Delay Activity and Sensory-Motor Translation During Planned Eye or Hand Movements to Visual or Tactile Targets

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Macaluso E, Frith CD, Driver J. Delay activity and sensory-motor translation during planned eye or hand movements to visual or tactile targets. J Neurophysiol 98: 3081–3094, 2007. First published September 26, 2007; doi:10.1152/jn.00192.2007. To perform eye or hand movements toward a relevant location, the brain must translate sensory input into motor output. Recent studies revealed segregation between circuits for translating visual information into saccadic or manual movements, but less is known about translation of tactile information into such movements. Using human functional magnetic resonance imaging (fMRI) in a delay paradigm, we factorially crossed sensory modality (vision or touch) and motor effector (eyes or hands) for lateralized movements (gaze shifts to left or right or pressing a left or right button with the corresponding left or right hand located there). We investigated activity in the delay-period between stimulation and response, asking whether the currently relevant side (left or right) during the delay was encoded according to sensory modality, upcoming motor response, or some interactive combination of these. Delay activity mainly reflected the motor response subsequently required. Irrespective of visual or tactile input, we found sustained activity in posterior partial cortex, frontal-eye field, and contralateral visual cortex when subjects would later make an eye movement. For delays prior to manual button-press response, activity increased in contralateral precentral regions, again regardless of stimulated modality. Posterior superior temporal sulcus showed sustained delay activity, irrespective of sensory modality, side, and response type. We conclude that the delay activations reflect translation of sensory signals into effector-specific motor circuits in parietal and frontal cortex (plus an impact on contralateral visual cortex for planned saccades), regardless of cue modality, whereas posterior STS provides a representation that generalizes across both sensory modality and motor effector.

INTRODUCTION

Representation of external space and performance of spatially selective actions require many combined neural computations. These will include encoding of the position of sensory stimuli, in relation to current posture, as well as translation of the locations indicated via senses into planning of a movement toward a specific location. Although in everyday life we can effortlessly direct gaze or move our hands to objects, brain structures that encode locations according to sensory input or motor output may be segregated anatomically. Moreover, we can acquire information about the position of an event or an object through different sensory modalities (e.g., vision and touch) and can spatially direct different parts of our body on the basis of information from these different modalities (e.g., shifting gaze and moving our hands to explore a seen and felt object that we are holding). The existence of distinct sensory modalities and motor modalities that can all encode spatial positions raises questions of whether and how the brain combines these different types of spatial representation, to achieve coherent perception of space and to control different types of spatially selective movement (Andersen et al. 1997; Colby and Duhamel 1996).

One possible architecture for integrating or translating between such spatial representations would be first to combine sensory information from different modalities into a common and unique representation of sensory space and then feed such a “supramodal” representation into different effector motor systems. Other possible architectures might include multiple, segregated representations of multisensory space, separately connected to each specific effector system. Intensive electrophysiological work on neurons in parietal cortex of awake behaving monkeys (Andersen et al. 1997; Batista and Andersen 2001; Colby and Goldberg 1999; Duhamel et al. 1992; Gottlieb et al. 1998; Quian et al. 2006; Snyder et al. 1998; Wurtz et al. 1982) has revealed the existence of distinct regions in and around the intra-parietal sulcus that may serve as sensori-motor interfaces, each selectively or predominantly connected with a specific effector system. The lateral intraparietal region (LIP) has been associated with planning and execution of eye movements and primarily with visual responses (e.g., Ben Hamed et al. 2001; Snyder et al. 1997) although also showing some auditory responses in trained animals (Grunewald et al. 1999; Mullette-Gillman et al. 2005). A more medial region of the intraparietal cortex (variably termed parietal reach region, PRR, and/or medial intraparietal area, MIP) is thought to play a role in pointing and reaching movements with the hands (Cohen et al. 2002; Johnson et al. 1996; Kalaska et al. 1997). This region, for several other intraparietal regions involved in spatial representation and movements (e.g., area AIP in the anterior part of the intraparietal sulcus, Murata et al. 2000; and area 5 in the superior parietal lobule, Kalaska 1996; Rushworth et al. 1997), has also been shown to receive afferent input from several distinct sensory modalities, including touch as well as vision (Colby and Duhamel 1991). Moreover, the anatomical connectivity of these different intraparietal regions mirrors their apparent functional specificity: LIP connects primarily with dorsal regions of premotor cortex (PM) involved in eye-movement control,
whereas PRR/MIP and AIP project to premotor regions involved in arm and hand movement control, in dorsocaudal PM and ventrorostral PM, respectively (Jones and Powell 1970; Luppino et al. 1999; Tanne-Gariepy et al. 2002; Wise et al. 1997). According to this anatomo-functional organization, spatial information concerning several sensory modalities may be brought together in distinct parietal-premotor circuits that ultimately specialize in different aspects of spatial movement.

Some recent human neuroimaging studies have adapted classical electrophysiological paradigms to test for possible analogies (or differences) between the organization of parietal cortex and related structures in human and non-human primates (Astafiev et al. 2003; Bremmer et al. 2001; Culham and Valyear 2006; Desouza et al. 2000; Greffes et al. 2004; Kawashima et al. 1994; Prado et al. 2005; Schluppeck et al. 2005; Simon et al. 2002). Many of these human studies typically employ visual cues specifying a location for subsequent eye (saccadic) or finger (e.g., pointing) movement. Overall, neuroimaging results from such studies have highlighted some segregation of saccade-versus-manual-related activations, although some overlap (or some degree of activation during the other task) has also been found (Astafiev et al. 2003; Connolly et al. 2003; Medendorp et al. 2005a; Simon et al. 2002). Overlapping responses across different effector systems (see also Wurtz et al. 1982 for related data from monkeys), when found, may indicate that location encoding in the affected area is primarily associated with sensory or attentional representations there rather than strictly motor output (Astafiev et al. 2003; Colby and Goldberg 1999; Macaluso et al. 2003a).

