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Title: Parietal Cortex Integrates Visual and Oculomotor Signals to Update Grasp Plans

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Abstract

Posterior parietal cortex participates in the spatial updating of *reach goals* during rapid eye movements (saccades), but the neural mechanisms for updating *grasp orientation* are unknown. Based on the role of the supramarginal gyrus (SMG) in transsaccadic perception, we hypothesized that it might also play a role in updating grasp plans. To test this, we employed a functional magnetic resonance imaging (fMRI) paradigm, where saccades sometimes interrupted preparation of a grasp toward an unpredictably oriented object. Right SMG and several parietal grasp areas (e.g., intraparietal/superior parietal cortex) were specifically modulated by transsaccadic changes in object orientation. Finally, a psychophysiological interaction analysis

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suggested that SMG interacted with both saccade-related cortical inputs and grasp outputs to dynamically update grasp plans during saccades. These data implicate SMG as a key module for updating object orientation for perception *and* action, and show how it interacts with sensorimotor areas to update grasp.

Introduction

We inhabit a dynamic visual environment, where brain and behavior must constantly compensate for changes in relative visual location induced by our own motion and/or external changes. For example, parietal cortex is thought to play an important role in updating reach goals in response to both unexpected changes in object location (*1*) and internally driven changes in eye position (*2*, *3*). The latter often compensates for rapid eye movements (saccades), allowing reaches toward targets that are no longer visible (*4*, *5*), and more precise aiming to visible targets (*6*, *7*). However, successful object interaction often requires more than transporting the hand towards the target, it also requires grasping: shaping of the hand to fit specific object attributes, such as shape and orientation (*8–10*). Reach transport and hand configuration must be intimately coordinated through space and time for successful grasp ((*11*); see (*12*) for review). Likewise, intended grasp location and orientation must remain linked and updated during saccades (*13*, *14*). However, to date, the cortical mechanisms that integrate saccade and object features for grasp updating have not been studied.

Clues to visual feature updating for grasp might be gleaned from studies of transsaccadic perception: the comparison and integration of visual information obtained before and after a saccade (*15–17*). Transcranial magnetic stimulation studies suggest that the frontal eye field (FEF) provides the saccade efference copy for transsaccadic integration of stimulus orientation,

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and that posterior parietal cortex is also involved (*18–20*). Recently, a functional magnetic resonance imaging adaptation (fMRIa) paradigm showed that the inferior parietal lobe (specifically, the supramarginal gyrus; SMG) is specifically sensitive to transsaccadic changes in visual stimulus orientation (*21*). Human SMG probably expands functionally and anatomically into the lateral intraparietal cortex in the monkey, which contains a mixture of saccade, visual feature, and spatial updating signals (*22*, *23*). Since the inferior parietal cortex is thought to play an intermediate role in perception and action (*24*), spanning both ventral and dorsal stream visual functions (*25*), we hypothesized that SMG might also play a role in updating stimulus orientation for grasp planning across saccades.

Feature updating, however, influences behavior only when it results in the updating of sensorimotor plans. Several parietal areas have been implicated in the visuomotor transformations for grasp, including the anterior intraparietal sulcus (aIPS) (*26*, *27*), superior parietal cortex (SPL) (*28*, *29*), and superior parieto-occipital cortex (SPOC) (*30*). Transcranial magnetic stimulation experiments suggest that SPOC is involved in early visuomotor transformations for setting reach goals (*31*), whereas more anterior areas along the intraparietal sulcus have also been implicated in updating grasp plans in response to external perturbations in object shape and orientation (*32–34*). However, it is not known if these (or other) areas are involved in the integration of saccade and orientation signals for transsaccadic updating when planning a grasping movement.

Based on this background information, we hypothesized that SMG and areas in the parietal grasp network provide the visuomotor coupling for transsaccadic grasp updating, by integrating visual feature input with internal saccade signals, originating from frontal cortex. To test this model, we performed a series of experiments in an MRI suite equipped with an eye

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tracker and a rotatable grasp stimulus that could be presented in complete darkness (Fig. 1*A*). Specifically, we merged two previously employed event-related fMRIa paradigms for transsaccadic integration (*21*) and grasp planning (*35*), respectively (Fig. 1*B*). We applied a set of criteria to identify areas involved in the integration of eye position and visual orientation changes for grasp updating: 1) these areas should be specifically sensitive to transsaccadic changes in visual orientation during grasping movements (*21*) (Fig. 1 *C1*), 2) they should show saccade modulations during grasp preparation (Fig. 1 *C2*), and 3) these modulations should be task-specific, especially in areas associated with the sensorimotor control of grasp (Fig. 1 *C3*). Finally, during grasp updating, these areas should show stronger functional connectivity for saccades than fixation, both with each other, and with the putative source of an oculomotor signal originating in the cortical saccade generator.

Results

Grasp Planning and Saccade Modulations during Action Preparation

As indicated in Fig. 1*B*, our task can be divided into three two-second phases: *Stimulus Presentation* (which begins with the original grasp stimulus orientation), *Action Preparation* (which included a saccade in 50% of trials, and ends with a Same or Different stimulus orientation that also acts as a ‘go’ signal), and *Action Execution* (where the actual reach and grasp occurs). By design, we expected brain activation to be dominated by: 1) visual signals during the *Stimulus Presentation* phase, 2) grasp preparation, saccade, and spatial updating signals during the *Action Preparation* phase, and 3) grasp motor signals and (in the case of Different stimuli) grasp orientation updating during the *Action Execution* phase of this task. We

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begin with an overview of the activation in the *Action Preparation* phase, where one might expect to find events related to the saccade-related updating of the original grasp stimulus.

Various psychophysical and neuroimaging studies have shown that humans can remember stimulus properties and use these to plan upcoming actions for several seconds or more, until a 'go' signal is provided (*27*). To isolate activity related to grasp preparation in our task, we contrasted activity during the *Action Preparation* phase against baseline activity in grasp fixation trials (Fig. 2*A*). This revealed activation in a parietofrontal network, including right SMG and several well-established reach/grasp areas: aIPS, lateral SPL (lSPL), precentral gyrus (PCG; corresponding to primary motor cortex), and dorsal / ventral precentral sulcus (PCSd/ PCSv; likely portions of these areas corresponding to dorsal and ventral premotor cortex, respectively) (*28*, *36*). Activation of this well-known parieto-frontal network (*28*) suggests that our participants began to prepare for a grasp as soon as they saw the illuminated stimulus.

Likewise, saccades also activate a well-known parieto-frontal network, but it is not clear how these signals interact with grasp plans. To see how these signals interact during our task, we compared grasp saccade trials to grasp fixation trials during the *Action Preparation* phase (Fig. 2*B*, sky blue areas), and compared this to activity from our saccade localizer task, where only saccades were made with no grasp ((Fig. 2*B*, fuchsia areas). These two contrasts produced overlap in some cortical regions (e.g., right frontal cortex and SMG), but saccades also produced extensive superior parietal and occipital modulations in the grasp task, including traditional grasp areas like aIPS and SPL. However, we could not assume that these additional modulations are related to grasp updating. They could be related to various other functions, such as updating reach *goals* (*2*, *3*), general aspects of eye-hand coordination (*37*), or expected sensory feedback

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(*38*). To identify activity specific to *transsaccadic grasp updating*, we used our *a priori* predictions (Fig. 1 *C.1, 2, 3)*, as shown in the following analyses.

