., Harel, M., Malach, R., 2001. A hierarchical axis of object processing stages in the human visual cortex. Cereb. Cortex 11(4), 287-297.
Lescroart, M.D., Kanwisher, N., Golomb, J.D., 2016. No evidence for automatic remapping of stimulus features or location found within fMRI. Front. Syst. Neurosci. 10, 53.
Livingstone, M., Hubel, D., 1988. Segregation of form, color, movement, and depth: Anatomy, physiology, and perception. Science 240(4853), 740-749.
Luna, B., Thulborn, K.R., Strojwas, M.H., McCurtain, B.J., Berman, R.A., Genovese, C.R., Sweeney, J.A., 1998. Dorsal cortical regions subserving visually guided saccades in humans: an fMRI study. Cereb. Cortex 8(1), 40-47.
Malik, P., Dessing, J., Crawford, J., 2015. Role of early visual cortex in trans-saccadic memory of object features. J. Vis. 15(11), 1-17.
Mathôt, S., & Theeuwes, J. (2010). Evidence for the predictive remapping of visual attention. Exp. Brain Res. 200(1), 117-122.
Maunsell, J.H., Van Essen, D.C., 1983. Functional properties of neurons in middle temporal visual area of the macaque monkey. I. Selectivity for stimulus direction, speed, and orientation. J. Neurophysiol. 49(5), 1127-1147.
McKeefry, D., Watson, J., Frackowiak, R., Fong, K., Zeki, S., 1997. The activity in human areas V1/V2, V3, and V5 during perception of coherent and incoherent motion. NeuroImage 5, 1-12.
McLaren, D., Ries, M., Xy, G. & Johnson, S., 2012. A generalized form of context-dependent psychophysiological interactions (gPPI): a comparison to standard approaches. NeuroImage 61, 1277-1286.
Medendorp, W.P., Goltz, H.C., Vilis, T., Crawford, J.D., 2003. Gaze-centered updating of visual space in human parietal cortex. J. Neurosci. 23(15), 6209-6214.
Melcher, D., Colby, C.L., 2008. Trans-saccadic perception. Trends Cogn. Sci. 12(12), 466-473.
Merriam, E., Genovese, C.R., Colby, C.L., 2003. Spatial updating in parietal cortex. Neuron 39(2), 361-373.
Merriam, E., Genovese, C.R., Colby, C.L., 2007. Remapping in human visual cortex. J. Neurophysiol. 97(2), 1738-1755.
Nakamura, K., Colby, C.L., 2000. Visual, saccade-related, and cognitive activation of

single neurons in monkey extrastriate V3A. J. Neurophysiol. 84(2), 677-692.
Nakamura, K., Colby, C.L., 2002. Updating of the visual representation in monkey striate and extrastriate cortex during saccades. Proc. Natl. Acad. Sci. 99(6), 4026-5031.
Neupane, S., Guitton, S., Pack, C.C., 2016. Two distinct types of remapping in primate cortical area V4. Nat. Commun. 7(1), 1-11.
O'Reilly, J., Woolrich, M., Behrens, T., Smith, S. & Johansen-Berg, H., 2012. Tools of the trade: Psychophysiological interactions and functional connectivity. Soc. Cogn. Affect. Neurosci. 7, 604–609.
Orban, G.A., Dupont, P., Vogels, R., Bormans, G., Mortelmans, L., 1997. Human brain activity related to orientation discrimination tasks. Eur. J. Neurosci. 9(2), 246-259.
Podrebarac, S., Goodale, M., Snow, J., 2014. Are visual texture-selective areas recruited during haptic texture discrimination? NeuroImage 94, 129-137.
Prime, S.L., Niemeier, M., Crawford, J.D., 2006. Transsaccadic integration of visual features in a line intersection task. Exp. Brain Res. 169(4), 532-548.
Prime, S.L., Vesia, M., Crawford, J.D., 2008. Transcranial magnetic stimulation over posterior parietal cortex disrupts transsaccadic memory of multiple objects. J. Neurosci. 28(27), 6938–6949.
Prime, S.L., Vesia, M., Crawford, J.D., 2011. Cortical mechanisms for trans-saccadic memory and integration of multiple object features. Philos. Trans. R. Soc. B. Biol. Sci. 366(1564), 540–553.
Ptak, R., & Müri, R. (2013). The parietal cortex and saccade planning: lessons from human lesion studies. Front. Hum. Neurosci. 7, 254.
Rao, H.M., Mayo, J.P., Sommer, M.A., 2016. Circuits for presaccadic remapping. J. Neurophysiol. 116(6), 2624-2636.
Rayner, K., Pollatsek, A., 1992. Eye movements and scene perception. Can. J. Psychol. 46(3), 342-376.