One well-established approach to such issues, for both electrophysiological work in nonhuman primates as well as for neuroimaging studies in humans, has utilized delayed-response paradigms (Calton et al. 2002; Desouza et al. 2000; Duhamel et al. 1992; Schluppeck et al. 2006; Snyder et al. 1997). In such delay paradigms, a variable period separates the sensory stimulus specifying the target location from the subsequent overt movement, triggered by a later go signal. Much recent interest has focused on the processes occurring during the delay period itself, when there is no sensory stimulus present at the cued location and as yet no overt motor behavior, although the target location for the upcoming movement has already been identified.

Location-specific delay activity has been found both in apparently saccade-related (Duhamel et al. 1992) and apparently manual-related (Snyder et al. 1997) regions of parietal cortex. Nonetheless, it should be noted that such delay activity in specific regions linked to particular effector circuits is also typically coupled with strong responses to the initial sensory (visual) onset, leading increasingly to the perspective that such regions should be viewed as sensori-motor interfaces (Gottlieb et al. 2005; Schluppeck et al. 2006; Snyder et al. 1998). For example, in a recent human fMRI study on delay-activity during preparation for saccadic eye movements, Schluppeck and colleagues (2006) showed that in medial and posterior intraparietal areas (IPS1, IPS2, and V7) activity increased during the delay period, but this sustained effect was relatively small compared with the initial response to the visual cue and the subsequent response to the overt movement (saccade). Further this study found spatially specific activation (greater activity for contralateral than ipsilateral target/saccades) for the visual cue and during the delay period, but no side-specific effects were found for saccade execution. These findings suggest (in accord with much monkey electrophysiological data) (e.g., Colby et al. 1996; Snyder et al. 1997) that location encoding in these apparently saccade-related parietal regions might not be fully segregated from sensory processing, with the same regions participating both in the “sensory” encoding of the relevant location, as well as the beginnings of motor preparation (see also Beurze et al. 2007; Connolly et al. 2000; Gottlieb and Goldberg 1999; Gottlieb et al. 2005; Medendorp et al. 2005b; Zhang and Barash 2000).

Such findings, in humans as in monkeys, that even those parietal regions that seems linked primarily to one or other type of upcoming movement can also show strong sensory-related responses, opens the issue of whether providing location cues in different sensory modalities (e.g., within touch not only vision) will modulate activity in these regions. Although several studies have examined this issue for the monkey brain (Cohen and Andersen 2000; Mullette-Gillman et al. 2005; Schlack et al. 2005), until recently there have been rather fewer human fMRI studies of the issue (though see Macaluso et al. 2003a) because most of the human neuroimaging studies examining different types of movements and/or delay periods have used only visual cues (e.g., Beurze et al. 2007; Connolly et al. 2003; Medendorp et al. 2005a; Schluppeck et al. 2005, 2006). If different sensory modalities can trigger activation of regions related to particular types of motor circuit, the new question then arises of whether delay activity in different regions may change as a function of the cue modality or if instead delay activity will solely reflect the type of upcoming movement. We tested this here in a human fMRI study of delay activity.

We investigated possible effects and interactions concerning the modality of the cue (visual or tactile stimuli in the left or right hemifield to specify the relevant spatial location for subsequent movement) and also concerning the motor effector used for the upcoming overt response at the end of the delay. Our design separated cue- and response-related activity from the critical sustained activity occurring during the delay period between sensory cue and motor response movement (e.g., Schluppeck et al. 2006). For motor responses, we used either saccades or lateralized manual responses but included a variable delay period between stimulus cue and motor execution with our focus being on the delay activity observed. The manual task involved button presses with the left or right hand on the corresponding target side. Thus although left versus right eye movements differed solely in term of end spatial position (i.e., with the same effector—the eyes being used for both left and right movements), our manual task did not dissociate effector (left or right hand) from spatial position (target location in left or right hemifield) (see also Beurze et al. 2007, who addressed the issue of position vs. effector specificity). Thus the present manual task of spatially compatible button pressing, after the delay after a visual or tactile stimulus cue, may require a step of effector selection (left or right hand) (see also Thoenissen et al. 2002) as well as the location selection involved in the oculomotor task also. Nonetheless, because the present paradigm factorially crossed cue modality (visual or tactile) with movement type (oculomotor or manual), this allowed us to determine whether during the delay phase the relevant position would be encoded according to the modality of the cue (visual or tactile), the type of upcoming overt
response (saccadic or manual), or some interactive combination of these two factors. Moreover, other potential designs (such as placing one hand in a central start position, analogous to central fixation for the eyes) would have prevented us from placing tactile stimuli at identical locations to the visual stimuli on either side. We return to such issues in our DISCUSSION. For now, the present design allowed us to assess whether brain activity as measured with fMRI, for the delay period, would depend on the stimulus modality, the response type (oculomotor or manual) or some interaction between these.

METH O D S

Participants

Nine right-handed healthy volunteers (6 males) participated (mean age: 26 yr). They gave written informed consent in accord with local ethics.

Paradigm

The experimental design was a $2 \times 2 \times 2$ factorial; with cue modality (vision/touch) and side (left/right) as orthogonal event-related factors and movement type (eyes/hand) as an orthogonal blocked factor. On each trial, a visual cue or tactile cue on the left or right indicated the relevant position for the subsequent movement. After a variable delay (see following text), an auditory “go-signal” instructed the subjects to execute the movement for the cued side. Eye movements to left or right or hand movements (button presses with left or right hand) were blocked within each fMRI run, so subjects always knew whether the eyes or hands were currently relevant but did not know which target side they should be directed to prior to the stimulus cue on each trial. The delay between the sensory cue and the subsequent go signal for movement initiation was varied (range: 0.3–12.8 s) to allow us to isolate preparatory activity in this delay period.