Prediction 1: Saccade-Specific Sensitivity to Stimulus Orientation Changes

The first step was to determine regions that are specifically involved in transsaccadic grasp updating. If our participants incorporated original object orientation into short term memory and grasp plans, and then update this information when they see the final object orientation, one should expect: 1) activity in the corresponding brain areas to increase when stimulus orientation changes, and 2) in order to maintain spatial coherence of the internal respresentations with the physical stimulus, at least some of these orientation-sensitive brain areas should account for changes in eye position. Based on previous literature, we hypothesized that this might involve both right SMG (*21*) and the intra/superior parietal grasp network (*32*). To test this, we applied prediction 1 (Fig. 1 *C.1*) to the *Action Execution* interval. Specifically, we used a voxelwise contrast applied to the trials wherein a saccade or fixation occurred (i.e., (Grasp Saccade Different Orientation > Grasp Saccade Same Orientation) > (Grasp Fixation Different Orientation > Grasp Fixation Same Orientation)). In other words, we looked specifically for cortical areas that showed responses to orientation changes that followed saccades.

As shown in Fig. 3*A*, this contrast predominantly resulted in parietal lobe activation. In particular, right SMG, left aIPS, and bilateral SPL showed saccade-specific orientation sensitivity. All four areas passed cluster threshold correction (see Methods for details and Table 1 for Talairach coordinates). Fig. 3*B* shows the same result, but presented in a more quantitative format (β-weights extracted from voxels of peak activation) designed to enable a direct visual

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comparison with prediction 1 (Fig. 1 *C.1)*. As expected, initial stimulus orientation was not disregarded: it influenced the *Action Execution* response in several areas. More specifically, right SMG, left aIPS, and bilateral SPL produced more grasp execution activity when orientation changed, and only after a saccade. Having met this first criterion, we will henceforth refer to these areas as putative grasp updating sites, and only apply our remaining criteria to the same four sites.

Predictions 2 and 3: Site-Specific Saccade Modulations and Task Specificity

The saccade-specific modulations observed in our four putative grasp areas were consistent with updating, but could have been caused just by the change in retinal location of the visual stimulus. In order to qualify as updating areas, we had to show that they also receive internal input from the saccade system. To test this directly, we examined *Action Preparation* phase activity of our task (prediction 2) and compared this to our separate saccade localizer data in our four putative updating areas (prediction 3). Panels *A* and *B* of Figure 4 show the locations of the peak voxels from our four putative grasp updating sites, superimposed on the overall preparatory activity during fixation only, and saccade modulations in our task and saccade localizer, respectively (derived as in Fig. 2). All four sites (right SMG, left aIPS, and bilateral SPL) fell within regions of grasp preparation (Fig. 4*A*), as well as within, or bordering on, regions of saccade modulation (Fig. 4*B*). To test saccade sensitivity in these regions (during *Action Preparation*), we applied prediction 2 on β-weights extracted from these locations (Fig. 4*C*). All four regions showed significantly higher preparatory activity in the presence of saccades, although SMG did not survive correction for multiple comparisons.

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Finally, we wished to ascertain which of these saccade modulations were task-specific (i.e., specific for grasp updating opposed to general saccade-related updating). To test this, we applied prediction 3, i.e., we tested if our putative grasp updating areas showed saccade modulations during our grasp task and not during our saccade localizer (Fig. 4*D*). In this case, only aIPS and bilateral SPL showed significant task specificity, but not SMG. This suggests a progression of task-specificity from SMG to the more motor areas. Overall, this series of tests show that right SMG, left aIPS, and bilateral SPL are modulated by saccades (the latter three in a grasp-specific fashion), and are sensitive to changes in object orientation that followed saccades, thus meeting our pre-set criteria. We next asked if these areas form a functional network with the saccade generator.

Functional Connectivity of SMG with Saccade and Grasp Areas

Our analyses so far have confirmed our perceptual updating result for SMG (*21*), and extended this function to sensorimotor updating in aIPS and SPL for grasp; but, do these regions participate in a coherent functional network for grasp updating? Based on our previous finding that right SMG is active for perceptual orientation updating (*21*), and its re-appearance in the current grasp updating task, we hypothesized that SMG is a key hub for updating visual orientation across saccades, and that it would communicate with both saccade regions (for signal input) and grasp regions (for signal output) during our grasp task. To do this, we identified a seed region within the right SMG from our independent saccade localizer data, and performed a psychophysiological interaction (PPI) analysis to examine which areas showed increased functional connectivity for saccade as compared with fixation trials with SMG during *Action Preparation* (Fig. 5*A*-*C*). This resulted in three sites that survived cluster threshold correction:

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right PCSd (likely a portion corresponding to FEF), left medial, superior frontal gyrus (likely the supplementary eye field, SEF), and SPL (including a region that overlaps with aIPS).

Discussion

In this study, we set out to identify the cortical areas associated with updating grasp plans during changes in gaze direction and/or object orientation. We reasoned that, in order to perform this function, the brain would have to integrate saccade signals in areas sensitive to visual orientation and/or grasp orientation updating. To identify these areas, we applied three specific criteria: transsaccadic sensitivity to orientation changes during grasp execution, sensitivity to intervening saccades during motor preparation, and task specificity in these modulations, at least in the more superior parietal grasp motor areas. We found four areas that met these criteria: right SMG, an area previously implicated in transsaccadic orientation perception (*21*), and three more dorsal areas that are associated with grasp correction (*19*, *39*). Finally, with the use of task-related functional connectivity analysis with area SMG, we identified a putative network for saccades that includes parietal and prefrontal regions.

Transsaccadic Updating of Object Orientation for Grasp

In a previous study, we found that the right anterior inferior parietal lobe (SMG) is involved in transsaccadic comparisons of object orientation for perception (*21*). Here, we hypothesized that SMG would contribute to feature updating for grasp execution, whereas some part of other areas involved planning/updating grasp orientation (*26*, *40*, *41*) would also be involved in the transsaccadic updating of orientation for grasp preparation. To test this, we compared orientation change specificity for saccades versus fixation during *Action Execution*,

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and found four areas (right SMG, left aIPS, and bilateral SPL) that fit this criterion and passed our standard statistical criteria. We further found that all of these areas were modulated by saccades during grasp preparation, although the motor task specificity of these modulations was clearer in aIPS and SPL. Finally, the laterality of these responses was consistent with our hypothesis, i.e., right SMG being consistent with the general role of right parietal cortex in spatial awareness (*42*), whereas left aIPS was opposite to the motor effector uses (the right hand). This supports a general-purpose role for right SMG in the transsaccadic updating of object orientation, and adds a more unique role for aIPS and SPL in updating grasp orientation.

