Title: Parietal Mechanisms for Transsaccadic Spatial Frequency Perception: An fMRI Study

Abbreviated Title: Cortical mechanisms for transsaccadic feature processing

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Abstract

Posterior parietal cortex (PPC), specifically right supramarginal gyrus, is involved in transsaccadic memory of object orientation for both perception and action. Here, we investigated whether PPC is involved in transsaccadic memory of other features, namely spatial frequency. We employed a functional magnetic resonance imaging paradigm where participants briefly viewed a grating stimulus with a specific spatial frequency that later reappeared with the same or different frequency, after a saccade or continuous fixation. Post-saccadic frequency modulation activated a region in the right hemisphere spanning medial PPC (ventral precuneus) and posterior cingulate cortex. Importantly, the site of peak precuneus activation showed saccade-specific feature modulation (compared to fixation) and task-specific saccade modulation (compared to a saccade localizer task). Psychophysiological interaction analysis revealed functional connectivity between this precuneus site and the precentral gyrus (M1), lingual gyrus (V1/V2), and medial occipitotemporal sulcus. This differed from the transsaccadic *orientation* network, perhaps because spatial frequency signaled changes in object *identity*. Overall, this experiment supports a general role for PPC in transsaccadic vision, but suggests that different networks are employed for specific features.

Introduction

The visual system tracks both low-level (e.g., orientation, spatial frequency) and high-level (e.g., objects, faces) components of our visual surroundings through space and time [1], despite the interruption of several saccades (rapid eye movements) per second [2,3]. To do this, visual features must be encoded, retained, updated, and integrated across saccades [4,5], through a process called transsaccadic perception [2,6,7,8]. As argued elsewhere [9-11], transsaccadic perception likely incorporates mechanisms for both visual working memory [12,13] and spatial updating [14,15]. However, the specific *neural* mechanisms for transsaccadic feature perception are not well understood.

When saccades occur, they cause both object locations and their associated features to shift relative to eye position. It is well established that human posterior parietal cortex (PPC; specifically, the mid-posterior parietal sulcus), is involved in transsaccadic spatial updating, i.e., the updating of object *location* relative to each new eye position [16-19]. Recently, we found that inferior PPC (specifically, right supramarginal gyrus; SMG) is also modulated by transsaccadic comparisons of object orientation [20]. This area is located immediately lateral to the parietal eye field / lateral intraparietal sulcus, so might be an evolutionary expansion of the monkey intraparietal eye fields, which show modest spatial updating of object information across saccades [21]. Consistent with these findings, transcranial magnetic stimulation (TMS) of PPC (just posterior to SMG) disrupted transsaccadic memory of multiple object orientations [22,23]. SMG activity is also modulated during transsaccadic updating of object orientation for grasp, along with other parietal sensorimotor areas [24]. These findings implicate PPC in the transsaccadic updating of *both* object location and orientation.

It is not known if these neural mechanisms generalize to other stimulus features. One might expect PPC to be involved in other aspects of transsaccadic feature memory and integration, because of its general role in spatial updating [17,25,26]; however, the specific mechanisms might differ. SMG seems to play a specialized role for high-level object orientation in various spatial tasks [27,28]. Thus, while SMG might play a general role in transsaccadic updating of all visual features, it is equally possible that the brain engages different cortical networks for transsaccadic processing of different features, as it does during prolonged visual fixations [29,30].

To address this question, we used an event-related fMRI paradigm, similar to Dunkley et al. [20], where participants briefly viewed a 2D spatial frequency grating stimulus, either while continually fixating the eyes, or while making a saccade to the opposite side, and then judged whether a re-presented grating was the same or different. But here, we modulated spatial frequency, rather than orientation (Fig. 1a,b). As in Dunkley et al. [20], we first localized clusters that were activated by changes in stimulus frequency following saccades; then, as in Baltaretu et al. [24] we determined if the site(s) of peak PPC activation passed two additional criteria: their feature modulations must be saccade-specific (Fig. 2, prediction 1), and 2) they must show task-specific saccade modulations relative to a simple saccade motor task (Fig. 2, prediction 2). Finally, we analyzed the functional connectivity of this area. Our findings confirm the involvement of PPC in processing transsaccadic feature interactions, but demonstrate that different PPC areas/networks are involved in transsaccadic processing of spatial frequency versus orientation.

--- Figure 1 Here ---

--- Figure 2 Here ---

Results

Overall, our task (Fig. 1) produced widespread and progressive activation in brain areas related to vision, visual memory and eye movements during the initial *Sensory/Memory Phase* (Fig. S1) and *Visual/Oculomotor Updating Phase* (Fig. S2). Here, we focus on the specific analysis pipeline that we used to identify and test if any parietal sites showed saccade- and task-specific feature modulations for spatial frequency (Fig. 2). For this analysis, we only analyzed the *Visual/Oculomotor Updating* phase of our task, i.e. the period after the first stimulus presentation, starting at the time when a saccade occurred and a second stimulus (either Same or Different) appeared (Fig. 1a). An *a priori* power analysis suggested that 14 participants were required for the voxelwise contrasts used in this pipeline (see Methods: Power analysis). To obtain this level, we continued testing participants (21 in total), until 15 of these passed our behavioural inclusion criteria for fMRI analysis (See Methods: Behavioural data and exclusion criteria).

Selection of parietal site for hypothesis testing.

Our overall aim was to identify parietal site(s) that showed post-saccadic feature modulations and then use these sites to test the predictions shown in Figure 2. As a first step in this analysis, we performed a whole-brain voxelwise contrast (*Different* Spatial Frequency > *Same* Spatial Frequency) on fMRI data derived from the

134 *Visual/Oculomotor Updating* phase of our saccade trials. The resulting group data are
135 shown in Fig. 3a, overlaid on a representative anatomic scan in 'inflated brain'
136 coordinates (note that while visually convenient, this convention results in small spatial
137 distortions). This contrast revealed two regions: First, a continuous region of change-
138 dependent activation in the right hemisphere spanning medial PPC (ventral precuneus
139 and the posterior cingulate gyrus, PCu/pCG). The other region (right medial frontal
140 gyrus, MFG), showed the opposite pattern, i.e., change suppression, but was not further
141 analyzed. Notably, unlike similar contrasts in studies of transsaccadic *orientation*
142 processing [20], SMG was not significantly modulated.

