Remapping the Remembered Target Location for Anti-Saccades in Human Posterior Parietal Cortex

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INTRODUCTION

The importance of the anti-saccade task (Hallet 1978) is that it can be used to study the neural processes that underlie flexible control of motor behavior. In this task, the location of the stimulus must be transformed into a voluntary motor command that directs the eyes away from, rather than toward, the visual target. Various brain regions have been implicated in this process, including prefrontal cortex, frontal eye fields, supplementary eye fields, posterior parietal cortex (PPC), primary visual cortex and superior colliculus (see Munoz and Everling 2004 for review).

In monkey PPC, neurons in the lateral intraparietal area (LIP) have been associated with the planning of saccades, but there is considerable debate about their precise role in the generation of anti-saccades. For example, in a pro- and anti-saccade task, Gottlieb and Goldberg (1999) showed that most neurons in monkey LIP seem to represent the visual cue rather than the direction of the saccade (or the target). However, in a memory-delayed version of the anti-saccade task, population activity in LIP turns from the visual direction to the motor direction during the memory period (Zhang and Barash 2000, 2004). This switching is accomplished very rapidly, within 50 ms from the arrival of the visual signals in LIP, and might represent a remapped visual response.

Neuroimaging studies have also implicated the PPC in pro- and anti-saccades (Connolly et al. 2000, 2002; DeSouza et al. 2003; Kimmig et al. 2001). Kimmig et al. (2001) reported a higher blood-oxygen-level-dependent (BOLD) activation for anti- than for pro-saccades in PPC. Other studies have shown that the superior parietal lobe is activated for both pro- and anti-saccades, whereas the inferior parietal lobe responds only to anti-saccades (Connolly et al. 2000; Matsuda et al. 2004).

Recently, Sereno et al. (2001) located a bilateral region in the human superior parietal lobe that shows topography for target direction in a delayed pro-saccade task. These authors suggested this region be a human homologue of monkey area LIP. More recently Koyama et al. (2004) have come to the same conclusion. Using fMRI, they compared brain activations in both monkeys and humans performing visually guided saccade tasks. They found that the dorsal lateral intraparietal area in monkeys and an area in the posterior superior parietal lobule in humans exhibited the highest selectivity to saccade directions.

Recently, event-related fMRI was used to show that the stored memory activity in the human PPC region is shifted to the opposite cortical hemisphere when eye movements reverse the remembered horizontal target location relative to the gaze fixation point (Medendorp et al. 2003; Merriam et al. 2003). This shows that this area has an eye-centered organization that is updated when the eyes move, which further confirms previous physiology of monkey LIP (Batista et al. 1999; Duhamel et al. 1992; Gnadt and Andersen 1988; Mazzoni et al. 1996).

Would this region also update, or remap, its activity to the opposite cortical hemisphere when a memorized spatial location of a visual stimulus must be reversed to establish a goal for an anti-saccade? To answer this question, we examined, using event-related fMRI, the time course of the activation invoked in this region (which we will refer to as retinotopic IPS, or retIPS) during anti- and pro-saccades.

METHODS

Eight subjects (5 male/3 female), aged between 24 and 33, gave informed consent to participate in the experiments. All subjects but one were right-handed. Each subject practiced all tasks before imaging to ensure that the tasks were performed correctly in the magnet. In addition, eye-movement recordings and psychophysical measures were taken to confirm correct behavior as described in the following text.
MRI scanning

Data were collected with a 4-Tesla Varian (Palo Alto, CA) Unity Inova whole-body MRI scanner equipped with a Siemens Sonata Gradient system (Siemens, Erlangen, Germany). During the experiments, nine contiguous slices were used to image the part of the parietal cortex that included the known regions of interest (Medendorp et al. 2003, 2005) using a quadrature radio-frequency surface coil centered on the posterior parietal lobe. Functional data were obtained using navigator echo corrected T2*-weighted spiral imaging (TE = 15 ms; FA = 45°; FOV = 19.2 × 19.2 cm; TR = 1 s; in-plane pixel size = 3 × 3 mm; thickness = 4 mm). Functional data were superimposed on high-resolution inversion prepared three-dimensional T1-weighted anatomical images of the brain (typically 128 slices, 256 × 256, FOV = 19.2 × 19.2 cm; TE = 5.5 ms, TR = 10.0 ms). In separate sessions, subjects were rescanned using a birdcage-style head coil to obtain whole brain anatomical images. A high-resolution inversion prepared three-dimensional (3D) T1-weighted sequence was used (FA = 15°; voxel size: 1.0 mm in-plane, 256 × 256, 164 slices, TR = 0.76 s; TE = 5.3 ms).