Stimuli and task

Subjects lay in the scanner with their hands on a plastic table positioned above the hips, where we placed LEDs for visual stimulation on either side; piezo-electric components (T220_H3BS_304, Piezo Systems, Cambridge, MA) to deliver unseen tactile stimulation to either hand; and electronic switches to record button presses with either hand when these were made (see Fig. 1A). Thus on each side, we could deliver visual or tactile cue stimuli (either of these in correspondence with the index finger of one hand) and could also record motor responses (i.e., key presses performed with either of the two thumbs, which were occluded to avoid any visual stimulation associated with manual responses and any eye-movements toward either side). The visual scene was filmed with a shielded camera placed outside the head-only magnetic resonance (MR) bore (SIEMENS, Allegra) and projected onto a screen at the back of the scanner (see Fig. 1A, left). The subjects viewed the visual scene through a mirror system that also allowed monitoring of eye-position with a remote infra-red eye-tracker (see following text). From inside the scanner, the scene appeared to the subjects as if they were looking down at their own hands resting on a table (see Fig. 1A, right) while they looked straight ahead into the mirror system. The soft illumination of the MR room permitted continuous viewing of the scene throughout the experiment. On the table, the index fingers (and the LEDs) rested at 10 cm to the left or right of the central fixation point. The distance between the camera and the table was adjusted so that the index fingers were at 7.8° visual angle in the projected image, thus maintaining a realistic size scaling for the seen hands.

Before the beginning of each fMRI run, the subjects were instructed verbally on whether they had to respond with eye movements or with
manual button presses for the upcoming block of trials. Irrespective of effector type, each trial began with the illumination of a central fixation point. After 1,500 ms this central fixation point was turned off, and either a visual or a tactile cue was presented on the left or on the right side for 200 ms. Cue modality and position were randomized and unpredictable. The lateralized sensory cue indicated the target position for subsequent movement, but subjects had to withhold their motor response until the auditory go signal. After a variable delay (see following text), an auditory tone (frequency of 500 Hz; duration of 200 ms) instructed the subject to execute the movement for the relevant location (go signal). In two fMRI runs, subjects responded by manually pressing the button on the relevant side, and in the other two fMRI runs, they made a saccade toward the relevant position (i.e., toward the index finger of one or the other hand, at the same locations as the possible visual target) and back to the central fixation point, with the order of tasks counterbalanced.

Each fMRI run consisted of 28 trials (intertrial interval = 16 s). There were 14 visual trials (7 on the left and 7 on the right side) and 14 tactile trials (7 left and 7 right) in random order. We used cue-to-go-signal delay periods of between 0.3 and 12.8 s. To reduce the correlation between cue-related activity, movement-related activity, and preparatory/delay activity, we used long delays for 57% of the trials (447–863 ms), and short delays for 14% of the trials (300–446 ms). The high variability of possible delays also ensured that subjects could not anticipate the exact time of the go signal and therefore should prepare for whenever the go signal might occur. The order of the four fMRI runs (2 runs with eye movements, and 2 runs with hand movements) was counterbalanced across subjects. Each run lasted for 8 min. Prior to the fMRI session, all subjects received approximately ten minutes of practice inside the scanner.

**Magnetic resonance imaging**

A Siemens Allegra (Siemens Medical Systems, Erlangen, Germany) operating at 3 T and equipped for echo-planar imaging acquired functional MR images. A quadrature volume head coil was used for radio frequency transmission and reception. Thirty-two slices of functional MR images were acquired using blood-oxygenation-level-dependent imaging (3 × 3 mm, 2.5-mm thick, 50% distance factor, TR = 2.08 s, TE = 30 ms), covering the entirety of the cortex.

**Data analysis**

We used SPM2 (http://www.fil.ion.ucl.ac.uk) for data preprocessing and statistical analyses. We acquired 920 fMRI volumes for each participant. After discarding the first four volumes of each run, all images were corrected for head movement. Slice-acquisition delays were corrected using the middle slice as reference. All images were normalized to the standard SPM2 EPI template, resampled to 2-mm isotropic voxel size, and spatially smoothed using an isotropic Gaussian kernel of 10 mm full-width half-maximum (FWHM) in accord with the SPM approach. Time series at each voxel for each subject were high pass filtered at 220 s and prewhitened by means of an autoregressive model AR(1).

Statistical inference was based on a random effects approach (Penny and Holmes 2004), and assigned corrected $P$ values as described later. The SPM analysis comprised two steps. First, for each subject, the data were best-fitted at every voxel using a combination of effects of interest. This represented the three phases of the trial: sensory cue, variable-length delay, and motor response. Within each fMRI run (either with eye or hand responses), these three phases (sensory, delay, motor) were modeled separately according to cue modality (vision or touch) and relevant side (left or right hemifield). Thus each fMRI-time series was fitted with 12 effects of interest (3 phases × 4 trial-types), plus some confounding effects of no interest that were modeled separately to remove their influence. These were rare trial phases when subjects moved their eyes when they should instead have maintained central fixation (see following text). Linear contrasts were used to average responses for the 12 effects of interest in the two fMRI runs requiring the same motor response (i.e., eyes or hands). This procedure resulted in 24 contrast-images per subject, representing the four possible sensory-motor combinations (eye to vision, eye to touch, hand to vision, hand to touch), for either hemifield (left or right), and for the three trial phases (sensory, delay, and motor).