143 The second step in this analysis was to determine specific parietal coordinates
144 for our hypothesis tests. To do this, we examined the medial PCu/pCG region shown in
145 Fig. 3a, but raised the statistical threshold until only the peak site of parietal activation
146 remained, corresponding to ventral precuneus (vPCu). We then used BrainVoyager
147 (BrainVoyager QX v2.8, Brain Innovation) to determine the cluster of activation around
148 the peak voxel and extract data for prediction testing [24,31,32]. This site is shown in
149 Fig. 3b, overlaid on sagittal anatomic slice (which is less susceptible to distortions).
150 Coordinates and supporting references for this site (and the other regions mentioned)
151 are shown Table 1.

152

153 **--- Figure 3 Here ---**

154

155 **Hypothesis 1: Saccade-specific feature modulations.**

156 According to prediction 1 (Fig. 2), cortical sites involved in transsaccadic feature
157 comparisons should show positive (Different > Same) feature modulations following
158 saccades, but not during sustained fixation. Figure 3a suggests that vPCu is modulated
159 by frequency changes after saccades, but does not show if this modulation is saccade-
160 specific. To test this directly (and independently from the contrast used to localize the
161 site), we extracted β-weights for all participants from a small cubic region surrounding
162 the peak voxel coordinates for vPCu (Table 1). We did this under four conditions for the
163 same site: Saccade Different frequency (SD), Saccade Same frequency (SS), Fixation
164 Different frequency (FD) and Fixation Same frequency (FD). To test hypothesis 1, we
165 then compared *Different* - *Same* feature for *Saccade* (SD-SS) versus *Fixation* data (FD-
166 FS), as shown in Fig. 3c. In short, vPCu followed the predicted pattern: it showed a
167 significantly greater *Different-Same* feature modulation after saccades compared to
168 sustained fixation ($t(11)= -2.07$, $p= 0.031$, effect size= 0.60).
169
170 **Hypothesis 2: Task-specific saccade modulations.**
171 According to prediction 2 (Fig. 2), cortical sites that are specifically involved in
172 transsaccadic feature comparisons should be modulated by saccades in a task-specific
173 fashion, i.e. not simply by the motor act of producing a saccade. Figure 4 provides this
174 test using similar conventions to Figure 3. Figure 4a provides a general overview of the
175 data used in this calculation, showing Saccade > Fixation modulations during the
176 updating portion of our task and for reference, the same contrast from our saccade
177 localizer task, where participants simply looked back and forth between two points (see
178 Methods for details). As in our previous study [24], saccade modulations were generally

more widespread when they accompanied a more complex task. Figure 4b shows that the location of the vPCu site used for our hypothesis testing bordered on the edge of a major cluster of saccade modulation.

Figure 4c provides the statistical test of prediction 2, using data derived from our vPCU site in a similar fashion to that described above. i.e. *Saccade-Fixation* difference in the experimental task (TS-TF) versus the same difference from the saccade localizer (S-F). Note that we could only do this for the 12 participants that passed behavioural/imaging criteria in both tasks. Once again these data followed the predicted pattern, showing task-specific saccade modulations in our main experiment compared to the saccade localizer data ($t(11)= 2.57$, $p=0.013$, effect size= 0.68). Overall, these findings suggest that activity in our ventral precuneus site reflects changes in spatial frequency in both a saccade-specific and task-specific manner.

-Figure 4 here-

Functional network for spatial frequency-specific transsaccadic perception.

Our previous study of transsaccadic orientation updating showed a functional network connecting right SMG to both saccade and grasp motor areas [24]. Here, we provide a similar analysis of precuneus activity for the current perceptual task. To do this, we used a *Saccade* > *Fixation* contrast in a psychophysiological interaction (PPI) analysis, wherein right precuneus served as the seed region. Figure 5a shows these data overlaid on a series of transverse brain slices. We observed statistically significant functional connectivity between precuneus (cyan region) and three other regions

(orange): 1) left lingual gyrus (LG), 2) a caudal portion of the left medial occipitotemporal sulcus (MOtS), and 3) right precentral gyrus (likely primary motor cortex, M1).

--- Figure 5 Here ---

Discussion

The goal of this study was to determine whether the involvement of PPC in transsaccadic updating of visual location and orientation generalizes to other object features, such as spatial frequency. We found that medial PPC and a lateral frontal region were modulated by spatial frequency changes across saccades. Further hypothesis testing on PPC showed that ventral precuneus passed our predefined criteria for putative transsaccadic updating [24]. Finally, our functional connectivity analysis suggests that this area interacts with other visual and motor areas to perform the task that we required of our participants.

Putative sites for transsaccadic integration of spatial frequency.

It has previously been shown that PPC, specifically intraparietal sulcus and adjacent portions of inferior PPC, are involved in transsaccadic processing of object location and orientation [17,20,24]. The current results extend this role to spatial frequency processing, but implicate a different portion of PPC: ventral precuneus, along with other sites in cingulate and frontal cortex. The latter three sites have several common characteristics. First, although they modulate with saccades, they do not overlap with

225 the classic saccade motor areas (Fig. S2) [33-35]. Second, they were all located in the
226 right hemisphere, consistent with the lateralization observed previously for spatial
227 attention [36,37], spatial updating [38], and transsaccadic orientation processing [20,24].
228 Finally, they are all relatively 'high level' (as opposed to early visual cortex), presumably
229 because our participants performed a top-down, instruction-based task, in contrast to
230 automatic, bottom-up feature integration [11].

231 Since the intent of this experiment was to explore the role of PPC in
232 transsaccadic integration, we focused our analysis on right ventral precuneus, which
233 met all of our criteria for transsaccadic feature processing. In general, precuneus is
234 associated with complex visuospatial transformations [39-41]. Dorsal precuneus is
235 associated with reaching [42-44], saccades [45,46], and visual memory [47]. Ventral
236 precuneus is involved in change detection [47] and egocentric processing [48], and
237 shows connectivity with the parahippocampus, cuneus, LG (positive connections), and
238 MFG (negative connections) [49]. In short, ventral precuneus has functions and
239 connectivity generally consistent with the task and observations in the current study.

240 In the current study, precuneus showed extensive functional connectivity with
241 other areas (see next section), and fell within a broad region of right medial posterior
242 cortex activation, that also included another peak in the posterior cingulate gyrus. The
243 posterior cingulate gyrus region is thought to contribute to several saccade-related
244 functions that might be related to transsaccadic perception, including attention orienting
245 [50], and retainment of information in working memory [51]. Saccade-related attention
246 has been closely linked with transsaccadic perception [52].