Stimulus presentation and eye movement recording

Stimulus presentation was performed using a Silent Vision SV-4021 projection system (Avotec, Sturt, FL). This system includes an MEyeTrack-SV (Silent Vision) eye tracker (SensoMotoric Instruments GmbH, Teltow, Germany). This device uses fiber optics housed in dual stalls that sit in front of a subject’s eyes, allowing presentation of visual stimuli and simultaneous CCD video-based infrared eye tracking. The visual display subtended 30° horizontally by 23° vertically with a resolution of 800 × 600 pixels and a refresh rate of 60 Hz. Eye position recordings were made at a 60-Hz sampling rate. Before scanning, we calibrated the system with a five-point calibration, with one point in each corner of the visual display as well as a central point. Eye movements were calibrated in visual display screen coordinates.

Location of retIPS

To identify retIPS, we used a delayed-saccade task, which was incorporated in block-design paradigm (see also Medendorp et al. 2003, 2005). Briefly, subjects fixated a central letter (S or F) referring to a delayed-saccade task (S). Then a brief peripheral dot was presented for 250 ms, either to the left or right at a random horizontal angle between 7.5 and 10° and at a random vertical angle <10°. Subsequently, a masking pattern (30° horizontal × 15° vertical, dot’s eccentricity 0.36°, density 0.3 dots/(deg^2) blinked (at 5 Hz) for 2.5 s during which the subjects maintained central fixation. Then, at distractor offset, subjects made a saccade to the remembered target location and immediately back to center. The time between successive movements was 5 s. Subjects made no movement during the fixation (F) task. Scans comprised 14 blocks (each 20 s): first two blocks of fixation, then 10 blocks in which four leftward targets were alternated with four rightward targets; and finally two fixation blocks that concluded the scan. Thus in each run, subjects made 20 leftward and 20 rightward delayed-saccades. Subjects were tested in four runs, each lasting for 4.67 min. Subjects were given one minute of rest between runs, so that the total time devoted to the localizer was ~22 min.

Memory-delayed pro- and anti-saccades

An event-related paradigm was used to test the response of the retIPS region for delayed pro- and anti-saccades. As shown in Fig. 1, subjects fixated centrally on a gray square, and a brief peripheral gray dot flashed for 200 ms, either left or right of central fixation at a random horizontal angle between 7.5 and 10° and at a vertical angle <10°. The masking pattern was then briefly presented for 100 ms to disrupt iconic visual memory. This was followed by a long 11.5-s memory delay during which the subject maintained fixation. Subsequently, 12 s after the trial began, the central fixation square changed to either a green (PRO) or a red square (ANTI), which indicated whether to plan immediately for a pro- or anti-saccade, respectively. Then after a further 12 s, the central square was turned off, signaling the subject to either look immediately toward the remembered location of the stimulus on pro-saccade trials or to its mirror location in the opposite hemifield on anti-saccade trials (panel 4) and then back to center when the fixation block reappeared (panel 5). Another 12 s later, the next trial started. Visual instructions related to the psychophysical measures taken (see text) are not shown.

Behavioral analysis

In six subjects we recorded the button presses during scanning; their performance was >90% correct. Eye-movement recordings in all eight subjects also confirmed that our subjects generally followed the instructions correctly: in <4% of the trials, subjects either broke fixation or made saccades in the wrong direction. We excluded these error trials from further analysis. Finally, the reaction times for anti-saccades and pro-saccades were not significantly different (t-test,
P = 0.52), indicating that pro and anti-trials were not anticipated differently by our subjects.

