Functional organization of human posterior parietal cortex: grasping- and reaching-related activations relative to topographically organized cortex

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Konen CS, Mruczek RE, Montoya JL, Kastner S. Functional organization of human posterior parietal cortex: grasping- and reaching-related activations relative to topographically organized cortex. J Neurophysiol 109: 2897–2908, 2013. First published March 20, 2013; doi:10.1152/jn.00657.2012.—The act of reaching to grasp an object requires the coordination between transporting the arm and shaping the hand. Neurophysiological, neuroimaging, neuroanatomic, and neuropsychological studies in macaque monkeys and humans suggest that the neural networks underlying grasping and reaching acts are at least partially separable within the posterior parietal cortex (PPC). To better understand how these neural networks have evolved in primates, we characterized the relationship between grasping- and reaching-related responses and topographically organized areas of the human intraparietal sulcus (IPS) using functional MRI. Grasping-specific activation was localized to the left anterior IPS, partially overlapping with the most anterior topographic regions and extending into the postcentral sulcus. Reaching-specific activation was localized to the left anterior IPS, partially overlapping with the medial aspects of the more posterior topographic regions. Although the majority of activity within the topographic regions of the IPS was nonspecific with respect to movement type, we found evidence for a functional gradient of specificity for reaching and grasping movements spanning posterior-medial to anterior-lateral PPC. In contrast to the macaque monkey, grasp- and reach-specific activations were largely located outside of the human IPS.

intraparietal sulcus; superior parietal lobule; prehension; functional magnetic resonance imaging

prehension involves the coordination between transporting the hand in space (i.e., reaching) and shaping the hand according to the target’s physical properties (i.e., grasping; Jeannerod 1981). One hypothesis is that these two components are controlled by independent frontoparietal systems, a dorsomedial network for reaching and a dorsolateral network for grasping (Jeannerod 1988; Jeannerod et al. 1995). Consistent with this hypothesis, physiology studies in macaque monkeys have revealed distinct areas in posterior parietal cortex (PPC) that are specialized for particular types of movements, such as grasping and reaching. Neurons in the anterior intraparietal area (AIP) preferentially encode grasping movements, whereas neurons in the parietal reach region (PRR) preferentially encode reaching movements.

Neurons in area AIP, which is located in the anterior-lateral part of the intraparietal sulcus (IPS), play a key role in preshaping of the hand for grasping (Murata et al. 2000; Sakata et al. 1992, 1997; Taira et al. 1990). These neurons exhibit selectivity for specific grasping movements, as well as the shape, size, and orientation of three-dimensional visual objects, regardless of the object’s position in visual space (Murata et al. 2000). Moreover, inactivation of AIP disrupts a monkey’s ability to utilize visual information for preshaping the contralateral hand (Gallese et al. 1994).

Neurons in PRR have been associated with the planning and execution of reaching movement. PRR is located on the posterior-medial bank of the IPS. It is a functionally defined area and likely overlaps with the medial intraparietal area (MIP) and area V6A (Andersen and Buneo 2002; Snyder et al. 1997). PRR appears to code the targets for a reach in visual coordinates relative to the direction of gaze (Buneo and Andersen 2006; Buneo et al. 2002; Pesaran et al. 2006). Moreover, PRR exhibits intention-related activation reflecting the plan for a reaching movement (for review see Andersen and Buneo 2002).

Recent evidence has suggested that the dorsolateral and dorsomedial networks are not simply independent networks for reaching and grasping. For example, reaching-related neurons in macaque area V6A (Fattori et al. 2001; Galletti et al. 1999) are sensitive not only to the direction of a reach (Fattori et al. 2004) but also to the orientation of a target (Fattori et al. 2009), the hand shape necessary to grasp different targets (Fattori et al. 2010), and the target shapes themselves (Fattori et al. 2012). The relative contributions of the dorsomedial and dorsolateral networks during prehension may instead reflect different requirements of specific movements in terms of planning (Glover et al. 2012), online control (Glover et al. 2012; Grol et al. 2007), or the integration of perceptual information (Verhagen et al. 2008).