In the second stage (group analyses), we modeled eight conditions (4 sensory-motor combinations on each side) separately in three SPM group analyses, one for each trial phase. Finally, within each such SPM analysis, linear compounds were used to compare the eight conditions, now using between-subjects variance (rather than between scans). Correction for nonsphericity (Friston et al. 2002) was used to account for possible differences in error variance across conditions and any nonindependent error terms for the repeated measures. In these group random-effects analyses, we retained as statistically significant only activations surviving correction for multiple comparisons ($P$ corr. < 0.05; see next section for more details).

Preliminary analyses assessed activity in the sensory cue phase and in the motor response phase. In the sensory cue phase, we tested for any modality-dependent activation, plus any common activations that generalized over modalities (conjunction analysis) (Friston et al. 1999; Price and Friston 1997). To assess this, we compared activity during sensory cueing versus rest (e.g., visual cue vs. rest) with a whole-brain corrected threshold ($P$ corr. < 0.05). Furthermore, to ensure the specificity of any modality-dependent activation during sensory stimulation, we included the additional constraint that such activity during cueing for one modality also had to be greater than for the other modality (e.g., visual vs. tactile cue; $P$ uncorr. < 0.001). Note that adding these additional constraints (i.e., requiring that a particular activation should pass a further uncorrected test also) can only make our analyses more conservative than the basic corrected contrast. Likewise, when testing for commonalities across vision/touch (whole-brain-corrected conjunction analyses), we also further required each of the individual modalities to activate at $P$ uncorr. < 0.001.

An analogous approach was used to assess brain activation in the motor response phase. Accordingly, we tested for any activation specific for a movement type (saccade or manual), plus any common activation that generalized over movement types (using conjunction analyses). We compared activity during motor-response versus rest (whole-brain-corrected threshold: $P$ corr. < 0.05) plus added the further constraint that activity for one movement type also had to be greater than for the other movement-type (e.g., saccade vs. manual responses; $P$ uncorr. < 0.001). When testing for commonalities across eye/hand (whole-brain-corrected conjunction analyses), we additionally required each of the individual movement-types to activate at $P$ uncorr. < 0.001.

For the critical analyses of the preparatory delay phase, again we tested for modality or effector-dependent delay activity and for any common activations that generalized across modality (and/or effector) versus rest (whole-brain $P$ corr. < 0.05). To confirm modality- and/or effector-specific activation, we added the further constraint that activity for one modality (or effector) also had to be greater than for the other modality/effector ($P$ uncorr. < 0.001) to count as specific in this sense.

Further, we tested for any side-dependent activations (left minus right targets or vice versa), separately for the sensory, delay, or motor phases described in the preceding text within those regions already highlighted by the comparisons mentioned in the preceding text (i.e., already characterized as modality specific or generalizing across modality; and as effector specific or generalizing across effectors). For these side-dependent contrasts, correction for multiple comparisons ($P$ corr. < 0.05) considered only the volumes already activated for the
main comparisons (i.e., modality/effectort-dependent or common activations).

Finally, for completeness only (and to allow some comparison with our prior work) (Macaluso et al. 2003a), we also tested for side-dependent activations in the anterior intraparietal sulcus (aIPS). In a previous study that had used a similar design but without the critical delay period introduced here, we had found that this region was activated contralaterally regardless of stimulus modality (vision or touch) or effectort (hand vs. eye) when immediate movements were made (Macaluso et al. 2003a). In the current experiment, we could assess whether any such side-dependent activations in the aIPS would be specific to the sensory cue phase, delay phase, or motor response phase. For this a priori defined aIPS region, we assigned corrected P values using as the volume of interest a 10-mm sphere (small volume correction) (Worsley et al. 1996) that was centered on the intraparietal peak found in Macaluso et al. (2003a).

Eye tracking
In all subjects but one, eye position was monitored using an ASL eye-tracking system with remote optics that was custom-adapted for use in the scanner (Applied Science Laboratories, Bedford, MA; Model 504, sampling rate = 60 Hz). Eye-position traces were examined in a 14.5-s time window, beginning with the cue onset until the end of the trial. For each subject the eye-tracking system was calibrated before fMRI scanning. The subject performed a series of saccades from central fixation to the left and to the right LEDs, visiting each lateral position twice (duration of each fixation = 1,500 ms). The calibration served to convert the (arbitrary) units of the eye-tracking system to degrees of visual angle. The eye-position data acquired during fMRI scanning were baseline adjusted using the average horizontal position in a 500-ms precue window. We identified losses of fixation as changes in horizontal eye-position > 2° with durations > 100 ms. To ensure that trials containing inappropriate losses of fixation would not affect our imaging results, these were modeled separately in the imaging data analysis (see Data analysis). After removal of those trials, no systematic gaze deviation could be found in any of the periods requiring maintenance of central fixation. For trials requiring saccadic responses, the first derivative of the eye position (eye velocity) was used to compute saccadic reaction time (i.e., here defined as the time between the auditory go signal and eye velocity exceeding 100°/s; see Fig. 1B).