**Image analysis and region of interest (ROIs)**

Analysis was performed using Brain Voyager 4.8 software (Brain Innovation, Maastricht, The Netherlands) and Matlab software (The Mathworks). Surface coil images were aligned manually to head-coil images. Anatomical images for each subject were segmented at the gray/white matter boundary, rendered and inflated for visualization purposes only. For functional data analysis, we excluded any scans in which motion artifacts were observed. Time courses within each voxel were corrected for linear temporal drift. Anatomical and functional images were transformed to Talairach space to obtain stereotaxic coordinates for the regions of interest (Talairach and Tournoux 1988).

Using the localizer scans, the retIPS region of interest was identified by contrasting the blocks devoted to leftward saccades with the blocks for rightward saccades. Within these areas, the point of peak activation was located (see Table 1). Our regions of interest contained all voxels within a cubic cluster of 8 mm centered on these points that exceeded a threshold of P < 0.01.

Using this independently defined bilateral retIPS region, fMRI time courses corresponding to all activated voxels within these ROIs were extracted for each of the subsequent event-related scans. The average percent signal change for the four conditions, RP, RA, LP, and LA, was computed using the fixation periods as a baseline. For each condition, these were then averaged across all runs for each sample point (each volume) within a subject and then across subjects. For plotting of the event-related average across subjects (see Fig. 3), data were temporally smoothed using a moving average filter (Bartlett filter) with a span of 5 volumes. Filtering was not applied for quantification of the data (see Fig. 4) to avoid contamination of the signal across events. In Fig. 4, we computed the difference between the mean signals of two conditions for each subject separately. The SD of this difference was computed using the error propagation formula. To compute the standard error, we divided this value by \( \sqrt{(n1 + n2 - 1)} \), with n1 and n2 the number of samples taken for the two conditions, respectively. Thus for each point in time, we determined the difference signal and its standard error. Then, for the intervals indicated in Fig. 3, we took the mean difference and the mean standard error, and plotted them in Fig. 4, A and B.

**RESULTS**

As in our previous studies (Medendorp et al. 2003, 2005), we used the delayed-pro-saccade task (normal saccades to the visual cue) to identify retIPS: a bilateral region in the human IPS that shows a preference for remembered targets in the contralateral visual hemifield. The results of this analysis are depicted in Fig. 2 for all subjects. Yellow regions indicate a stronger activation for remembered target locations in the right visual field than in the left, whereas blue voxels represent the opposite pattern. All subjects tested demonstrated an equivalently organized area in their PPC. More specifically, the area was located in the posterior superior parietal lobule, within a small sulcus running medially from the intraparietal sulcus. For all subjects, the Talairach coordinates (in mm) and peak t values of their retIPS regions are presented in Table 1. These coordinates are consistent with previous studies (Koyama et al. 2004; Medendorp et al. 2003, 2005; Sereno et al. 2001).
The important question addressed here is whether this area represents the spatial location of the visual stimulus or the saccadic goal that it specifies. Obviously, without knowing the action plan, the representation can only be of the stimulus. However, after a response selection is cued—anti- or pro-saccade—the brain can determine the location of the saccadic goal. For anti-saccades, this means that the coordinates of the visual stimulus must be rotated through 180°, or mirrored, to specify the goal for action. If the retIPS region is involved in this process, or if it reflects the outcome of this process, we would expect its activity to be updated after being instructed to produce an anti-saccade. More specifically, we would expect a remapping of activation to occur across the two hemispheres to represent the goal—and not the location of the visual stimulus—for anti-saccades. We tested this hypothesis using an event-related fMRI paradigm in which subjects first saw a target and then, after a 12-s delay, were cued to plan for either a pro- or anti-saccade; then, after another 12-s delay, subjects executed the movement (see Fig. 2). As illustrated by Fig. 3A, the paradigm consisted of four different conditions: either a pro-saccade (P) or an anti-saccade (A) to a target either presented in the right (R) or left (L) visual hemifield. The four conditions are represented as RP, RA, LP, and LA, respectively.

Figure 3B shows the mean response of eight subjects in the left parietal region for each of the four conditions. As shown, after the brief presentation of the target, cortical activation during the first delay period shows first a phasic response followed by a tonic response. This activity is higher when the remembered spatial location of the stimulus is in the right (contralateral) hemifield than when it is in the left (ipsilateral) hemifield. Left and right patterns of activation are reversed for initial responses in the right parietal cortex (Fig. 3C). This confirms the topographical nature of the region, as identified by our localizer task and as shown in previous studies (Medendorp et al. 2003, 2005; Sereno et al. 2001).