SMG is an area that has largely been implicated in perception tasks, such as those requiring spatial processing of orientation (*43*) and visual search (*44*), or those requiring crossmodal spatial attention (*45*). In contrast, SPL has been implicated in both saccade- and grasp-related populations (*29*) that make it an ideal site to respond to changes in retinal visual information about the position and orientation of an object. This may alter any hand preshaping signals that will be sent from SPL (*42*) to PMd (*47*, *48*), which possesses both mixed saccade-and-reach or reach-only populations of neurons (*29*). Finally, aIPS is sensitive to object orientation information for grasp (*23*, *46*). It is thought that populations of neurons in aIPS may process object features such as its orientation in order to ultimately shape and orient the hand to match the object's shape and orientation (*40*, *51*). Information related to grasping is then proposed to travel to PMv to engage specific reach/grasp-related neuronal populations to generate motor commands (*44*, *48*). Thus, our result appears to be consistent with the known functions of these areas, and extends our understanding of how these functions might be linked to update grasp signals in the presence of saccades.

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A Putative Network for Transsaccadic Updating of Grasp Plans

An important goal for this study was to understand how distributed cortical regions might work as a network to update grasp plans during saccades. Based on the computational requirements of this function, we hypothesized that such a network should involve: 1) areas specific to transsaccadic updating of orientation features, 2) saccade areas for oculomotor input, and 3) and grasp updating areas for motor output. Given our previous (*21*) and current results, we hypothesized that right SMG to plays a general role in trans-saccadic update of orientation for both perceptual and sensorimotor control (i.e., here, it would update object features during the *Action Preparation* phase so that these could be spatially integrated with new visual information for *Action Execution*). Based on this conjecture, we chose right SMG as the seed region for our functional connectivity analysis. As described in the Introduction, we expected prefrontal saccade areas to play the second role, and parietal grasp areas to provide the final role (based on our current results, aIPS/SPL). Indeed, this analysis revealed a functional network for saccades versus fixation involving right SMG, right SPL, right aIPS, right PCSd, and the left superior frontal gyrus. Taken together with the overlapping areas that fit the previous three criteria, this suggests a saccade-dependent network with the specific properties needed for updating grasp orientation.

PPI analysis does not provide directionality, but based on the functional requirements of the task and known physiology of these areas, we conceptualized this network as shown in Fig. 5*D*. PCSd likely corresponds to the right FEF (*53*, *54*). The FEF is a key component of the cortical saccade generator (*54*), and is known to provide reentrant feedback to earlier visual areas (*55*, *56*). The superior frontal gyrus likely corresponds to the supplementary eye field (*54*, *57*), which has reciprocal connections with FEF. Thus, FEF/SEF could be the source of saccade

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signals for SMG and the entire network. As discussed above, aIPS (*58*) and SPL are implicated in grasp planning / corrections, show saccade signals (*29*, *46*), and of course were already implicated in transsaccadic grasp updating in our other analyses. Thus, this putative network appears to possess all of the signals and characteristics that one would expect to find in a transsaccadic updating circuit during grasp preparation.

Eye-hand coordination is relatively understood in terms of the transport component of reach, but little is known about the integration of saccade and visual signals for updating grasp configuration across eye movements. We set out to identify a putative human grasp updater and found a remarkably consistent cluster of regions including SMG and aIPS/SPL, (likely) receiving oculomotor inputs from prefrontal eye fields. This network provides the necessary neural machinery to integrate object features and saccade signals, and thus ensure grasp plans remain updated and coordinated with gaze-centered reach transport plans (*2*, *3*). These new findings have several general implications: First, this circuit might explain some of the various symptoms of apraxia that results from damage to the posterior parietal cortex (*59*, *60*). Second, the role of the inferior parietal cortex in both transsaccadic perception (*21*) and grasp updating supports the notion that inferior parietal cortex (a very late phylogenetic development) has high-level visuospatial functions for both ventral and dorsal stream vision (*25*). Finally, the various roles of specific parietal modules in spatial updating (*61*), visual feedback corrections (*62*), and (here) a combination of the two for action updating, support a general role for parietal cortex for detecting, differentiating, and compensating for internally and externally induced spatial perturbations.

Materials and Methods

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Participants

Seventeen graduate students with normal or corrected-to-normal vision from York University, Toronto, Ontario, Canada participated in the study. Participants were compensated financially for their time. These participants were all right-handed and were of 26.5 +/- 3.7 years of age (from 22 to 32). All participants provided written consent and had no neurological disorders. On the basis of motion correction parameters (described below), four participants were excluded, leaving thirteen participants for the analyses described in the Results section. The York University Human Participants Review Subcommittee approved all experiments.

Experimental set-up and stimuli

Participants were asked to fill out an MRI screening form. Upon passing MRI screening, participants were informed about the task. Once they felt comfortable with what the experiment entailed, they were asked to assume a supine position on the MRI table, with their head in a six-channel coil tilted forward at a 20° angle (in order to allow for direct visibility of the objects) (*40*). To obtain a complete signal, we also placed a four-channel coil anteriorly on the head (*40*).

This experiment was conducted in complete darkness. In our set-up, we had red fixation light emitting diodes (LEDs) for participants to focus on during the entire duration of a trial. A fixation LED was placed to the left and right of the central stimulus (between 10-12° from the center of the stimulus to each LED; (*40*)). There was also a white LED that was used to illuminate the stimulus only when participants would grasp at a particular time point in each trial (Fig. 1*A*, *B*). These LEDs were mounted onto a rotatable platform that was placed above each participant's pelvis. LEDs were held in place by MRI-compatible rigid tubes (which were made

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of many units to allow for movement of the overall tube in order to position the LEDs accordingly).

The stimulus that participants had to grasp was a six-degree long bar with rounded ends (Fig. 1*A*, *B*) and centered on the platform. The bar could be rotated, but two MRI-compatible pins were placed in the surrounding area to ensure that the bar could only be oriented horizontally (0°) or obliquely (135°).

For each participant, right eye position was recorded using an infrared (IR) camera affixed to the right side of the MRI table (Fig. 1*A*). Eye movement signals were recorded using iViewX software (SensoMotoric Instruments) for offline analysis. We recorded, using a hand camera (Fig. 1*A*), the reaching and grasping movements of participants during each trial of every run.

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

General paradigm/procedure

Experiment

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We used an event-related fMRI design to determine the cortical underpinnings of saccade-modulated activity during grasping. We also had the additional factor of object orientation change and examined how object orientation might affect cortical activity during the task and how these two factors (saccades and object orientation) interacted.

Before running the experiment, subjects were trained to reach at specific times within each trial (Fig. 1*A*, *B*). Moreover, participants were instructed to use all digits of their right hand to grasp the object centrally (Fig. 1*A*). When not reaching, participants rested their arm, bent at the elbow, on their abdomen in a position that was within comfortable reaching distance of the stimulus (distance was determined before the experiment started).