247 Finally, we found the opposite pattern of post-saccade activation (*Different* <
248 *Same* frequency) in the right middle frontal gyrus. This is consistent with negative
249 functional connectivity between precuneus and MFG [49]. MFG is located within the
250 dorsolateral prefrontal cortex (dlPFC), which contains various subregions, some
251 saccade-sensitive [53], critical for spatial working memory and top-down control [54-
252 56]. This area has previously been implicated in high-level aspects of transsaccadic
253 perception: e.g., online TMS to dlPFC disrupted memory of multiple objects during
254 fixation, but enhanced transsaccadic memory [57]. In general, dlPFC, has been
255 implicated in various other relevant visual functions, including monochromatic
256 perception of texture [58-60] (although see [61]), attention orientation [62], and retention
257 of perceived information in working memory [55,63,64].
258
259 **Putative functional network for transsaccadic perception of spatial frequency.**
260 In our previous study of transsaccadic updating of grasp orientation, SMG mainly
261 showed connectivity with sensorimotor areas, including the frontal and supplementary
262 eye fields, anterior intraparietal cortex, and adjacent portions of superior parietal cortex
263 involved in grasp control [24]. Here we observed a very different pattern of connectivity:
264 our seed region (right ventral precuneus) showed task-related functional connectivity
265 with right precentral gyrus (likely M1) [65], left LG, and left MOtS. Although PPI analysis
266 is limited in the sense that it does not provide directionality [66], this analysis suggests a
267 bilateral network for transsaccadic perception of spatial frequency involving both lower
268 and higher-level visual areas. Based on these results, we propose the network model
269 illustrated in Figure 5b, where (as discussed above) ventral precuneus is the central

(PPC) hub for spatial frequency processing in this task, and contiguous activity in posterior cingulate contributes saccade-related attention signals [52].

LG (likely corresponding with visual areas V2/V3) processes low-level information about spatial frequency in this network [67-70], and has also been implicated in spatial updating [16,71]. MOtS, located within occipitotemporal cortex, is thought to be involved in higher-level aspects of spatial frequency processing related to objects and scenes [72]. Involvement of precentral gyrus most likely reflects preparatory activity for the final response, the button press [73-75]. Finally, although MFG/dlPFC did not reappear in our connectivity analysis, it was suppressed by feature changes that followed saccades (Fig. 2a) and has been shown to be functionally connected with ventral precuneus in previous studies [49]; a blue dotted line in the model (Fig. 5b) from this area denotes its putative role in top-down control [57,76,77].

Feature- and task-related aspects of transsaccadic perception.

As noted above, our previous experiments showed transsaccadic modulations for object orientation in inferior parietal cortex (specifically SMG) along with some task-dependent extrastriate and superior parietal areas [20,24]. Why would the sites and networks observed for transsaccadic spatial frequency processing in the current study be so different? In part, it is likely that transsaccadic perception builds on computations already used during fixation, which are themselves feature- and task-dependent [21,78,79,80], especially in the higher-level visual areas activated in our tasks [48,65]. At early levels like V1, there is clear multiplexing of orientation and spatial frequency [67,81,82], but at higher levels these may tap into entirely different processes. For

example, in our experiment, a change in orientation might influence how one can orient to an object [24,83], but a change in spatial frequency can denote more fundamental changes in perceived identity and affordance, evoking very different cortical mechanisms [84]. Moreover, changes in motor aspects of the task can readily explain why the functional connectivity in the current task (with an abstract button press response) was very different from that in our previous experiment where the perceived object was then grasped [24]. Finally, it is likely that more automatic bottom-up aspects of transsaccadic integration (such as the automatic integration of motion signals across saccades) [85] involve different mechanisms again, perhaps involving earlier visual centres [11,16,71]. Thus, the notion of a dedicated 'transsaccadic integration centre' is likely naïve: transsaccadic vision, not prolonged fixation, is normal biological vision, and has likely developed different and nuanced mechanisms, depending on feature and task details.

Conclusion

In this fMRI study, we set out to explore the cortical mechanism for transsaccadic updating of spatial frequency, with emphasis on the role of PPC. We found that PPC (and likely other cortical areas) play a key role, but in contrast to involvement of SMG for transsaccadic orientation perception [20], the key parietal hub for transsaccadic spatial frequency processing was ventral precuneus. We also found different patterns of functional connectivity compared to our previous grasp updating experiment, i.e., where SMG activity correlated with saccade and grasp motor areas [24]. Overall, these

315 findings support the role of parietal cortex in transsaccadic vision, but suggest that
316 specific network recruitment is feature- and task-dependent.
317
318 **Materials and Methods**
319 **Participants.**
320 We tested 21 (human) participants from York University (Toronto, Canada) of
321 whom 15 met our inclusion criteria for analyses (see Behavioural analysis and exclusion
322 criteria), thus exceeding the requirement for sufficient statistical power (see Power
323 analysis) [86]. These 15 individuals (average age: 26.6 +/- 4.3 years; age range: 21-37;
324 11 females and 4 males; all right-handed) had no neurological disorders and normal or
325 corrected-to-normal vision. Each participant provided written consent and was
326 remunerated for their time. This experiment was approved by the York University
327 Human Participants Review Subcommittee.
328
329 **Experimental set-up.**
330 Participants passed initial MRI safety screening and were then informed about the
331 experimental task. Participants practiced before taking part in the experiment. Once
332 they felt comfortable with the task, they assumed a supine position on the MRI table,
333 with their head resting flat within a 32-channel head coil. An apparatus, holding a mirror
334 to reflect images from the screen in the MRI bore, was attached to the head coil. An
335 MRI-compatible eye-tracker (iViewX, SensoMotoric Instruments) was also attached to
336 the apparatus in order to record the position of the right eye. Participants held an MRI-
337 compatible button box in their right hand. Their right index and middle fingers rested on

two buttons, used to provide the task responses when presented with the ‘go’ cue (see General paradigm).

Stimuli.

During the experiment, participants were presented with an 18° stimulus that contained a vertical sine-wave grating pattern, averaged to the mean luminance of the screen. Stimuli were presented in the centre of the screen on a light gray background (MATLAB; Mathworks, Inc.). The two spatial frequencies that were tested were 0.7 or 1.1 cycles/degree (cpd) (see Fig. 1a).