RESULTS
Behavioral data
Overt responses were measured throughout each scanning session using an eye-tracking system with remote optics (see preceding text), plus electronic switches on each side to record manual button presses. The percent of misses was 5% in the manual task and 2% in the saccade task. Subjects never responded with a button press on saccade trials, but in the manual task, we detected losses of fixation after target onset on 18% of the trials. All error trials were excluded from the fMRI analyses. A within-subject ANOVA with cue modality, movement type, and target side as independent factors was used to compare the reaction times in the eight conditions. This revealed a main effect of type of movement [F(1,7) = 49.1; P < 0.001] with saccades yielding faster reaction times [422 ± 36 (SE) ms for saccades and 567 ± 23 ms for button presses]. The main effect of side and the side-by-movement interaction almost reached significance (P = 0.058 and 0.051, respectively) due to faster responses with the right than the left hand [539 ± 29 vs. 595 ± 22 ms; F(7) = 2.6; P = 0.036], especially on button-press trial as might be expected in these right-handed subjects. Overall the reaction times were quite slow (but similar to Macaluso et al. 2003a, who used a similar experimental setup). A possible reason for this is because of the demanding fMRI environment in which subjects had to perform the tasks (i.e., a noisy surrounding where subjects have to lay still for ~1 h, including setup time). However, any such effect of the environment should presumably affect all conditions similarly, thus having no specific influence on our fMRI results.

fMRI results: sensory-cue-phase and movement-phase

SPM analyses of the sensory-cue phase highlighted sensory circuits for touch or vision, plus any “common” multisensory activation (see Fig. 2A, and Table 1); whereas fMRI analyses of the movement phase revealed motor circuits involved in eye or hand movement and effectort-independent responses (Fig. 2B and Table 2).

Analyses of brain activity associated with the sensory cues revealed “common” regions responding to both visual and tactile cues in and around the intraparietal sulcus and premotor regions, plus the occipito-temporal junction (see Fig. 2A, magenta). Selective responses for the visual cues were found in ventral, lateral, and dorsal occipital cortex, plus posterior parietal cortex (see Fig. 2A, in cyan), as would be expected. For tactile cues, we found activation of the postcentral gyrus plus parietal operculum (see Fig. 2A, in yellow), again as expected.

Within both “bimodal” regions (activated in common by both vision and touch) and “unimodal” (visual or tactile specific), we then tested for any effect of stimulus position (left minus right and vice versa; see Table 1, rightmost columns). The bimodal regions in frontal, parietal and posterior temporal cortex did not show any significant effect of stimulus position at our whole-brain corrected threshold. But for completeness, we examined the anterior intraparietal sulcus (aIPS) region previously reported by Macaluso et al. (2003a) as showing a contralateral response that generalized across vision and touch. We considered a spherical region of interest (10 mm radius) centered at the coordinates reported in that study (left hemisphere: x, y, z = −38, −36, 54; right hemisphere: x, y, z = −48, −32, 46). This confirmed a significant (P corrected < 0.05) main effect of contralateral minus ipsilateral cue side, regardless of cue modality (see also Table 1).

For areas responding selectively for visual cues, greater responses for contralateral minus ipsilateral stimulation were found within the occipital lobe (i.e., in ventral, lateral, and dorsal occipital cortex; see Table 1). The visually selective posterior parietal cortex did not show any lateralized effect in our study. A possible reason for this is that—unlike several studies that did find some spatiotopic responses in high-order visual areas—here we used small low-contrast and brief visual stimuli to signal the relevant position rather than the intensive periodic stimulation required for phase-mapping techniques (cf. Hagler and Sereno 2006; Schluppeck et al. 2005). For tactile cues, contralateral effects were found both in the postcentral gyrus and in the parietal operculum as expected.

We highlighted motor circuits by considering activity after the auditory “go signal” that prompted movement execution (see Fig. 2B and Table 2). All movement conditions activated the medial frontal cortex and superior premotor areas (Fig. 2B,
in blue). In addition, regions along the superior temporal gyrus were activated but probably as an auditory response to the go signal (common for all movement conditions). Saccadic eye movements resulted in selective activation of posterior parietal cortex and superior premotor regions. The peaks of the dorsal premotor activation were located on the lateral side of the precentral sulcus, thus in a somewhat more lateral location than the classical localization of the frontal eye fields (e.g., see Petit et al. 1997, who reported peak activation in the depth of the sulcus but with the activation cluster also extending to the lateral surface as here). Nonetheless, the current finding is consistent with our previous study that also directly compared eye versus hand movements revealing nearly identical coordinates (Macaluso et al. 2003a). The entirety of occipital cortex, including visual cortex in the calcarine fissure, also showed increased activity during eye movements, presumably as a consequence of the changes of retinal input due to saccadic execution (see Fig. 2B, in red). Hand movements resulted in the activation of peri-central regions, extending posteriorly to the anterior part of the superior parietal lobule (see Fig. 2B, in green). In addition we also found increased activity in the supplementary motor areas (partially overlapping with the region showing activation for both types of movements, cf. transverse section in Fig. 2B), in the temporo-occipital junction and in the parietal operculum (see Table 2).

Analogously to the sensory cue phase, we then tested the motor response phase data for any effect of movement side, comparing leftward minus rightward trials and vice versa (see Table 2, rightmost columns). For hand responses, this showed activation in the precentral gyrus with greater activity for button presses using the contralateral versus ipsilateral hand as would be expected in primary motor regions. In addition, hand responses activated also the anterior parietal cortex, parietal operculum, SMA, and temporo-occipital junction. Fronto-parietal regions that activated selectively for eye movements did not show any significant effect of the target side, possibly because each saccade to the target was followed by a saccade in the opposite direction, re-orienting gaze to the central fixation point (see also Macaluso et al. 2003a). Primary visual cortex in the calcarine fissure showed greater activity for ipsilateral than contralateral saccades, possibly due to changes of retinal input during the eye movements. Auditory and medial frontal regions that activated in common for both hand and eye movements (see preceding text) did not show any effect of movement side.