Each trial started with the illumination of one of the two LEDs to the right and left of the central target. Then, the central target was illuminated for 250 ms. The target could be oriented at 0° or 135° (pseudorandomized and counterbalanced within and across runs). Participants were required to keep fixating for another 1.75 s. This first two-second phase was referred to as the '*Stimulus Presentation*' phase (Fig. 1*B*). After this period, participants kept fixating on the same LED for another 1.75 s ('Fixate' condition) or make a saccade to the other LED, which would be illuminated while the previous LED would be extinguished ('Saccade' condition). Following this 1.75 s period, the object was illuminated for 250 ms. This was referred to as the '*Action Preparation*' phase (Fig. 1*B*). The object could now be oriented in the same orientation as in the first illumination/presentation ('Same' condition, e.g., 0° orientation first and then, another 0° orientation; same for the 135° orientation) or a different orientation as compared to the first ('Different' condition, e.g., 0° orientation first, followed by a 135° orientation and vice versa). Participants were then given 4 s to reach out to grasp the object in its final orientation as described above ('*Action Execution'* phase) while still fixating the illuminated LED, and then

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move their hand back to the resting position on the abdomen. Following this phase, the LED was set up for the next trial and participants had 16 s to rest while maintaining fixation (intertrial interval, ITI), so as to allow the BOLD signal to come back to baseline. The illumination of the stimulus marked the beginning of each trial and the end of the 16 s period of relaxation marked the end of the trial.

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

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

Compared to our previous studies (*21*, *63*), we used a shorter stimulus period (total of 2 s for each stimulus presentation) in order to match a TR time of 2 s, and to ensure a reasonably long run/ experiment (given that a long ITI is needed to allow the BOLD to return to baseline). This is more than enough time for transsaccadic integration to occur: recent studies have suggested that this process can occur on the order of tens of ms (*64*). In addition, we chose a fixed ITI (no jitter) because we did not investigate timing in this study and we wished to maximize our statistical power to detect relatively subtle transsaccadic integration signals (*21*).

Saccade Localizer

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To determine which regions are involved in the production of saccadic eye movements, we used a localizer that had a sequence similar to that of the experimental runs. This localizer comprised alternating periods of fixation and saccadic eye movements. First, a baseline of activity would be established as a result of participants fixating the illuminated LED for 18 s (two runs total of data were collected, where participants fixated the left LED first and right LED second, or vice versa). Then, every second for 6 s, the LEDs would alternate in illumination, resulting in saccades. After this, participants would then fixate the initial LED for 16 s. This fixation-saccade sequence was repeated eight times in the localizer run. There was a last fixation period of 18 s. For each of these two runs, 98 volumes were acquired, with 35 slices per volume (TR= 2000 ms, TE= 30 ms; in-slice resolution of 3 mm x 3 mm; slice thickness= 3.5 mm, no gap).

Imaging Parameters

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

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Analysis

Behavioral data

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

Functional imaging data: Experimental

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

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were four predictors for the first 2 s of the grasp event. These predictors were based on the direction of the preceding saccade and upon whether the orientation of the object that was being grasped was the same in the *Action Preparation* phase as in the *Stimulus Presentation* phase (Same condition) or different (Different condition). Thus, the four predictors were: "Motor Execution_Sacc_NovFeature", "Motor Execution_Sacc_RepFeature", "Motor Execution_Fix_NovFeature", and "Motor Execution_Fix_RepFeature". The following 2 s of the *Action Execution* phase were provided a "Motor Execution" predictor. These predictors comprised each GLM for each participant (BrainVoyager QX 2.8, Brain Innovation). Each predictor variable was convolved with a haemodynamic response function (standard two-gamma function model) (*21*). GLMs were modified through the addition of confound predictors for eye movement or hand movement errors. If a GLM had more than 50% of the trials being modelled in the confound predictor, the GLM for that run was not included in the overall population level GLM (random effects GLM, RFX GLM).

Additionally, functional data for all runs across all participants was preprocessed (slice time correction: cubic spline, temporal filtering: <2 cycles/run, and 3D motion correction: trilinear/sinc). Data for runs that had abrupt motion of over 2 mm were excluded from the RFX GLM and additional analysis. As a result, four participants' data were excluded because more than half of the runs were unusable due to abrupt, excessive head motion of over 2 mm. The anatomical data was transformed to a Talairach template (*65*) and the functional data from the remaining 13 participants were coregistered using gradient-based affine alignment (translation, rotation, scale affine transformation) to raw anatomical data. Lastly, functional data were smoothed using an FWHM of 8 mm.

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We used voxelwise analysis of β-weights obtained during the *Action Preparation* and *Action Execution* phases in order to determine whether there are any cortical regions that are modulated by saccades during the period of preparation and by transsaccadic integration of object orientation during grasping. β-weights were extracted from the selected regions and were used to test our hypotheses. For each *a priori*-motivated t-test conducted within hypothesized regions, we indicate the relevant statistical values (i.e., t-statistic and p-values).

Functional Imaging Data: Localizer

For the preprocessing of functional data for the localizer, see above section. On the basis of excessive head motion (>2 mm), two participants' localizer data were excluded for when the starting fixating LED was on the left and two for when the starting LED was on the right (one of these participants had their data excluded from both the left and right LED conditions, thus leaving a total of ten participants' data to analyze further). Using the remaining functional data, we ran an RFX GLM on the data for each of the localizers. For the saccade localizers, we had three predictors: a 9 s "Baseline" predictor, a 16 s fixation "Fix" predictor, and a 6 s saccade "Sacc" predictor. The results of the saccade localizer were used to identify which regions are involved in saccade production in our task specifically (Figs. 2*B*, 4*B*).

Functional Connectivity: Psychophysiological Interaction Analysis

In order to determine the network of cortical regions that interact to update saccade signals during the preparation of a grasp, we conducted psychophysiological (PPI) analysis (*66–68*) during the *Action Preparation* phase. In order to carry out this analysis, we had three predictors: 1) physiological component (z-normalized time courses obtained from the seed regions for each participant for each included run), 2) psychological component (predictors of the model were convolved with a haemodynamic response function), and 3) psychophysiological

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interaction component (multiplication of z-normalized time courses with task model in a volume-by-volume manner). For the task model produced for the psychological component, the Saccade predictors were set to a value of '+1', whereas the Fixation predictors were set to a value of '-1;' all other and baseline predictors were set to a value of '0'. Single design matrices (SDMs) were created for each participant for each included run. These were subsequently included in an RFX GLM for right SMG (*66*) in order to determine functional connectivity with each of these regions.

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B.R.B. and J.D.C. designed the study. G.N.L and J.V.-I. collected and analyzed data. B.R.B. and J.D.C. wrote the manuscript. S.M. provided advice on analysis and edited the manuscript.