General paradigm.

In order to identify the cortical activity correlates of transsaccadic perception of spatial frequency, we used a modified 2 (Gaze: Fixate or Saccade) x 2 (Spatial Frequency: 0.7 or 1.1 cpd) slow event-related fMRI design [20]. Here, we modulated the spatial frequency (repeated or changed within the same trial; *‘Same’* and *‘Different’* conditions, respectively) and/or position of the eyes (continued fixation of gaze or a saccade was produced; *‘Fixation’* and *‘Saccade’* conditions). This resulted in four main conditions: 1) Fixation/Same, 2) Fixation/Different, 3) Saccade/Same, and 4) Saccade/Different. These were randomly intermingled and repeated four times within each run; there were six runs in total for each participant.

Trial sequence.

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

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

Saccade localizer.

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

MRI parameters.

A 3T Siemens Magnetom TIM Trio MRI scanner at the York MRI Facility was used to acquire fMRI data. An echo-planar imaging (EPI) sequence (repetition time [TR] = 2000 ms; echo time [TE] = 30 ms; flip angle [FA] = 90°; field of view [FOV] = 240 x 240 mm, matrix size = 80 x 80, in-plane resolution = 3 mm × 3 mm; slice thickness = 3 mm) was acquired in ascending, interleaved order for each of the six functional runs and for the two separate saccade localizer runs. Thirty-three contiguous slices were acquired per volume for a total of 192 volumes of functional data in each experimental run, and 128 volumes of data for each saccade localizer run. A T1-weighted anatomical reference volume was obtained for each participant using an MPRAGE sequence (TR= 1900 ms; FA= 256 mm x 256 mm; voxel size= 1 x 1 x 1 mm^3). 192 slices were acquired per volume of anatomical data.

Analysis

Power analysis.

To determine the appropriate number of participants to provide a sufficient effect size and level of power, we used results from the most recent, relevant findings [24]. Specifically, we used the effect size (0.887, Cohen's d) from the most relevant region of activation in parietal cortex (i.e., SMG) and applied the following properties: 1) two-tailed t-test option, 2) an α value of 0.05, and 3) a power value of 0.85. Using G*Power 3.1 [87], we determined that a minimum of 14 participants would be required to achieve an actual power value of 0.866. As noted above, we tested a total of 21 participants in order to exceed this minimal number, after application of exclusion criteria in the next section.

Behavioural data and exclusion criteria.

In our previous studies [20,24], we found that experiments such as this are highly sensitive to head motion. Due to excessive head motion, data were excluded from analyses on the basis of two criteria: 1) presence of head motion over 1 mm/degree and/or 2) any abrupt motion of the head over 0.5 mm/degrees. If more than 50% of all data (i.e., at least 3 runs out of the total 6 runs for a given participant) were removed from analysis, the entire data set from that participant was removed. On this basis, data from six participants were removed. From the remaining 15 participants, one run was removed from data analysis for each of two participants, and two runs were removed for each of another two participants, for a total of six runs (6.7%).

Eye tracking and button-press data were analyzed post-image acquisition in order to determine whether the task was completed correctly or not. Eye position data (e.g., Fig. 1b) were inspected visually to confirm that the eye fixated on the fixation

428 crosses and/or moved to the correct saccade location when prompted to do so in all
429 trials. Button press responses were also inspected offline to ensure that participants
430 responded correctly to the *Same*/*Different* condition trials. On these bases, 41 trials
431 were excluded from further analysis (3.1% of the remaining data). Overall, accuracy of
432 the 15 participants included in the final data analysis was 97.4% ± 3.1%. Only data for
433 correct trials were included in all further analyses.
434
435 **Functional imaging data: experimental.**
436 To model the fMRI BOLD response, we used a general linear model (GLM) analysis. In
437 this model, a standard two-gamma haemodynamic response function (BrainVoyager QX
438 2.8, Brain Innovation) was convolved with predictor variables [20]. We had five major
439 classes of predictors for each trial: 1) a baseline predictor ("Baseline"), corresponding to
440 the first and last 16 s of each run; 2) "Fixate", which represented initial trial fixation
441 (either left or right); 3) "Adapt", which modeled the activity in response to the first
442 stimulus presentation; 4) "Fixate/Same", "Fixate/Different", "Saccade/Same", or
443 "Saccade/Different" to model activity in response to the second stimulus presentation in
444 one of the four main conditions; and 5) "Response", which modeled the activity for the
445 button press response period. GLMs were generated using the eight predictors per run
446 for each participant (BrainVoyager QX 2.8, Brain Innovation).
447 Preprocessing of functional data from each run for all participants included slice
448 scan-time correction (cubic spline), temporal filtering (for removal of frequencies < 2
449 cycles/run), and 3D motion correction (trilinear/sinc). Anatomical data were transformed
450 to a standard Talairach template [88]. Functional data were coregistered using gradient-

based affine alignment (translation, rotation, scale affine transformation) to the raw anatomical data. Lastly, the functional data were spatially smoothed using a Gaussian kernel with a FWHM of 8 mm.

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

Functional imaging data: saccade localizer.

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

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

Voxelwise map contrasts: Analysis and statistical considerations.

473 We conducted voxelwise contrasts on data from the 15 participants included in the
474 analysis (for task, and on the remaining 12 participants for the localizer). For analysis
475 purposes, we divided the experimental task data into the *Sensory/Memory* phase (when
476 participants saw and initially remembered the stimulus) and *Visual/Oculomotor Updating*
477 phase (when saccades occurred and the stimulus reappeared). For all (voxelwise)
478 contrasts, we first applied a False Discovery Rate (FDR) of $q < 0.05$, followed by cluster
479 threshold correction (BrainVoyager QX v2.8, Brain Innovation) to our contrasts. This
480 included the Saccade > Fixation contrast shown in Fig. 4a/b, and the contrasts shown in
481 supplementary figures (Sensory/Memory phase activity > Baseline, Fig. S1;
482 Visual/Oculomotor Updating > Sensory/Memory contrast, Fig. S2).
483
484 **Hypothesis testing: Analysis and statistical considerations.**
485 In order to localize our site-of-interest testing, we used a similar approach to site
486 localization as in Song and Jiang [31]; Baltaretu et al. [24]; and Tsushima et al. [32] by
487 first applying a whole-brain contrast of interest: Saccade Different – Saccade Same at a
488 liberal p-value ($p < 0.05$) with cluster threshold correction (Fig. 3a). We then used
489 reduced the p-value in order to localize the centre of our *a priori* predicted parietal
490 activation (i.e., within the larger pCU/pCG area, Fig. 3b), and then used BrainVoyager
491 (BrainVoyager QX v2.8, Brain Innovation) to determine a cluster within a 1000 mm^3
492 volume ($p < 0.05$, cluster corrected; Table 1). Finally, we extracted the β-weights from
493 associated voxels around the peak voxel for the experimental data and saccade
494 localizer data (separately) in order to test our hypotheses within the parietal, ventral
495 precuneus (i.e., first, to determine the presence of a transsaccadic feature-specific

effect and, second, whether transsaccadic effects are task-specific). These analyses were carried out for the 12 participants who survived our behavioural criteria for the task and localizer.