In summary, analyses of brain activity in the sensory cue phase and in the movement phases revealed the expected effects according to the sensory stimulation (Fig. 2A and Table 1) or the type of movement (Fig. 2B and Table 2). We found unimodal visual, unimodal tactile, and bimodal visuo-tactile activations during the sensory cue phase and effector-specific plus some effector-independent activations in the movement-phase. Several of the sensory and motor regions also showed...
Preparing to perform an eye movement toward the cued hand or eye (see Table 2), here visual areas activated contralaterally during saccade execution (see Table 2), here visual areas activated contralaterally during saccade preparation (i.e., specifically during the delay, prior to an actual saccade). Hence this preparatory activity is unlikely to represent changes of retinal input due to small eye movements that survived our exclusion criteria (see METHODS) but may instead reflect visual enhancement of the target location for an upcoming saccade. Crucially, we thus show a modulation of activity in visual cortex that was selective for the type of upcoming movement (oculomotor vs. manual) but that generalized across both visual and tactile cues.

Analyses of delay activity preceding button-press responses (hand-movement trials) revealed selective activation of motor regions in the precentral gyrus, plus supplementary motor areas.
Eye movements. We found that delay activity clearly reflected the interaction of these. We examined brain activity in the interval used for the upcoming lateralized motor response (or some a relevant position during a delay period follows primarily the different effector systems. Here we asked whether encoding of combination of signals from different modalities (as when we

DISCUSSION

TABLE 2. Target-related activity (motor responses)

<table>
<thead>
<tr>
<th>Main Effects</th>
<th>Coordinates</th>
<th>z Score</th>
<th>P-Corr.</th>
<th>Spatial Effects</th>
<th>Coordinates</th>
<th>z Score</th>
<th>P-Corr.</th>
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<td>Eye movements</td>
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<td>L posterior parietal cortex</td>
<td>-26 – 62 52</td>
<td>6.1</td>
<td>&lt;0.001</td>
<td>L Occipital cortex*</td>
<td>-10 – 78 4</td>
<td>&gt;8</td>
<td>&lt;0.001</td>
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<tr>
<td>R posterior parietal cortex</td>
<td>-28 – 62 56</td>
<td>5.1</td>
<td>0.006</td>
<td>R Occipital cortex*</td>
<td>14 – 72 6</td>
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<td>Common responses for eye and hand movements</td>
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</table>

Target-related activity (motor responses). Main effects: anatomical location, peak coordinates, z values, and corrected P values for regions activated in the movement- phase. Areas are divided according to whether the activation was effector-specific (eye movement; hand movement) or it generalized across effectors (i.e., common activation for eye and hand movements). P values are corrected for multiple comparisons considering the whole brain as the volume of interest. Spatial effects: within areas responding in the movement phase, we tested for any effect of movement-direction (left vs. right and vice- versa). P values are corrected for multiple comparisons considering all voxels showing a main effect of the movement (effector specific or effector independent), as the volumes of interest, whereas for hand movements all side-specific effects were contralateral to the responding hand, during saccade execution the side-effects in visual cortex (*) were ipsilateral to the movement/target direction.

(see Fig. 4B and Table 3, 2nd section). The medial activation did not show any selectivity according to relevant side, whereas the precentral regions showed greater activity for preparation of movement with the contralateral hand (see signal plots in Fig. 4B, green bars) as would be expected for a manual motor-plan.

Finally, we tested for any brain regions showing increased preparatory activity irrespective of both the modality of the cue and the type of upcoming motor response. This revealed robust bilateral activation in the posterior part of the superior temporal sulcus (see Fig. 5 and Table 3, 3rd section). Here activity increased during the delay phase of all trial types, responding also here irrespective of target side (see cyan bars in Fig. 5).

Discussion

Spatial orienting to external events or objects often requires combination of signals from different modalities (as when we can both see and feel an object) and also coordination of different effector systems. Here we asked whether encoding of a relevant position during a delay period follows primarily the sensory modality signaling the location or the motor system used for the upcoming lateralized motor response (or some interaction of these). We examined brain activity in the interval between sensory cue and delayed motor response (delay activity) in the absence of any current sensory stimulation or motor response. We found that delay activity clearly reflected the type of upcoming movement rather than the sensory modality of the cue stimulus. Activity increased in contralateral precentral cortex when subjects prepared for a button press with either the left or the right hand, irrespective of whether the left/right position had been cued with a visual or a tactile stimulus. When subjects prepared for an eye movement instead, activity increased in the posterior parietal cortex, dorsal premotor cortex, and ventral occipital cortex, again irrespective of the modality of the sensory cue. In occipital cortex, the delay activity was strongly lateralized to the hemisphere contralateral to the relevant location, whereas posterior parietal cortex activated for both contra- and for ipsilateral locations but with larger effects during the preparation of saccades to the contralateral hemifield. In addition, a region in the superior temporal sulcus activated during the delay, irrespective of cue modality, relevant side, and type of movement. Our findings suggest that during a delay period intervening between a stimulus cue to target location and a later motor response to that location, the relevant location is coded according to the movement type rather than the cue modality, and—critically—that these effector-specific areas can be cued by spatially specific signals from different sensory modalities.