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Figures and Tables

Fig. 1. Experimental set-up, paradigm, and predictions. (**A**) Set-up of the experiment, showing participant lying supine on MRI table with head tilted at 20° under the head coil, along with MRI-compatible eye tracker for right eye and hand tracker. Participants rested their hand on the abdomen in a comfortable position and were asked to transport their hand to the platform to grasp an oriented 3D bar; a strap across the tor-so was used to ensure minimal-to-no movement

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of the shoulder and arm during transportation of the hand to the platform. The blue stalk above the platform was used to illuminate the central grasp object, whereas those to the left and right contained LEDs and were used to ensure fixation of gaze. A black ellipse has been placed on top of the model's face to ensure anonymity. (**B**) Stimuli and task. An example of an initial trial condition is shown (0° grasp bar, gaze left) followed by the four possible conditions that might result: Fixate / Different Feature, Fixate / Same Feature, Saccade / Different Feature; and Saccade / Same Feature). Each trial lasted 24 seconds and was comprised of three major phases: 1) Stimulus Presentation, during which the grasp object was illuminated in one of two possible orientations (0° or 135°) and gaze could be left or right; 2) *Action Preparation*, when participants maintained fixation on the same LED as in the previous phase (Fixate condition) or they made a saccade to the opposite LED (Saccade condition) – the object was illuminated a second time at the end of this phase and was presented either in the Same orientation as in phase 1 (0° if the initial was 0° or 135° if the initial orientation was 135°; Same condition) or at a Different orientation (0° if the initial was 135° or vice versa; Different condition); and 3) *Action Execution*, which required participants to grasp the oriented object for 2 s and then, return to rest. (**C**) The possible predictions for sensitivity to saccade signals in grasp areas in three conditions. **C.1**. The first prediction suggests that, during the *Action Execution* phase, cortical regions that specifically update object orientation across saccades should show a greater difference in activity between the Same and Different orientation conditions in the Grasp Saccade condition, as compared with the Same – Different orientation difference in the Grasp Fixate condition (GSDO, GSSO, GFDO, GFSO, respectively). **C.2**. The second prediction indicates that, if a grasp area is modulated by saccade signals, the BOLD activity should be greater for the Saccade condition (Grasp Saccade condition, GS), as compared with the Fixate condition (Grasp Fixation

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condition, GF). **C.3**. The third prediction tests whether modulations due to saccade signals during the grasp *Action Preparation* phase (**C.2**) are specific to grasp-related activity. This predicts a greater difference between the Saccade and Fixate conditions in the grasp experiment compared to a separate saccade localizer that only required participants to either saccade between our two LEDs or fixate on one of the LEDs ((Grasp Saccade - Grasp Fixate) > (Saccade – Fixate); GS - GF > S - F).

Fig. 2. Lateral view of (A) reach/grasp cortical regions and (B) saccade modulations during Action Preparation. (**A**) Shown is an inflated brain rendering of an example participant (left and right hemispheres from the lateral view, respectively). An activation map obtained using an RFX GLM (n=13) is shown for the contrast, Grasp Fixation > Baseline (chartreuse). Abbreviations: PCSd: dorsal precentral sulcus, PCSv: ventral precentral sulcus, PCG: precentral gyrus, aIPS: anterior intraparietal sulcus, SPL: superior parietal lobe, SMG: supramarginal gyrus. (**B**) Activation maps for a Saccade > Fixate contrast obtained using an RFX GLM (n=13) on grasp experiment data (sky blue) and on a separate saccade localizer (fuchsia) were overlaid onto an inflated brain rendering from an example participant (left and right hemispheres shown in the lateral views). Abbreviations: PCSd: dorsal precentral sulcus, PCSv: ventral precentral sulcus, PCG: precentral gyrus, lSPL: lateral superior parietal lobe, aIPS: anterior intra-parietal sulcus, mIPS: middle intraparietal sulcus, SMG: supramarginal gyrus, SOG: superior occipital gyrus, TOS: transverse occipital sulcus, MOG: middle occipital gyrus, IOG: inferior occipital gyrus, STS: superior temporal sulcus.

Fig. 3. Post-saccadic Different vs. Same orientation responses during Action Execution. (**A**) Voxelwise statistical map overlaid onto inflated brain rendering of an example participant obtained using an RFX GLM (n=13) for Different > Same in the Grasp Saccade condition as

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compared with the Grasp Fixate condition ($p<0.05$). Top panels show the lateral views of the inflated brain rendering on which can be seen activation in right superior lateral lobe (SPL) and supramarginal gyrus (SMG). In the middle, bottom panels, the top view of the left and right hemispheres can be seen, which display activation also in the left anterior intraparietal sulcus (aIPS) and SPL. The left and rightmost panels contain transverse slices through the average brain of all the participants onto which the activation in these five regions can be viewed in more detail. (**B**) Bar graphs of β-weights plotted for the difference between the Grasp/Saccade Different and Same orientation conditions (dark orange) versus the difference between the Grasp/Fixation Different and Same conditions (light orange). Data were extracted from peak voxels from the transsaccadic regions shown in (**A**). Statistical tests were carried out on β-weights extracted from peak voxels on these areas in order to test Prediction 1. Values are mean ± SEM analyzed by dependent t test. * indicates a statistically significant difference between the GS and GF β-weights during the *Action Preparation* phase (Bonferroni corrected at a $p<0.0125$). Δ indicates an uncorrected significant difference between the GS and GF β-weights during the preparatory period (not Bonferroni corrected, $p<0.05$).

Fig. 4. Location of putative transsaccadic reach updating sites (from Fig. 3) relative to grasp areas (A) and saccade modulations (B) during Action Preparation, followed by prediction tests 2 (C) and 3 (D). (**A**) Shown is an inflated brain rendering of an example participant (left and right hemispheres viewed from above, respectively). An activation map obtained using an RFX GLM (n=13) is shown for the contrast, Grasp Fixation > Baseline (chartreuse). The four transsaccadic regions from the *Action Execution* phase are overlaid onto this *Action Preparation* activation. aIPS: anterior intraparietal sulcus, SPL: superior parietal lobe, SMG: supramarginal gyrus. (**B**) Activation maps for a Saccade > Fixate contrast obtained using

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an RFX GLM (n=13) on grasp experiment data (sky blue) and on a separate saccade localizer (fuchsia) were overlaid onto an inflated brain rendering from an example participant (left and right hemispheres shown from a bird's eye view). These overlaid activation maps allow for comparison of which cortical regions respond to saccade signals in a grasp task-specific manner. Abbreviations: aIPS: anterior intraparietal sulcus, SPL: superior parietal lobe, SMG: supra-marginal gyrus. (**C**) Bar graphs of β-weights plotted for Grasp Saccade conditions (dark blue) versus Grasp Fixation conditions (light blue) from all thirteen participants. Data were extracted from peak voxels from the transsaccadic regions represented by the black dots above in A and B in order to test prediction 2. Values are mean ± SEM analyzed by dependent t test. (**D**) Bar graphs of β-weights plotted for Grasp Saccade conditions (pale blue) versus Grasp Fixation conditions (magenta). Data were extracted from peak voxels from the transsaccadic regions shown in Fig. 2A and B, which com-pared for only the ten participants whose data were analyzed for the saccade localizer. Statistical tests were carried out on β-weights extracted from peak voxels in these are-as in order to test prediction 3. Values are mean ± SEM analyzed by dependent t test. * indicates a statistically significant difference between the GS and GF β-weights during the preparatory period (Bonferroni corrected at a $p<0.0125$). Δindicates an uncorrected significant difference between the GS and GF β-weights during the preparatory period (not Bonferroni corrected, $p<0.05$).