Using the β-weights, we looked for specific directionality in the two predictions that we tested (Fig. 2), so we used one-tailed repeated measures t-tests for each of the two predictions (one to identify saccade/feature-related specificity and another to determine transsaccadic task specificity). For the results of these analyses, we provided all relevant t-statistics, p-values, and effect sizes (Cohen's d, determined using G*Power) [87].

Psychophysiological interaction.

Lastly, we were interested in uncovering the functional network for saccade-related updating during transsaccadic perception. In order to do this, we conducted psychophysiological interaction (PPI) analysis [24,66,89,90] on data extracted from the posterior parietal region that showed transsaccadic effects from the *Visual/Oculomotor Updating* phase. 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. [66] and Baltaretu et al. [24].) We created single design matrices for each run for each of the 15 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. We applied the p-value threshold (0.05) to the volumetric map and cluster threshold correction to identify clusters of activation. We used similar region localization as Song and Jiang [31], Baltaretu et al. [24], and Tsushima et al. [32] to pinpoint specific regions of activation for this analysis.

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Figure Legends

Figure 1. Experimental paradigm and eye movement traces. **A.** An example trial is shown (0.7 cycles per degree, cpd, left fixation) with the four possible conditions:

774 Fixation Same, Fixation Different, Saccade Same, and Saccade Different. Each 22 s
775 trial had three major phases: 1) *Sensory/Motor,* for the first presentation of the stimulus
776 at one of the two possible spatial frequencies (0.7 or 1.1 cpd) while gaze could be to the
777 left or right; 2) *Visual/Oculomotor Updating*, for the second presentation of the stimulus
778 at the same spatial frequency (e.g., 0.7 cpd for first and second stimulus presentations;
779 *Same* condition) or different (e.g., 0.7 cpd for first presentation and 1.1 cpd for second
780 stimulus presentation, or vice versa; *Different* condition) while participants maintained
781 fixation on the same cross (*Fixate* condition) or made a directed saccade (*Saccade*
782 condition); and 3) *Response*, for the button press response period where an indication
783 of whether the spatial frequency across the two stimulus presentations was the same
784 ('R') or different ('N'). **B.** An example eye position trace (º) for an example fixation and
785 saccade trial. In this figure, each of the two trials started with initial fixation on the right
786 (13.5º from center), then diverged after the initial presentation of the stimulus (1st visual
787 stimulus) and mask (black vertical bar), whereby gaze remained fixed for the fixation
788 trial or moved to the other fixation cross position (-13.5º from center) for the saccade
789 trial, where it remained after the second stimulus presentation (2nd visual stimulus), and
790 button press period.
791
792 **Figure 2.** Predictions used to test transsaccadic feature- and task-specificity. Prediction
793 1: For an area that shows saccade-related feature-specific modulations, there should be
794 a larger response 1) for a change in spatial frequency than a repetition, and 2) when a
795 saccade is produced than for fixation (i.e., (Saccade Different – Saccade Same) >
796 (Fixation Different – Fixation Same); SD, SS, FD, FS, respectively). Prediction 2: The