Regardless of the specific functional role of the regions in these networks in the control of object-directed arm and hand movements, neuroimaging studies in humans and monkeys have consistently reported grasp-specific activity in the anterior IPS (e.g., Beglioni et al. 2007; Binkofski et al. 1998; Culham 2004; Culham et al. 2003; Frey et al. 2005; Nelissen and Vanduffel 2011) and reach-related activity in medial IPS extending into the superior parietal lobe (SPL; e.g., Cavanagh et al. 2010; Connolly et al. 2003; Filimon et al. 2009; Nishimura et al. 2007; Prado et al. 2006). However, due to interindividual differences in IPS anatomy (Caspers et al. 2006; Konen and Kastner 2008a; Scheperjans et al. 2008) and the blurring of spatial information, traditional analyses in normalized reference frames have yielded inconsistent results regarding the precise anatomic localization of human parietal grasp- and reach-related regions (for review see Culham et al. 2006). Additionally, although the detailed knowledge gained
from electrophysiological studies in macaque monkeys provides a useful model for understanding the functionality of human PPC, the anatomic differences between monkeys and humans present a challenge for bridging research across species.

One approach to circumvent these challenges is to characterize the relationship between human parietal grasp- and reach-related regions relative to other functionally defined regions at the single-subject level. The human PPC contains at least seven topographically organized areas (for review see Silver and Kastner 2009), six along the IPS (V7/IPS0, IPS1–IPS5) and one in the SPL (SPL1). Each area contains a representation of the contralateral visual field and is separated from adjacent areas by reversals in the visual field sign. These regions can be readily identified in individual subjects with paradigms such as the memory-guided saccade task (Sereno et al. 2001), thus permitting the systematic investigation of the core functions of the human PPC using a region-of-interest (ROI) approach while accounting for differences in individual anatomy. Additionally, the properties of these areas can be compared with neurophysiological studies in monkeys to gain insight into putative functional relationships across species. Previous studies using such an approach have identified differential response properties of these regions related to motion processing (Konen and Kastner 2008a), arm and eye movements (Konen and Kastner 2008a; Levy et al. 2007), spatial attention (Lauritzen et al. 2009; Silver et al. 2005; Szczepanski et al. 2010), short-term memory (Schluppeck et al. 2006; Sheremata et al. 2010), and object processing (Konen and Kastner 2008b; Mruczek et al. 2013).

In the present study, we determined the anatomic location of grasping- and reaching-related activations relative to topographically organized areas in human PPC in individual subjects. We found that grasping-specific activation was partially overlapping with IPS5 and extending laterally and anteriorly into the postcentral sulcus, whereas reaching-specific activation was located medially in the precuneus and partially overlapping with IPS1/2 and SPL1. From posterior-medial to anterior-lateral PPC, movement-specific activation smoothly changed in between. The functional properties of these regions are reminiscent of those observed in macaque AIP and PRR, although we have chosen the nomenclature human parietal grasp region (hPGR) and human parietal reach region (hPRR) to avoid implying direct homologies between areas across species. In contrast to macaque monkeys, grasp- and reach-specific activation was largely located outside of the human IPS.

METHODS

Subjects

Six subjects gave informed written consent for participation in the study, which was approved by the Institutional Review Panel of Princeton University. All of the subjects (4 men, 2 women; 24–36 yr of age) were right-handed and in good health with no history of psychiatric or neurological disorders. Subjects had normal or corrected-to-normal visual acuity. All subjects participated in two scanning sessions: one for the movement study and one for localizing topographically organized areas in PPC.

Stimulus Presentation

Auditory stimulation. For the movement experiments, the auditory stimuli were generated on a Macintosh G4 computer (Apple Computers; Cupertino, CA) using MATLAB software (The MathWorks, Natick, MA) and Psychophysics Toolbox functions (Brainard 1997; Pelli 1997). Auditory stimuli were delivered through MR-compatible hearing tubes.

Visual stimulation. For the memory-guided saccade experiments, the visual stimuli were generated on a Macintosh G4 computer (Apple Computer) using MATLAB software (The MathWorks) and Psychophysics Toolbox functions (Brainard 1997; Pelli 1997). Stimuli were projected from a PowerLite 7250 liquid crystal display projector (Epson; Long Beach, CA) outside the scanner room onto a translucent screen located at the end of the scanner bore. Subjects viewed the screen at a total path length of 60 cm through a mirror attached to the head coil. The screen subtended a circular region with a radius of 30° of visual angle.

For both experiments, a trigger pulse from the scanner synchronized the onset of stimulus presentation to the beginning of the image acquisition.

Movement Experiment

Experimental design. Grasping and reaching movements were directed at a grasping apparatus (Fig. 1A; adapted from Culham et al. 2003). The metal-free apparatus consisted of a rotating cube with four faces. Each face contained two objects of a particular size (small, medium-small, medium-large, and large). The metal-free apparatus consisted of a rotating cube with four faces. Each face contained two objects of a particular size (small, medium-small, medium-large, and large).