Fig. 5. Functional connectivity network involved in processing saccade signals during Action Preparation. (**A-C**) Using a Saccade > Fixation contrast and the right supramarginal gyrus (SMG) as a seed region, psychophysiological interaction is shown in the activation maps (yellow for positive correlation; copper for negative correlation) overlaid onto the inflated brain

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renderings of an example participant. Right frontal eye field (FEF), SPL (that extends into the anterior intraparietal sulcus, aIPS) and left supplementary eye field (SEF) show significant, cluster-corrected positive correlation with right SMG. Only areas that passed a $p<0.05$ and cluster threshold correction are labeled. (**D**) A potential network for the communication between right SMG and other saccade and grasp regions.

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Figure 1

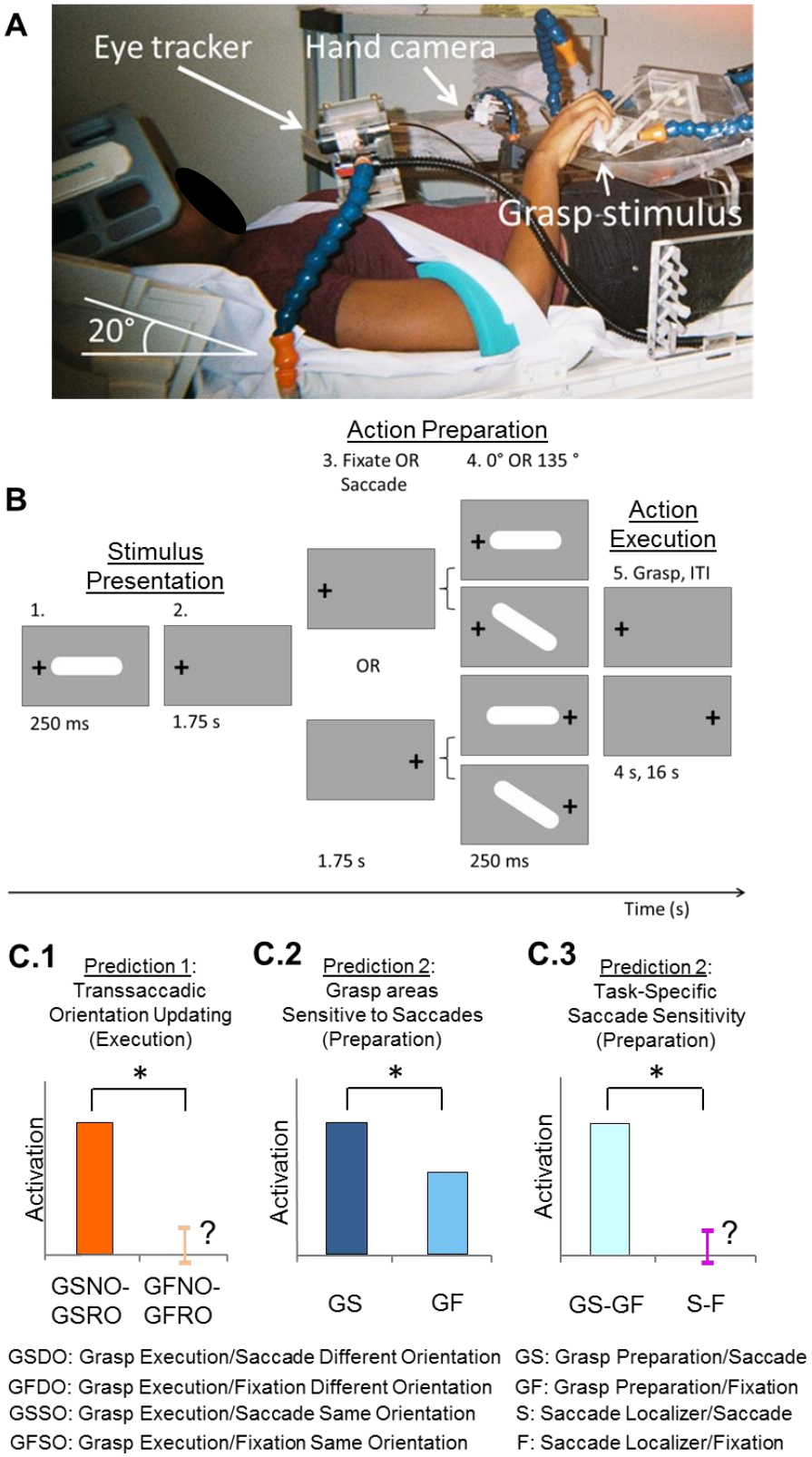

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Figure 2

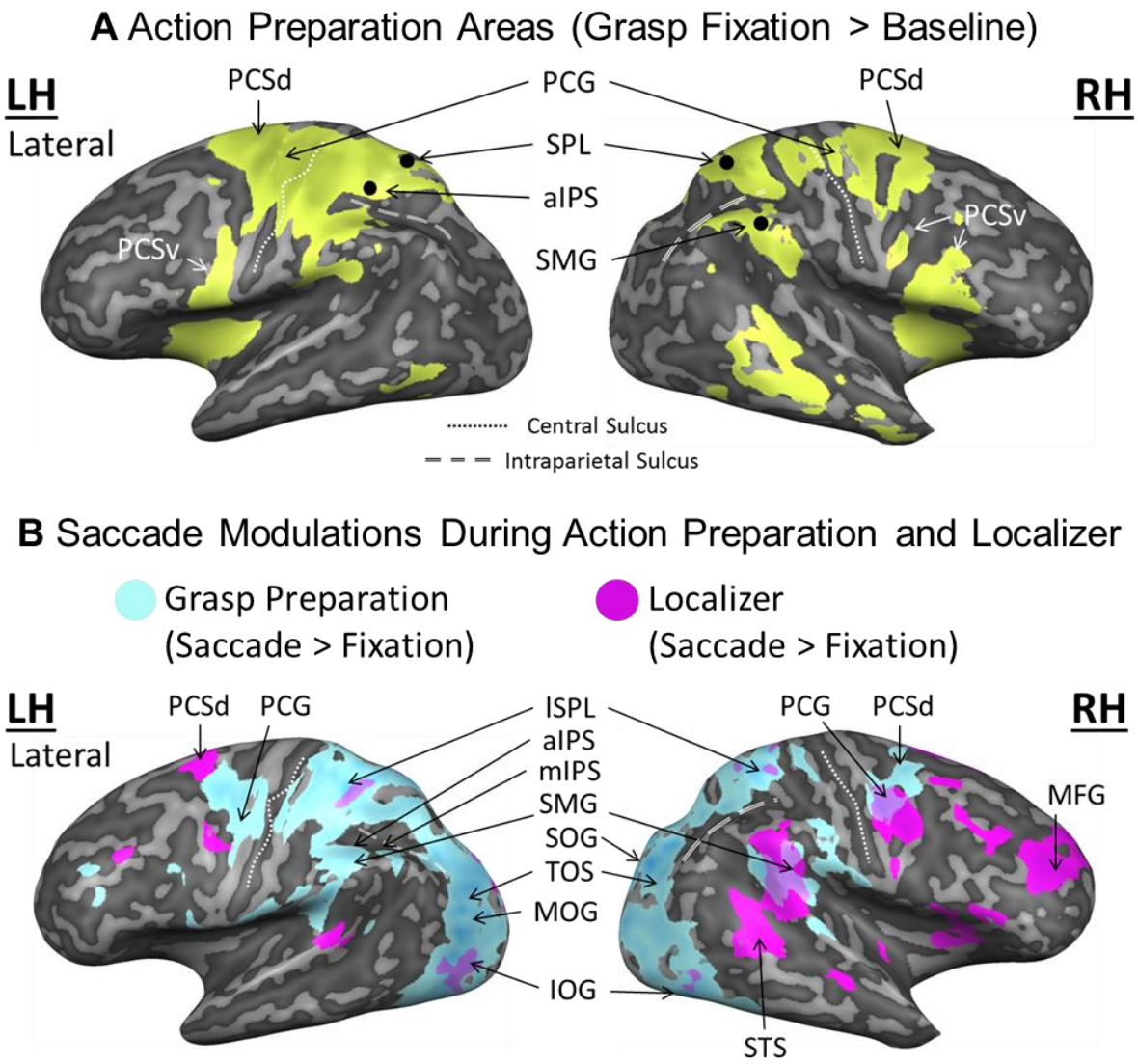

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Figure 3

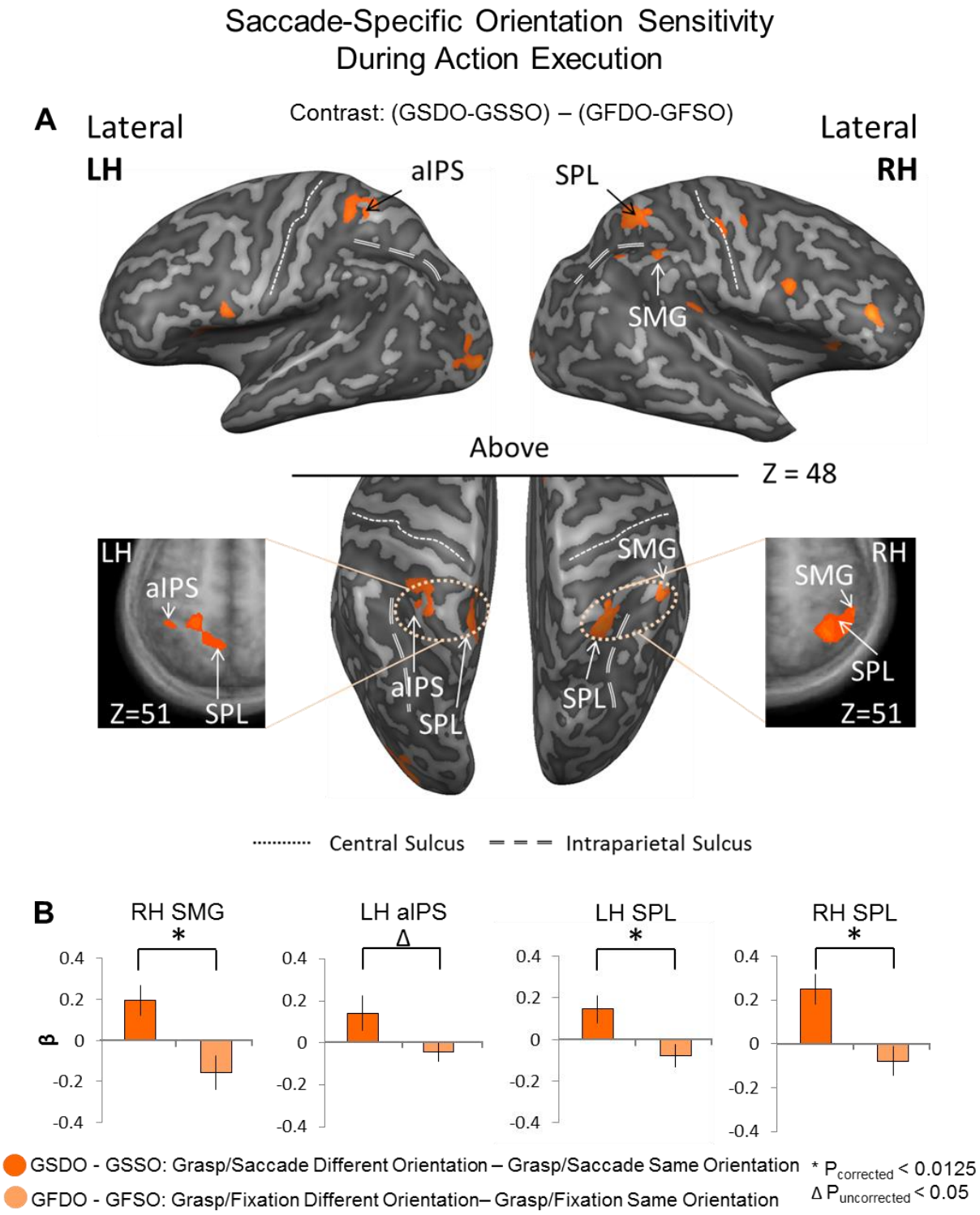