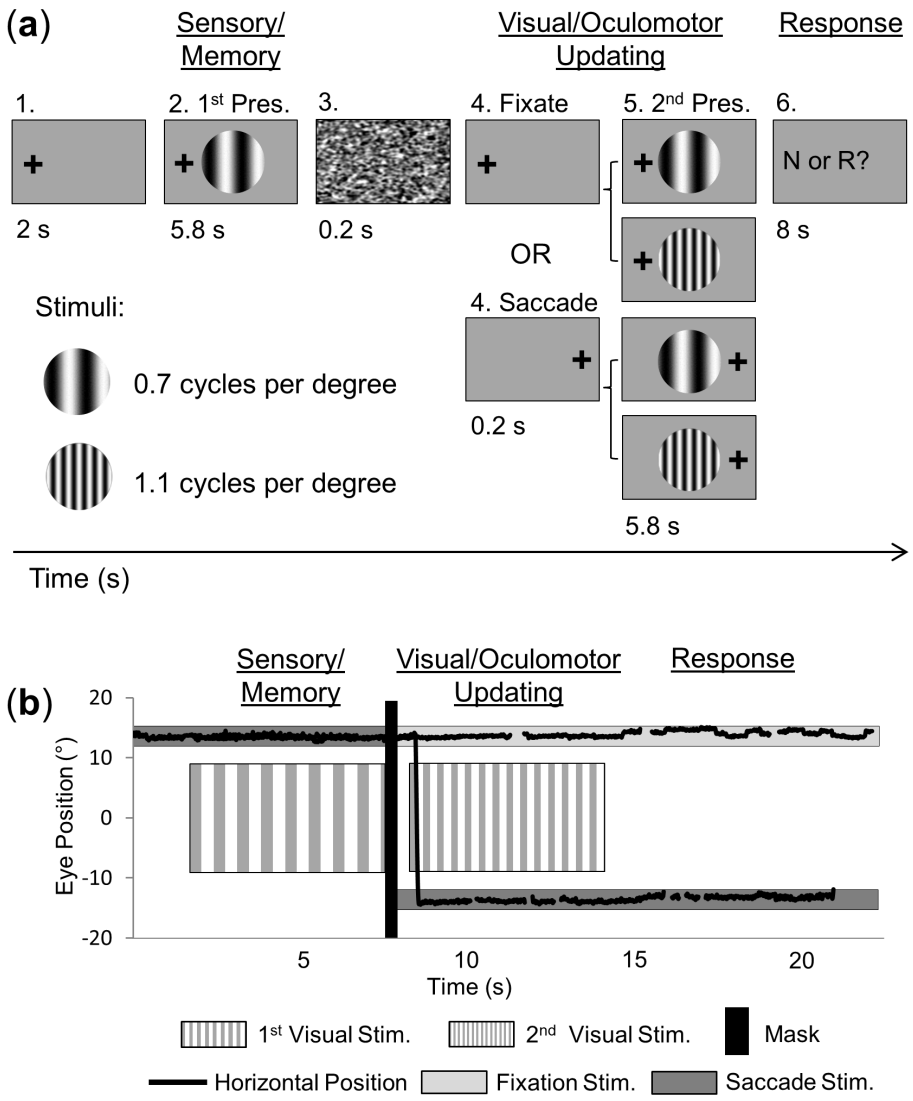
797 saccade-related effects in this region should also show task-specificity – i.e., there
798 should be larger modulations in the Saccade condition than the Fixation condition for
799 the experimental task compared with the independent saccade localizer (i.e., (Task,
800 Saccade – Task, Fixation) > (Saccade Localizer, Saccade – Saccade Localizer,
801 Fixation); TS, TF, S, F, respectively).
802
803 **Figure 3**. Testing Prediction 1: Saccade specificity in PPC during the *Visual/Oculomotor*
804 *Updating* phase. **A.** Upper panels: Voxelwise statistical map from an RFX GLM (n=15)
805 for Different > Same in the *Saccade* condition (orange) is overlaid on inflated cortical
806 surface renderings of right hemisphere of example participant (lateral view on left and
807 medial view on right). Regions in medial precuneus/posterior cingulate gyrus
808 (PCu/pCG) and frontal (MFG, middle frontal gyrus) cortex show saccade-related
809 feature-specific effects. **B.** Specific parietal site localization was performed, where the
810 site-of-interest is shown in white (i.e., ventral PCu, vPCu). The white dot corresponds to
811 location of peak voxel(s) of the site-of-interest. **C.** β-weights were extracted from vPCu,
812 analyzed, and plotted in bar graphs (n=12). In order to meet the first criterion (Prediction
813 1) to be considered a putative *transsaccadic integrator,* precuneus would need to show
814 a larger feature-related β-weight difference for the *Saccade* and *Fixation* conditions
815 (SD-SS: Saccade Different – Saccade Same; FD-FS: Fixation Different – Fixation
816 Same). As shown in the left bar graph, there is a (significantly) greater feature-related
817 difference for the *Saccade* than for the *Fixation* condition [(SD - SS) > (FD - FS)].
818 Values are mean differences ± SEM analyzed using one-tailed repeated measures t-
819 tests. (Please see Results for specific statistical values.)

820

821 **Figure 4**. Testing Prediction 2: Task specificity in PPC during the *Visual/Oculomotor*
822 *Updating* phase. **A.** Upper panels: Voxelwise statistical maps from an RFX GLM (n=15)
823 for Saccade > Fixation in the experimental task (orange; FDR ($q < 0.05$) and cluster
824 correction) versus the localizer (n=12; fuchsia; FDR ($q < 0.05$) and cluster correction)
825 are overlaid onto inflated cortical surface renderings of example participant (left
826 hemisphere on the left, right hemisphere on the right; upper panels showing the lateral
827 views, and lower panels showing medial views). There is substantial overlap in activity
828 in medial occipital regions for task and localizer. However, (experimental) task-specific
829 saccade modulations can be observed in particular occipital (middle occipital gyrus,
830 MOG), parietal (medial precuneus, mPCu; inferior parietal lobe, IPL; and superior
831 parietal lobule, SPL), and frontal saccade regions (medial superior frontal gyrus, mSFG
832 – likely pre-supplementary eye field; dorsal precentral sulcus, PCSd – likely frontal eye
833 field). **B.** The site-of-interest (i.e., ventral PCu, vPCu) is shown in white on the sagittal
834 view of the average brain of all the participants, which lies outside of the saccade-
835 specific activation for the task (orange) or localizer (fuchsia). The white dot corresponds
836 to location of peak voxel(s) of the site-of-interest. **C.** β-weights were extracted from
837 vPCu, analyzed, and plotted in bar graphs. To meet the second criterion (Prediction 2),
838 the observed saccade-related modulations for spatial frequency would have to be
839 greater for the task than for a separate saccade-only localizer. The β-weight difference
840 between *Saccade* and *Fixation* conditions is plotted for the task (TS-TF, Task, Saccade
841 and Task, Fixation) and localizer (S-F, Saccade Localizer, Saccade and Saccade
842 Localizer, Fixation). Precuneus also showed a (significant) saccade-related task-specific

843 effect [(TS - TF) > (S – F)]. Values are mean differences ± SEM analyzed using one-
844 tailed repeated measures t-tests. (Please see Results for specific statistical values.)
845
846 **Figure 5**. Functional connectivity network (A) and model (B) engaged in transsaccadic
847 updating of spatial frequency. **A.** Transverse slices through the average brain of all
848 participants are shown from most superior to inferior along the vertical axis. 'Z'
849 components of each region's Talairach coordinates are reported for reference. Shown in
850 cyan is the seed region, right precuneus (vPCu). Using a Saccade > Fixation contrast,
851 the psychophysiological interaction (PPI) analysis revealed statistically significant
852 communication between precuneus and right precentral gyrus (PCG, likely primary
853 motor cortex), as well as left lingual gyrus (LG) and medial occipitotemporal sulcus
854 (MOtS). This suggests that parietal precuneus communicates with frontal motor and
855 early/late object perception regions. **B.** A network model proposed to highlight the
856 potential interactions between right precuneus and saccade, memory, and object
857 perception regions. Expt. Region refers to a region that showed activation in our task;
858 Non-expt. Region refers to a region we did not find in our task (e.g., early visual cortex,
859 EVC); PPI connection refers to a connection derived from our PPI results; Hyp.
860 Connection refers to a hypothesized connection between regions in our model; Inhib.
861 Hyp. Connect. refers to the possible inhibitory connection between the medial PCu/pCG
862 region and MFG/dorsolateral prefrontal cortex (dlPFC).
863

Figure 1


(a)
Sensory/ Memory
Visual/Oculomotor Updating
Response
1.
2. 1st Pres.
3.
4. Fixate
5. 2nd Pres.
6.
N or R?
2 s
5.8 s
0.2 s
OR
8 s
Stimuli:
4. Saccade
0.7 cycles per degree
1.1 cycles per degree
0.2 s
5.8 s
Time (s)
(b)
Sensory/ Memory
Visual/Oculomotor Updating
Response
Eye Position (°)
20
10
0
-10
-20
5
10
15
20
Time (s)
1st Visual Stim.
2nd Visual Stim.
Mask
Horizontal Position
Fixation Stim.
Saccade Stim.