Rossit, S., McAdam, T., Mclean, D.A., Goodale, M.A., Culham, J.C., 2013. fMRI reveals a lower visual field preference for hand actions in human superior parieto-occipital cortex (SPOC) and precuneus. Cortex 49(9), 2525-2541.
Rottschy, C., Caspers, S., Roski, C., Reetz, K., Dogan, I., …, 2013. Differentiated parietal connectivity of frontal regions for "what" and "where" memory. Brain Struct. Funct. 218(6), 1551-1567.
Salin, P.-A., Bullier, J., 1995. Corticocortical connections in the visual system: structure and function. Physiol. Rev. 75(1). 107-154.
Salmon, E., Van der Linden, M., Collette, F., Delfiore, G., Maquet, P., Degueldre, C., …, 1996. Regional brain activity during working memory tasks. Brain 119(5), 1617-1625.
Sapir, A., Hayes, A., Henik, A., Danziger, S., Rafal, R., 2004. Parietal lobe lesions disrupt saccadic remapping of inhibition location tagging. J. Cogn. Neurosci. 16(4), 503-509.
Segaert, K., Weber, K., de Lange, F.P., Petersson, K.M., Hagoort, P., 2013. The suppression of repetition enhancement: a review of fMRI studies. Neuropsychologia 51(1), 59-66.
Sincich, L.C., Horton, J.C., 2002. Divided by cytochrome oxidase: a map of the projections from V1 to V2 in macaques. Science 295(5560), 1734-1737.

Sincich, L.C., Horton, J.C., 2005. The circuitry of V1 and V2: integration of color, form, and motion. Annu. Rev. Neurosci. 28, 303-326.
Snow, J.C., Pettypiece, C.E., McAdam, T.D., McLean, A.D., Stroman, P.W., …, 2011. Bringing the real world into the fMRI scanner: Repetition effects for pictures versus real objects. Sci. Rep. 1, 130.
Subramanian, J., Colby, C.L., 2014. Shape selectivity and remapping in dorsal stream visual area LIP. J. Neurophysiol. 111(3), 613-627.
Talairach, J., Tournoux, P., 1988. Stereotaxic Atlas of the Human Brain.
Ten Brink, A.F., Fabius, J.H., Weaver, N.A., Nijboer, T.C.W., Van der Stigchel, S., 2019. Trans-saccadic memory after right parietal brain damage. Cortex 120, 284-297.
Tootell, R., Silverman, M., Hamilton, S., Switkes, E. & De Valois, R., 1988. Functional anatomy of macaque striate cortex. V. Spatial frequency. J. Neurosci. 8, 1610-1624.
Tong, F., 2003. Primary visual cortex and visual awareness. Nat. Rev. Neurosci. 4, 219-229.
Treisman, A., 1998. Feature binding, attention and object perception. Phil. Trans. R. Soc. Lond. B. 353(1373), 1295-1306.
Umeno, M.M., Goldberg, M.E., 1997. Spatial processing in the monkey frontal eye field. I. Predictive visual responses. J. Neurophysiol. 78(3), 1373-1383.
Utochkin, I.S., Brady, T.F., 2020. Independent storage of different features of real-world objects in long-term memory. J. Exp. Psychol. Gen. 149(3), 530-549.
Valyear, K.F., Culham, J.C., Sharif, N., Westwood, D., Goodale, M.A., 2006. A double dissociation between sensitivity to changes in object identity and object orientation in the ventral and dorsal visual streams: a human fMRI study. Neuropsychologia 44(2), 218-228.
Van Essen, D.C., Zeki, S.M., 1978. The topographic organization of rhesus macaque monkey prestriate cortex. J. Physiol. 277(1), 193-226.
Wade, N.J., Tatler, B.W., Heller, D., 2003. Dodge-ing the issue: Dodge, Javal, Hering, and the measurement of saccades in eye-movement research. Perception 32(7), 793-804.
Webster, M.J., Bachevalier, J., Ungerleider, L.G., 1994. Connections of inferior temporal areas TEO and TE with parietal and frontal cortex in macaque monkeys. Cereb. Cortex 4(5), 470-483.
Yantis, S., Schwarzbach, J., Serences, J.T., Carlson, R.L., Steinmetz, M.A., Pekar, J.J., Courtney, S.M., 2002. Transient neural activity in human parietal cortex during spatial attention shifts. Nat. Neurosci. 5, 995-1002.
Zeki, S.M., 1973. Colour coding in rhesus monkey prestriate cortex. Brain Res. 53(2), 422-427.
Zirnsak, M., Steinmetz, N.A., Noudoost, B., Xu, K.Z., Moore, T., 2014. Visual space is compressed in prefrontal cortex before eye movements. Nature 507(7493), 504-507.