Grasping and reaching movements were manually rotated to display different faces. Each face had 2 objects of a particular size (small, medium-small, medium-large, and large). The hand position depicted in A reflects the end position of a grasping movement. C: experimental design. Each run consisted of 4 movement blocks containing 2 grasping and 2 reaching movements each (GR, grasp to the right target; GL, grasp to the left target; RR, reach to the right target; and RL, reach to the left target). For each movement block, the grasping apparatus was manually rotated to display 1 of the 4 faces of the grasping apparatus.
faces covered with Lego support plates. Each face (14.5 × 13.3 cm) was attached with a central Lego cylinder (0.7-cm diameter), which served as the fixation point, and two identical Lego bricks mounted 3.6 cm to the left and right of the fixation point. The peripheral bricks differed in width and length across faces of the grasping apparatus. Small-sized objects were 1.6 × 1.6 cm, medium-small sized objects were 1.5 (width) × 2.4 cm, medium-large sized objects were 3.2 × 3.2 cm, and large-sized objects were 1.5 (width) × 4 cm. All objects had a depth of 1.1 cm. The rotating cube was fixed to an L-shaped frame (Fig. 1A). The vertical piece was adjustable in height, and the horizontal piece stabilized the grasping apparatus as subjects were laying on it with their lower backs. The grasping apparatus was positioned near the entrance of the scanner bore. The exact position and arrangement of the apparatus was individually adjusted for each subject in order to present the stimuli at a comfortable grasping/reaching distance without the need for shoulder movements. The approximate movement distance from the resting position (hand resting on the navel) to the target objects was 15 cm. The approximate viewing distance was 68 cm, yielding a target eccentricity of ~3°.

One of the experimenters was positioned next to the scanner bore throughout the experiment and manually rotated the grasping apparatus in between movement blocks. The experimenter rotated the apparatus according to a predetermined, randomized stimulus presentation sequence of small, medium-small, medium-large, or large objects. Although movement of any mass within the scanner’s magnetic field can induce artifacts (Culham 2006), the experimenter only moved in the middle of a 28-s fixation period between blocks, and these movements were not correlated with any of the experimental conditions. Thus any potential artifacts affected all conditions similarly and could not account for the specific results reported below.

Subjects lay supine on the horizontal scanner bed with their heads surrounded by foam to reduce head movements (Fig. 1A). The subjects’ heads were slightly tilted (~20–30°), which allowed them to look through the opening of the head coil and to fixate the fixation point attached to the grasping apparatus. The subjects were instructed to perform four different actions with their right hand: grasp the target to the right of fixation (GR), grasp the target to the left of fixation (GL), reach toward the target to the right of fixation (RR), and reach toward the target to the left of fixation (RL). In the grasping conditions, subjects grasped the vertical axis of the rectangular target using a precision grip with the right index finger and thumb (Fig. 1B). The objects were firmly mounted on the grasping apparatus, so the subjects could not remove the objects. In the reaching conditions, subjects transported their right hand to the target location and touched the object with the knuckle of their index finger (Fig. 1B). This form of reaching has been used in previous studies (Beglioni et al. 2007; Cavina-Pratesi et al. 2007; Culham et al. 2003) and was used in the present study to minimize the configuration of the hand needed to manipulate the target objects. After each movement, subjects returned their hand to the resting position by placing their right hand on their navel while maintaining fixation. We did not measure movement kinematics during the scanning sessions. Therefore, any potential differences between the reaching and grasping movements (e.g., reaction time, duration, etc.) are not accounted for in our analysis. Given the sluggishness of the hemodynamic response and the integration of the underlying neural activity across relatively long time windows, we expect that subtle differences in kinematics do not contribute significantly to the presented results.

Before each scan, subjects participated in a behavioral session consisting of four runs to become familiar with the task demands and to learn how to perform the different movements with consistency. During the training session and throughout the scanning sessions, subjects were reminded to maintain stable fixation throughout the task. Although we did not measure eye movements, all subjects were highly trained at maintaining stable fixation in a variety of psycho-physical tasks.
of the general linear model (GLM; Friston et al. 1995). Additional regressors to account for variance due to baseline shifts between time series, linear drifts within time series, and head motion were included in the regression model. Although motion correction algorithms correct for artifacts due to changes in head position, they do not correct for distortions of the magnetic field caused by the moving mass during limb movements. To check for the possibility that motion artifacts could account for the brain activation observed during the task, we performed the multiple regression analysis either including or excluding motion correction parameters as nuisance regressors. The comparison of these two analyses revealed no qualitative differences in activation patterns, as assessed by visual inspection of the statistical maps.