871 **Figure 2**

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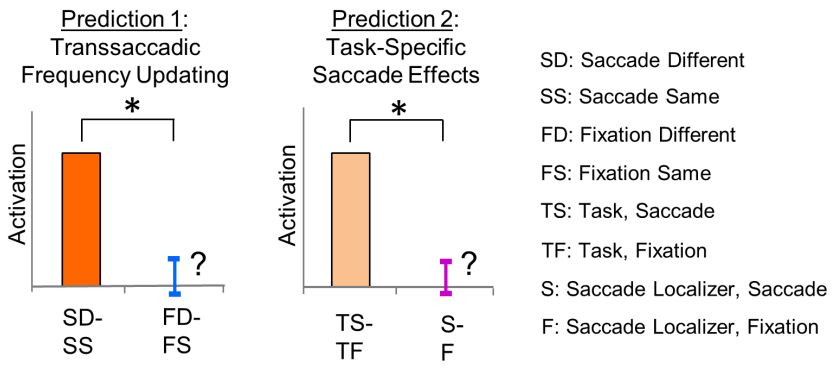

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894 **Figure 3**

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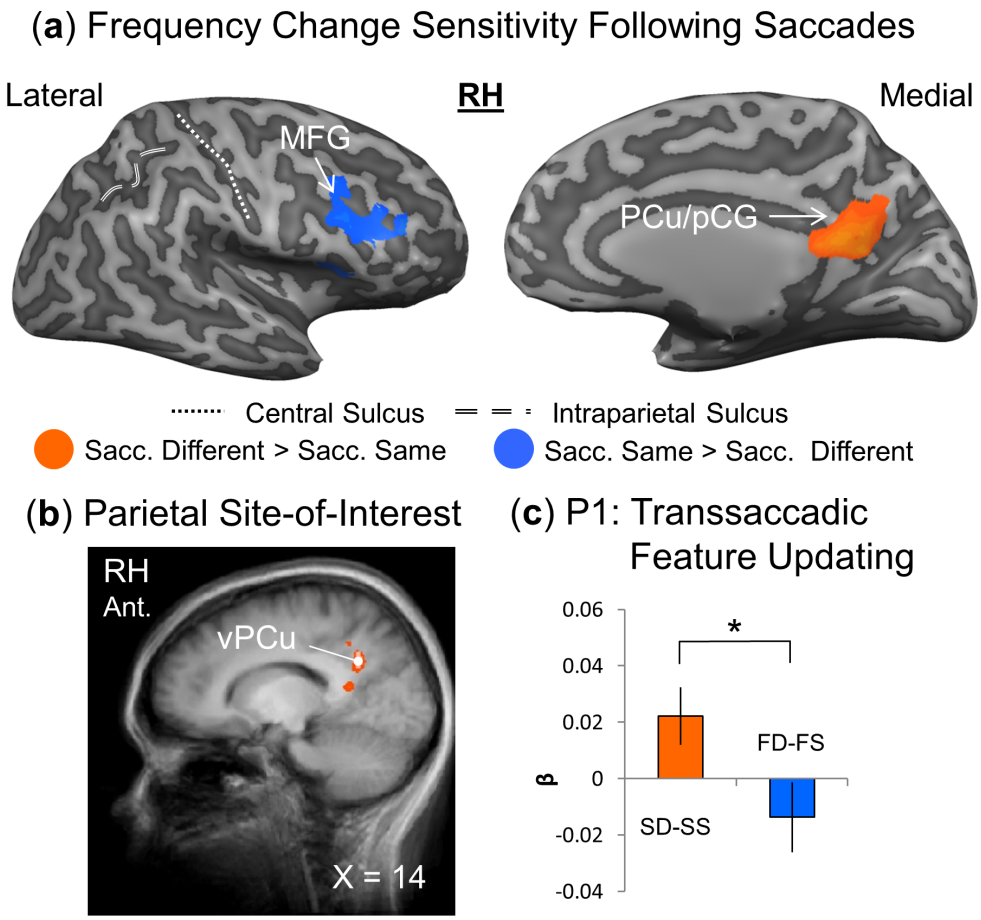