Our finding of effector-dependent responses during the cue-to-movement delay is in general agreement with previous electrophysiological studies in non-human primates (Andersen et al. 1997; Barash et al. 1991; Cohen et al. 2002; Kalaska et al. 1997; Snyder et al. 2000) and with more recent fMRI experiments in humans (Astafiev et al. 2003; Bremmer et al. 2001;
Culham and Valyear 2006; Desouza et al. 2000; Grefkes et al. 2004; Kawashima et al. 1994; Prado et al. 2005; Schluppeck et al. 2005; Simon et al. 2002). We found preparatory activity in the posterior parietal cortex that was selective for eye movements. This activation was located in the posterior part of the superior parietal gyrus, in an area that may correspond to the IPS2 region reported by Schluppeck and colleagues (2005), who showed some retinotopic organization there in a detailed study using an overt saccade task. In a later study (Schluppeck et al. 2006), the same group reported that this area is active during saccade preparation with greater activity during preparation of contralateral versus ipsilateral saccades. In the present study, we demonstrate that preparatory activity in this posterior parietal region is selective for eye movement when comparing eye-versus hand-movement preparation directly for the first time in a delay paradigm using both visual and tactile cues. As in previous studies (Schluppeck et al. 2006; Sereno et al. 2001), we also found larger activity during preparation of contralateral than ipsilateral saccades, albeit only the right hemisphere reached full statistical significance. A possible reason for the relatively weak lateralization within posterior parietal cortex in the current study might be that here we did not use a phase and/or polar-angle mapping approach that requires predictable and extended sequences of saccades (Schluppeck et al. 2005; Sereno et al. 2001). But instead, we did introduce here for the first time both visual and tactile lateralized cue stimuli to show that either of these can trigger effector-specific preparatory activity in posterior IPS. Thus spatial information from different sensory modalities seems to converge on posterior parietal cortex that exhibit sustained activation selectively while subjects prepare for a saccadic eye movement.

Together with the activation of the posterior parietal cortex, we also found saccade-specific preparatory activity in dorsal premotor cortex and in ventral occipital cortex. In premotor cortex, the activity increased irrespective of planned saccade direction, whereas the occipital activation was contralateral to the side of the up-coming saccade. The finding of effector-specific modulation within visual occipital cortex suggests a link between motor preparation and visual processing as predicted by premotor theories of spatial selection (Rizzolatti et al. 1987). Recent micro-stimulation experiments in monkeys...
found that stimulation of oculomotor control structures can change the response proprieties of single neurons in occipital visual cortex (Armstrong et al. 2006; Tolias et al. 2001). Such interactions between anatomically distant neural populations emphasizes the potential for interplay between higher associative regions and lower sensory areas during eye-movement guidance and attention selection (Moore 2006; see also Astafiev et al. 2003). Here, we show effector- and side-specific sustained activity in human occipital cortex that also generalized across the sensory modality of the cue for the prepared saccade. The finding of these spatially specific crossmodal effects is consistent with proposals that spatial information from the somatosensory system can reach and modulate spatial representations within visual occipital cortex, possibly via higher-order control structures in frontal and parietal cortex (Macaluso and Driver 2005; Macaluso et al. 2002), such as those involved in saccade preparation.

Unlike most previous studies on preparatory activity for saccadic eye movements (Desouza et al. 2000; Schluppeck et al. 2006; Sereno et al. 2001), our paradigm included not only left/right saccades, but also left/right manual button presses (see also Connolly et al. 2000, 2007; Simon et al. 2002 for studies that also used more than one effector-system in a within-subject fMRI design). Due to this, we could show here that our occipital, premotor, and posterior parietal findings for saccade preparation are truly effector specific (specific to oculomotor preparation) and cannot be accounted for by any more general process common to the two spatial-motor tasks (such as general shifts of spatial attention). Nonetheless, we should note that our manual button-press task differed from the pointing/reaching tasks used in most electrophysiological studies to date (Batista and Andersen 2001; Calton et al. 2002; Johnson et al. 1996; Snyder et al. 1997) and in some neuroimaging studies (Connolly et al. 2003; Desouza et al. 2000; Prado et al. 2005). We used a simple button-press task with the left or the right hand (see also Macaluso et al. 2003a). One potentially important difference between traditional pointing tasks and the current button-press task is that here we did not dissociate the left/right location of the manual response from the selection of one or other hand (i.e., here the left hand always pressed the left button, and the right hand pressed the right button, within their respective hemis-
Delay activity INDEPENDENT of cue-modality, motor-effector and target side

Delay-related activity (preparatory activity). Main effects: anatomical location, peak coordinates, $z$ values, and corrected $P$ values for regions activating during the delay phase. We could distinguish between areas showing selective preparatory activity depending on the type of upcoming movement (preparation for an eye movement; preparation for a hand movement); plus areas showing sustained activity irrespective of effector (last section). Critically, all areas activated irrespective of the modality (vision or touch) that was used to cue the relevant position. $P$ values are corrected for multiple comparisons considering the whole brain as the volume of interest. Spatial effects: within regions responding during the delay phase, we tested for any effect of relevant location (left vs. right and vice-versa). $P$ values are corrected for multiple comparisons considering all voxels showing effector-specific or effector-independent preparatory activity, as the volumes of interest. For the right ventral occipital cortex and the left pre-central gyrus, the side-specific effects did not overlap with the main effects (n.v.: not in volume of interest), hence we do not report corrected $P$ values. (n.s.: not significant).

### TABLE 3. Delay activity (preparatory activity)

<table>
<thead>
<tr>
<th></th>
<th>Main Effects</th>
<th>Spatial Effects</th>
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</thead>
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<tr>
<td>Delay activity specific for eye responses</td>
<td></td>
<td></td>
</tr>
<tr>
<td>L superior premotor cortex</td>
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</tr>
<tr>
<td>R superior premotor cortex</td>
<td>$58 0 44$</td>
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</tr>
<tr>
<td>L posterior parietal cortex</td>
<td>$-22 - 64$</td>
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</tr>
<tr>
<td>R posterior parietal cortex</td>
<td>$24 - 62$</td>
<td>4.4</td>
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<td>L ventral occipital cortex</td>
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<td>Delay activity specific for hand responses</td>
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<td>L pre-central gyrus</td>
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<td>R pre-central gyrus</td>
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<td>Delay activity independent of cue-modality and motor-effector</td>
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<tr>
<td>L superior temporal sulcus</td>
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<td>7.6</td>
</tr>
<tr>
<td>R superior temporal sulcus</td>
<td>$68 - 22$</td>
<td>$&gt;8$</td>
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</tbody>
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FIG. 5. Activations in the delay-phase common to the preparation of eye and hand movements. In the posterior part of the superior temporal sulcus, activity increased during the delay phase, irrespective of both cue modality (touch or vision) and movement effector (eyes or hands). The signal plots show activity for all sensory-motor combinations (crossing sensory modality of the cue with effector type), for the 3 trial phases (C, cue; D, delay; T, target/response) and separately for left and right hemifield trials. The bars in cyan highlight the bimodal, effector- and side-independent activation in the delay-phase. Activations are rendered on anatomical sections at a threshold of $P$ corr. = 0.05 (cluster level).
bution of each potential spatial framework to each stage of the sensory-motor spatial translation.