What happens after the instruction cue, which specifies the selected response, in the second delay period? As shown, in all conditions, there is a phasic response to the cue, even when the cue is for a pro-saccade. Later, when the phasic response has diminished, the region’s sustained activation encodes the spatial goal of the saccade, which requires an update of activation in the anti-saccade trials. That is, for the left cortex (Fig. 3B), if the remembered location of the stimulus required a transformation from the left (ipsilateral) hemifield into a saccadic goal in the right (contralateral) hemifield (LA condition), a high sustained activation was observed in the second delay period. But if the instruction required the stimulus location in the right hemifield to be transformed into an action goal in the left hemifield (RA condition), the level decreased. When, after the response instruction, the saccadic goal corresponded to the original stimulus location (i.e., the pro-saccade trials), the activation remained high if the location was contralateral (RP condition) but decreased if the location was ipsilateral (LP condition). Furthermore, the activation for a target on the right seems suppressed when it is a target for an anti-saccade (RA) compared with when it is a target for a pro-saccade (RP). The right parietal region (Fig. 3C) showed a similar, but mirrored, pattern of activation. In other words, the anti-saccade cue led to symmetrically yoked activation between the left and right PPC. The activity in retIPS in both hemispheres immediately prior to an anti-saccade seems indistinguishable from the activity prior to a pro-saccade in the same direction. Taken together, when the remembered stimulus coordinates must be reversed (left-right) to specify the goal for the saccade, dynamic shifts in cortical activity occur from one hemisphere to the other. This suggests that the parietal area identified here encodes and stores the location of a saccadic goal, and not the coordinates.

**Fig. 3.** RetIPS encodes and stores the location of saccadic goals, rather than the coordinates of the visual stimulus by which they are specified. A: RP, LP, RA, LA signify 4 possible conditions of our paradigm; the 1st letter signifies initial location of the 2 targets (R, right hemifield; L, left hemifield); the 2nd letter refers to either a pro-saccade (P) or an anti-saccade (A). B and C: left (B) and right (C) parietal activation (mean ± SE across 8 subjects) for each of the 4 conditions. −−−, presentation of stimulus, time of instruction (anti/pro), and time of saccade, respectively.
of the visual stimulus, after the instruction to plan for an anti-saccade.

To analyze these findings quantitatively in individual subjects, we have plotted, in Fig. 4A, the difference in activation between the RA condition and the LA condition after the anti-instruction cue (in the 2nd delay period, time period 22–26 s) versus the difference before the anti-cue (time period 10–14 s, 1st delay period; see METHODS). If the activation of the region matched the location of the goal for action, or the movement direction, we would expect these differences to have opposite signs. Accordingly, data from the right parietal cortex should be represented in the second quadrant, whereas left parietal data should be confined to the fourth quadrant (gray zones). In contrast, if the region only encoded the physical location of the stimulus after the anti-cue, or if it was not involved in the inversion process, the data points should lie in the opposite white zones. As Fig. 4A shows, nearly all of the data fell within the target remapping zones. Thus almost all of our subjects remapped the location of the target in our anti-saccade paradigm, or in other words, encoded the location of the target for action, rather than the location of the visual stimulus. As a control, we applied the same analysis to the pro-saccades; that is, the RP and LP conditions. In this case, if the region encoded the goal for action, we would expect that the differences in activation between these conditions in either delay period would have the same signs. This is exactly what we found, as clearly indicated by almost all data points falling in the first and third quadrants (Fig. 4B).

Consistent with these observations, a repeated measures multivariate ANOVA (MANOVA) with hemisphere (left/right), saccade task (pro/anti), and delay period (1st/2nd) as factors, revealed a significant three-way interaction \([F(1,7) = 45.7, P < 0.001]\). Separate analyses for the pro- and anti-saccade conditions revealed a significant two-way interaction between hemisphere and delay period in the anti-saccade condition \([F(1,7) = 89.6, P < 0.001]\) and no such significant interaction in the pro-saccade condition \([F(1,7) = 0.1, P = 0.81]\), which also confirms that the region encodes a goal for action. Even within hemispheres, statistical analysis provided validation for this claim. That is, for the left hemisphere, the difference between the RA and LA condition (RA-LA) for the first delay period was significantly different from that during the second delay period (paired \(t\)-test, \(P < 0.001\)), whereas this was not the case for the difference between the RP and LP conditions (RP-LP: \(P = 0.97\)). The same was observed for the right hemisphere (i.e., for RA-LA, \(P = 0.02\) and for RP-LP, \(P = 0.80\)).