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Figure 4

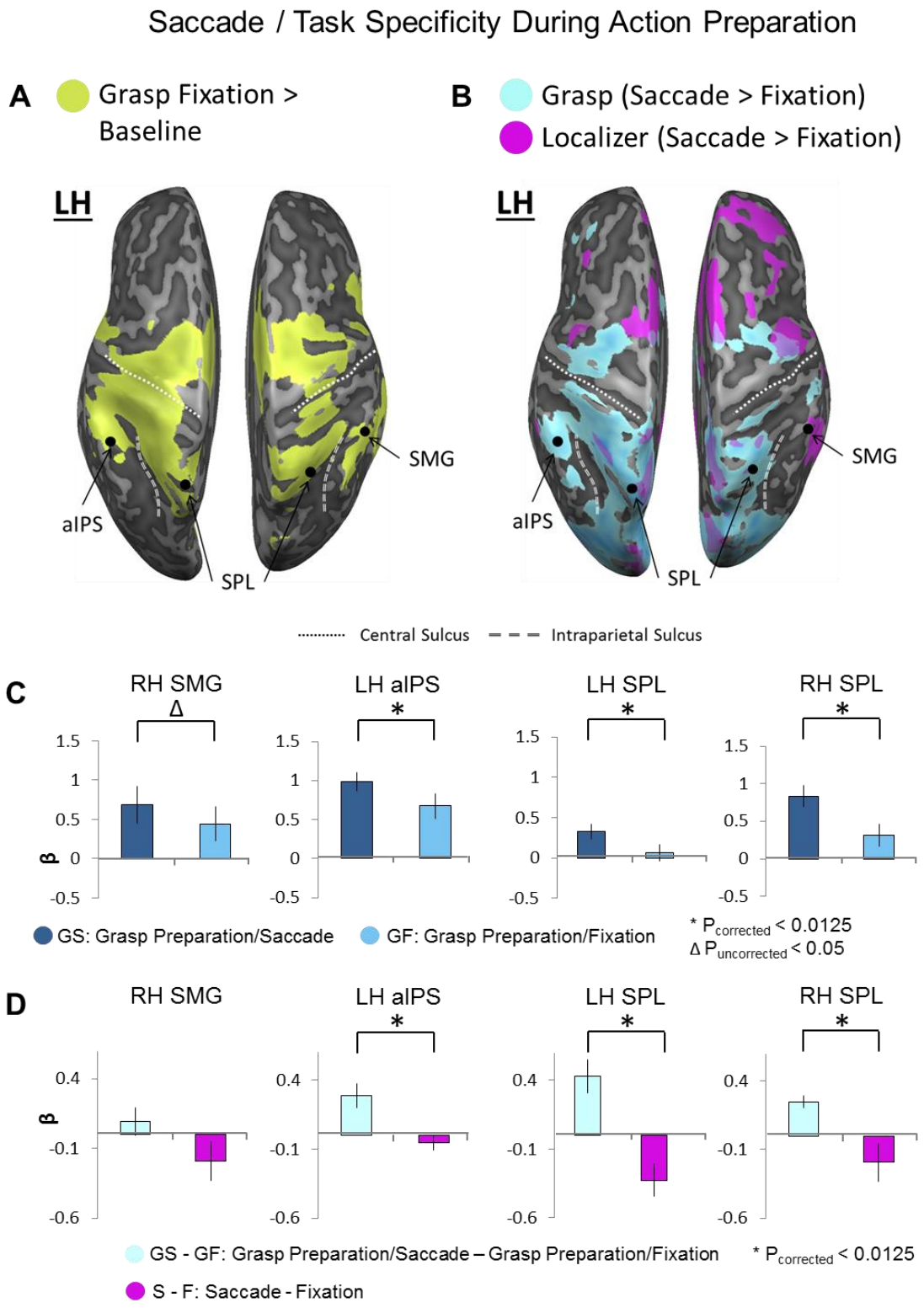

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Figure 5

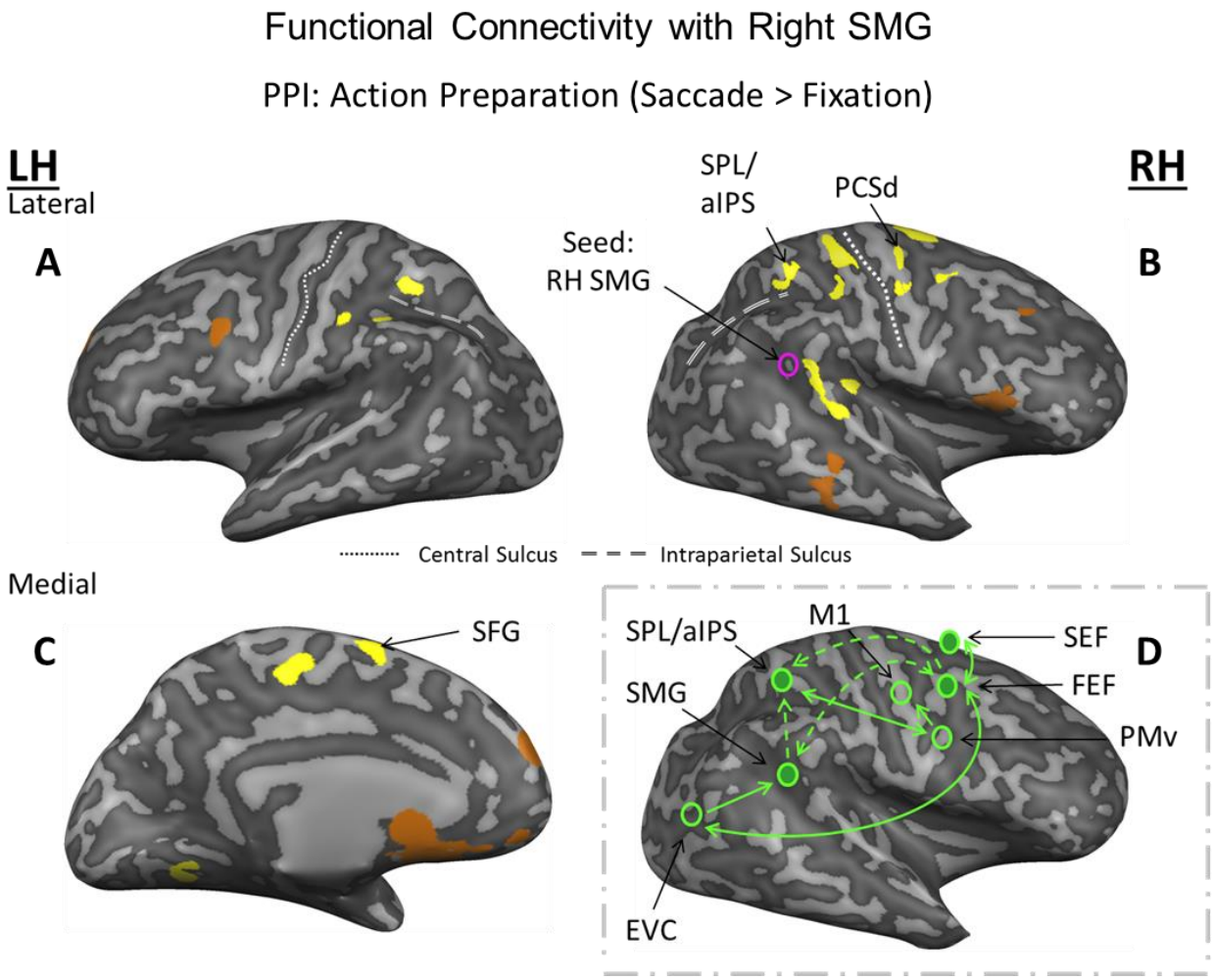

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Table 1. Talaraich coordinates for regions-of-interest extracted from the *Action Execution* phase.

ROI Name	**Talairach coordinates**						**ROI size**
	x	y	z	Std x	Std y	Std z	*n* voxels
LH aIPS	-38	-41	53	2.3	1.6	1.9	217
LH SPL	-13	-51	54	2.4	2..3	2.7	642
RH SMG	49	-40	48	2.0	2.2	2.1	361
RH SPL	35	-49	53	2.8	2.8	2.7	875