Within our current paradigm, it might be even argued that the sensory cues acted as “symbolic” signals instructing subjects to move one or the other hand (somewhat similar to presenting verbal cues: “move left” or “move right”) or to saccade left or right. But although it is indeed possible that subjects converted the exogenous lateralized sensory-cue signals into some other form of representation and then issued an endogenous motor command on presentation of the auditory go signal, we note that in fact we found strong motor-specific activations during the delay period. Moreover, prior to obtaining our actual results, it was entirely possible that subjects might maintain an internal representation of the relevant location in sensory rather than motor terms. Thus in principle, subjects could process the cue and then select a sensory representation endogenously to represent the critical location during the delay (e.g., simply “attending” to the relevant visual or tactile location during the delay). Our results show decisively that this does not happen; instead, the activity during delay reflects only the motor requirements.

Concerning the IPS, Medendorp et al. (2005) also reported greater activity during saccades than pointing, but note that their study did not explicitly separate cue, delay and movement phases unlike here. Delay activity during pointing or saccades was recently investigated in a fMRI study that dissociated position versus effector cuing (Connolly et al. 2007). This revealed increased activity in IPS, even when the instruction cue concerned only the relevant effector system (i.e., not specifying relevant location). IPS activation was observed both for saccadic and pointing preparation but with greater effects for saccade than pointing. Our IPS findings during the delay phase (larger activation for saccade task versus manual task, see Fig. 3A) appear consistent with Medendorp’s and Connolly’s findings (Connolly et al. 2007; Medendorp et al. 2005a), although our button-press task differs from previous pointing tasks as noted earlier. For present purposes, an advantage of the button-press task was that it allowed us to present tactile cue stimuli on each side (to the index-finger) at exactly the same location as the possible visual stimuli and that always required spatially compatible motor responses to the corresponding location. Pointing or reaching tasks would have precluded the possibility of using tactile cues in the same way, which was critical for the current aim of assessing the possible role of cue-modality (as well as movement type) during the cue-to-movement delay phase. But these differences in the type of hand-motor responses between the current study and previous pointing/reaching tasks may explain also why here we found preparatory activity in precentral cortex but not within the parietal cortex itself for hand movements. A possible alternative design could have used tactile cues on the left/right hand to instruct leftward/rightward pointing movement. Although this design might reveal tacitly triggered pointing activity in parietal cortex, it would have required placing visual and tactile cue stimuli at different positions or using different target locations for saccade and pointing tasks.

Together with our effector-specific findings (i.e., posterior parietal, dorsal premotor plus ventral occipital cortex for saccade preparation vs. precentral cortex for button-press preparation), we also found sustained delay activity in the superior temporal sulcus, but now irrespective of movement type. Also in this region, the delay response was observed irrespective of the modality that had cued the relevant location. Several previous studies implicated the STS in spatial covert orienting (Macaluso et al. 2001; Yamaguchi et al. 1994; see also Luh et al. 1986 for related studies in non-human primates). Using PET, we previously reported STS activation when subjects sustained attention either to the left or to the right hemifield (Macaluso et al. 2001) and—as in the current study—irrespective of whether vision or touch was used to define the currently relevant position. Our present results of sustained activity in the delay phase thus appear consistent with the interpretation that STS may be involved in committing spatial attention to a given spatial location prior to the go signal for executing a movement, and that this process can happen supramodally.

Although the primary aim of the current study was to investigate preparatory activity in the absence of any sensory stimulation or motor response, we also examined brain activity in the cue phase and the movement phase to highlight patterns of sensory (cue phase) and motor (movement phase) activity. For the movement phase, we observed the expected activation of the contralateral precentral gyrus for button press responses, and posterior parietal plus dorsal premotor regions (FEF) for saccade execution. In the cue phase, we could discriminate between “unimodal” (i.e., specific just for vision or touch) versus bimodal sensory activations. This revealed the expected unimodal effects in occipital cortex for vision versus postcentral gyrus plus parietal operculum for touch. Bimodal responses were observed at the occipito-temporal junction, posterior parietal cortex, and premotor regions. Several of these regions are likely to contain neurons responding to more than one modality (Bruce et al. 1981; Colby and Duhamel 1991; Graziano et al. 1994), although more general attentional or task-related processes might also explain some “common, bimodal” responses in fronto-parietal regions (Corbetta and Shulman 2002; Gitelman et al. 1999; Mesulam 1998; Yantis and E. MACALUSO, C. D. FRITH, AND J. DRIVER

In summary, sustained delay activity while subjects prepared for an overt response toward a cued location was found to reflect primarily motor preparation rather than sensory or attentional encoding of the relevant location. We found separate, effector-specific responses in posterior parietal cortex, frontal-eye-field, and ventral occipital cortex for saccade preparation versus contralateral precentral cortex for hand responses. Our findings are in general agreement with single-cell work in monkeys by indicating that sensory input is transformed into nascent motor plans during the delay. Critically, here we show that this generalizes across sensory modalities with spatial signals from vision and touch feeding into effector-specific motor representations in the human brain.
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