Finally, it is important to point out that our design employed fixed delays (~12 s) to separate the different cues. One could argue that, after the pro-anti cue had been given, subjects could plan their saccade at any time during the second delay interval, even though the instruction was immediately after the cue. Thus we had no direct control over subjects’ mental strategies in relation to their movement planning. On the other hand, the robust and clear time courses observed on average for the different conditions (see Fig. 3) would be surprising if subjects had followed different strategies. Also, the psychophysics is completely correlated with oculomotor performance (see METHODS). Nevertheless, in an attempt to examine the possibility that subjects planned their saccades arbitrarily during the second delay interval, we performed two further analyses. First, we checked whether the SD of the signal was greater during the second delay period than that during the first time interval, which could be expected if subjects were to use arbitrary planning strategies. For the four conditions and two hemispheres, the variability ranged between 0.05 and 0.09% signal change for the first delay period and between 0.05 and 0.08% for the second delay period. A \(t\)-test revealed that the observed differences were not statistically significant (\(P = 0.70\)), suggesting that our subjects followed the instruction to plan the saccade in direct response to the cue. Second, we compared the difference between the signals for the anti- and pro-saccade trials over the entire second delay interval. Our conclusion of target updating would further be warranted if anti > pro for ipsilateral stimulus locations, and anti < pro for contralateral stimuli. Indeed, for the left hemisphere, we found a difference of 0.18 ± 0.03% signal change for leftward (ipsilateral stimuli) and −0.06 ± 0.05 for contralateral stimuli, respectively. For the right hemisphere, we found 0.18 ± 0.05% for rightward (ipsilateral) stimuli and −0.03 ± 0.05 for contralateral stimuli. These results resemble the findings of Figs. 3 and 4. A MANOVA on the difference between anti and pro trials, with hemisphere (left/right) and target location (left/right) as factors, revealed a significant two-way interaction \([F(1,7) = 16.03, P = 0.005]\). This indicates that the effects of arbitrary planning strategies, if any, have been marginal. Together, the results of the latter two analyses provide further support for the claim that the retIPS region updates its activity when the remembered location of stimulus must be reversed to serve as a goal for a saccade.

FIG. 4. A comparison of activation before and after instruction cue (pro/anti) in retIPS in each subject. A: anti-saccades, B: pro-saccades. x axis: the difference (±SE) in the average activation between the stimulus right and stimulus left conditions just prior to the instruction. y axis: same for the saccadic goals after instruction cue. • right PPC; ○ left PPC. Before the instruction (1st delay period) activation should be contralateral. After the instruction (2nd delay period) activation should switch hemispheres for anti-saccades but not for pro-saccades if the region encodes the target location of a desired saccade. For anti-saccades, this requires right PPC data in the 2nd quadrant and left PPC data in the 4th quadrant, whereas for pro-saccades, the data should lie in the opposite 1st and 2nd quadrants. These quadrants are indicated by the gray zones.
DISCUSSION

In this paper, we have exploited the laterality of the PPC so that the goal for a saccade can be brought in and out of a given hemisphere depending on instruction. In this manner, we overcame the coarse spatial resolution of functional MRI and demonstrated that retIPS, the putative human homologue of monkey area LIP, codes the target location of the saccade and not the location of the visual stimulus in a delayed anti-saccade paradigm. Our study extends previous findings about anti-saccades in human PPC (Connolly et al. 2000, 2002; DeSouza et al. 2003; Kimmig et al. 2001) by demonstrating the dynamic exchange of activity between the hemispheres that occurs when the location of a visual stimulus must be reversed to specify the goal for a saccade.

Another requirement for generating anti-saccades is the suppression of the memory of the initial visual stimulus. There is clear evidence for this in our results. As Fig. 3 shows, in the left retIPS, the activation for a target on the right is less when it is a target for an anti-saccade than when it is a pro-saccade target (RA < RP in the 2nd delay period). The same occurs in the right retIPS for targets on the left. But note that the role of retIPS is not simply suppression: it also participates in the coding of the new target location.