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Figure 4

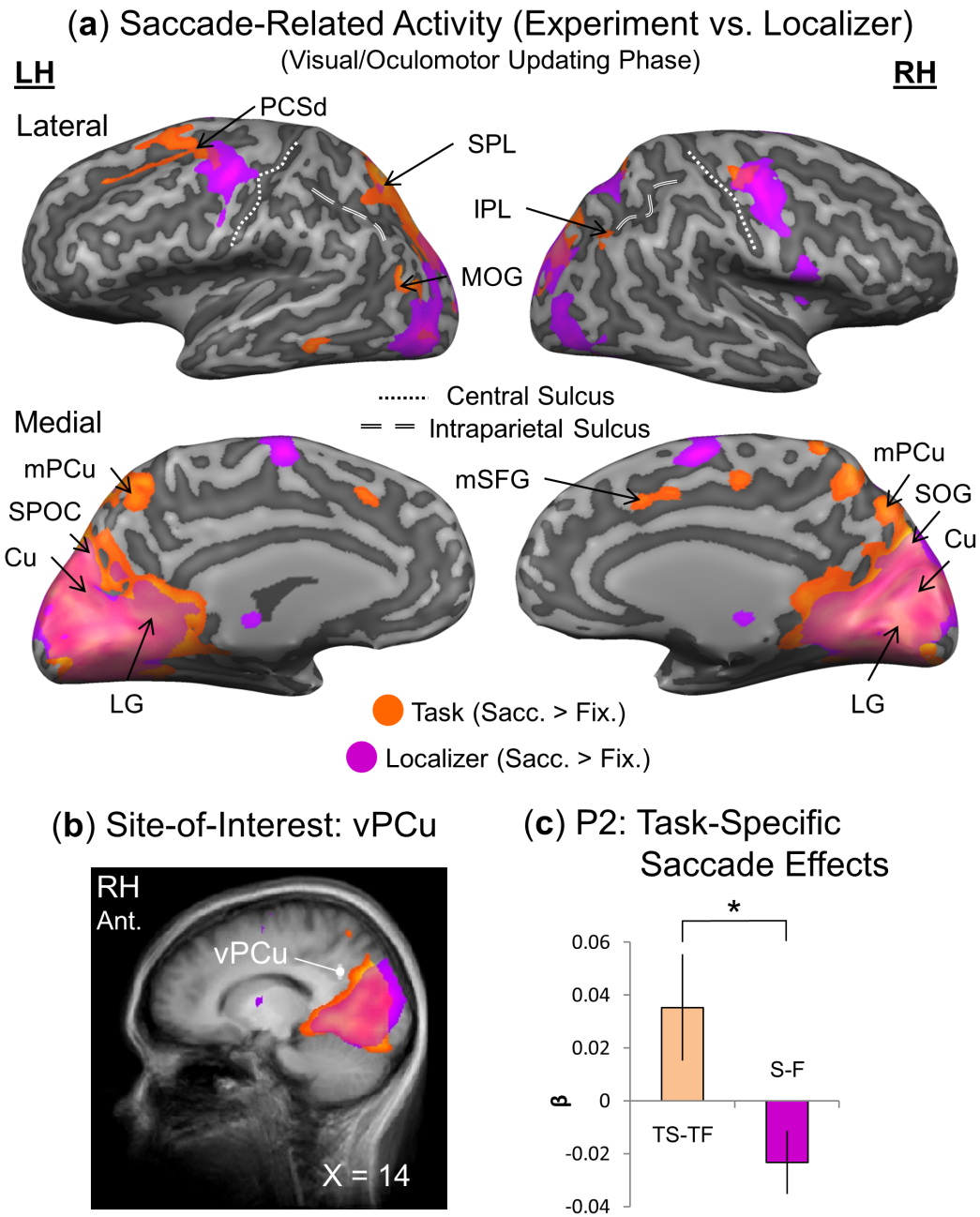
(a) Saccade-Related Activity (Experiment vs. Localizer)
(Visual/Oculomotor Updating Phase)
LH
RH
Lateral
PCSd
SPL
IPL
MOG
Central Sulcus
Intraparietal Sulcus
Medial
mPCu
SPOC
Cu
LG
mSFG
mPCu
SOG
Cu
LG
Task (Sacc. > Fix.)
Localizer (Sacc. > Fix.)
(b) Site-of-Interest: vPCu
RH
Ant.
vPCu
X = 14
(c) P2: Task-Specific Saccade Effects
*
0.06
0.04
0.02
0
-0.02
-0.04
β
TS-TF
S-F

Figure 5

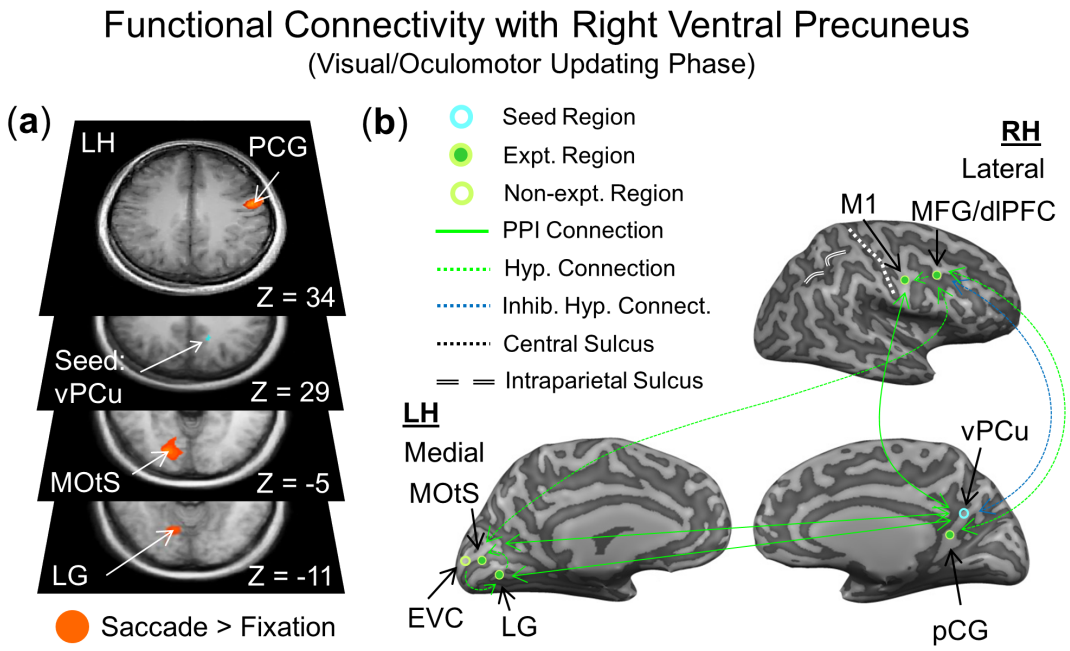
Functional Connectivity with Right Ventral Precuneus
(Visual/Oculomotor Updating Phase)
(a)
LH
PCG
Z = 34
Seed:
vPCu
Z = 29
MOtS
Z = -5
LG
Z = -11
Saccade > Fixation
(b)
Seed Region
Expt. Region
Non-expt. Region
PPI Connection
Hyp. Connection
Inhib. Hyp. Connect.
Central Sulcus
Intraparietal Sulcus
RH
Lateral
M1
MFG/dlPFC
LH
Medial
MOtS
vPCu
EVC
LG
pCG

Table 1. Names, Talairach coordinates, and sizes of regions of interest (ROIs) observed during the *Visual/Oculomotor Updating* phase.

Region of Interest	**Talairach coordinates**						**Active Voxels**	**References**
	x	y	z	Std x	Std y	Std z	*n* voxels	
RH ventral Precuneus	14	-55	29	1.3	1.3	2.8	142	[48,91]
RH posterior Cingulate Gyrus	9	-49	14	2.5	2.8	2.1	641	[91,92]
RH Middle Frontal Gyrus	39	17	37	2.7	2.5	2.7	790	[93,94]
RH Precentral Gyrus	51	-8	34	2.8	2.7	2.8	876	[95]
LH Lingual Gyrus	-13	-65	-11	2.4	2.4	2.6	618	[96]
LH Medial Occipitotemporal Sulcus	-18	-77	-5	2.4	2.7	2.4	665	[97]