Our results are consistent with the findings of Zhang and Barash (2000, 2004), who demonstrated, using delayed anti-saccades, that a stimulus direction is remapped in monkey LIP to code the direction for a saccade. In this respect, our results constitute an opportunity to validate that a certain electrophysiological finding in monkeys also applies to the human brain. Note, however, that not all neurons in the Zhang and Barash (2004) study showed the remapping effect: some neurons coded consistently the location of the stimulus, whereas others exclusively encoded the movement goal. The present study shows, at least, that the goal for a saccade is represented more strongly in the massed activation of retIPS than memory for the visual stimulus.

There are important differences between our anti-saccade paradigm and those of previous studies. In our case, the visual target location was presented first, and then the cue was given for either an anti- or pro-saccade. In the Zhang and Barash studies, target location and saccade type cues were presented simultaneously. In Gottlieb and Goldberg (1999), the monkeys were first cued to the appropriate saccadic response, and then were shown the visual target location. It is thus possible that response to the visual target was preprogrammed to be different, which may explain the differences between these and the present results.

Recently, Awarter and Lappe (2004) reported that the same distortions of visual space are produced during anti-saccades as during pro-saccades. They attributed these distortions to the remapping process in parietal cortex, in accord with the present findings. In this regard, our results are also compatible with earlier results on gaze-centered updating in retIPS that show a similar remapping of activation in PPC when eye movements reversed the remembered horizontal target location relative to the gaze fixation point (Medendorp et al. 2003; Merriam et al. 2003).

Several studies have emphasized the importance of the frontal lobe in the generation of anti-saccades (Sato and Schall 2003). Also, patients with lesions of the frontal lobe tend to make more errors when attempting to generate anti-saccades (Guitton et al. 1985; Machado and Rafal 2004). Our study does not contradict these findings. It simply demonstrates that the target location for an anti-saccade is coded in the parietal cortex. The decision to make an anti-saccade may in fact also be a function of the frontal lobe. Indeed, fMRI studies have suggested that the increase in activity seen during anti-saccades is associated with preparatory set, coding the readiness and intention to perform the saccade (Connolly et al. 2002; DeSouza et al. 2003).

Finally, it has been a subject of longstanding debate whether the posterior parietal cortex is more important for spatial attention and sensory memory (Colby and Goldberg 1999; Corbetta and Shulman 2002) or for response or action planning (Andersen and Buneo 2002). In our study, we did not explicitly control spatial attention, only the eye movements. Clearly, when subjects plan an anti-saccade, they will shift and maintain their attention to the opposite location (Findlay and Walker 1999; Klein 1980; Posner 1980; Rizolatti et al. 1987). Thus one could argue that the topography and dynamic shift of activation for anti-saccades represents a topographic shift of spatial attention. That is, shifting attention from one location to another contralateral location leads to a corresponding, contralateral shift in activation (Colby and Goldberg 1999; Corbetta and Shulman 2002; Nobre et al. 2000). Recently, Yantis et al. (2002) reported fMRI evidence for phasic, not tonic, changes in activity in human parietal cortex, related to attentional shifts in a visual recognition task. Other fMRI studies have demonstrated sustained activity in human parietal cortex during preparing and maintaining expectations for stimulus locations (Corbetta et al. 2002; Kastner et al. 1999). Our results showed clear sustained responses, which suggests that PPC also responds in a sustained fashion to a task that involves an action. However, the attention explanation would also imply that the same effects should be seen in retIPS regardless of motor effector. In that respect, it is important to note that we have recently shown that the activation in retIPS is dependent on which effector, that is, eye, right hand or left hand, is used for action (Medendorp et al. 2005). All together, is seems entirely plausible that the retIPS region is involved in both attentional and motor planning processes.

In summary, the neural mechanisms underlying flexible motor behavior, studied by means of anti-saccade paradigms, have been, and will be, an important and active area for research in primate neurophysiology and human neuro-imaging. Here we have shown how the human parietal cortex is engaged in this process. The results presented here advance our understanding of how the human parietal cortex processes spatial information, and they highlight the synergy between primate neurophysiology and human functional imaging.

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