Activated voxels resulting from the comparison between grasping or reaching movements vs. baseline were assigned to ROIs. Statistical maps were thresholded at \( P < 0.001 \) (uncorrected for multiple comparisons). To quantify the preferential encoding of grasping and reaching movements in and around topographically organized areas of PPC (defined using a memory guided saccade task, see below), the following analyses were performed.

**VOLUMETRIC ANALYSIS.** For each subject and area, we determined the number of voxels that were activated during the execution of either grasping or reaching movements or that were commonly activated during the execution of both types of movements (at a fixed threshold of \( P < 0.001 \)). The resulting volumes were normalized to the percentage of the overall activated volume within an area. These normalized volumes were then averaged across all subjects to yield group data. Statistical significance was assessed with a repeated-measures ANOVA followed by a \( t \)-test.

**MEAN SIGNAL CHANGE.** For each subject, the time series of functional MRI (fMRI) signals were corrected for hemodynamic lag (3 s) and averaged over all activated voxels in a given ROI and normalized to the first time point of each trial. All time course analyses were performed on unsmoothed data, and ROIs were included in these analyses only if the cluster of activated voxels was greater than 15 voxels. The fMRI signals obtained during the first four time points of each movement condition were averaged, resulting in mean signal changes that were then averaged across subjects to yield group data. Statistical significance was assessed with a paired \( t \)-test.

**MOVEMENT PREFERENCE INDEX.** A movement preference index (MPI) was computed to quantify the preferential encoding of grasping or reaching movements and to compare them across areas \( [\text{MPI} = R_{\text{grasping}} - R_{\text{reaching}}]/(R_{\text{grasping}} + R_{\text{reaching}}) \), where \( R_{\text{grasping}} = \text{mean fMRI signal change during grasping movements} \) and \( R_{\text{reaching}} = \text{mean fMRI signal change during reaching movements} \). This index ranges from 1 to \(-1\), with positive values indicating stronger responses evoked by grasping movements, negative values indicating stronger responses evoked by reaching movements, and values around 0 indicating no preferential encoding for one movement or the other. For each subject, the MPI was determined in a given area. The MPIs were then averaged across subjects to yield group data. Statistical analysis was assessed with a nonparametric bootstrap analysis (Efron and Tibshirani 1993). The mean fMRI signals evoked during the grasping and reaching tasks were pooled together across subjects for each ROI. Values were then randomly drawn, without replacement, from this pool and assigned as mean fMRI signals for each subject for both movement tasks. By using these randomly drawn numbers, the MPIs were again calculated separately for each subject and then averaged across subjects. This was repeated 10,000 times to yield a distribution of average MPIs for each ROI. Finally, the values obtained from the original data were compared with this distribution, and values that were outside of the 2.5–97.5 percentile range were deemed significant (i.e., 2-tailed test with \( \alpha = 0.05 \)). Additional bootstrap analysis was performed to compare the index values across ROIs.

**Functional ROI definitions.** The ROIs for hPGR and hPRR were functionally defined based on differential responses evoked by grasping and reaching trials compared with baseline (\( P < 0.001, \) uncorrected for multiple comparisons). We defined hPGR as a region that showed significant activation during grasping trials but not during reaching trials. Given the somatosensory and motor components of the task, this region was anatomically constrained to be posterior to the fundus of the postcentral sulcus. We defined hPRR as a region that showed significant activation during reaching trials but not during grasping trials. For the time course analysis and the calculation of MPI, the hPGR and hPRR ROIs were limited to nontopographic regions to maintain independence from the analysis of V7/IPS0, IPS1–IPS5, and SPL1 (defined below). It should be noted, however, that the ROI-based analyses of hPGR and hPRR are circular given that they were functionally defined using the same data sets. However, these analyses are included for the purposes of comparing with the topographic ROIs, which were defined using the independent memory-guided saccade task (see below). Finally, we directly contrasted grasping and reaching movements (\( P < 0.05, \) uncorrected for multiple comparisons), as has been done in previous studies (e.g., Begliomini et al. 2007; Cavina-Pratesi et al. 2010; Culham et al. 2003; Frey et al. 2005).

**Memory-Guided Saccade Task**

**Experimental design.** The memory-guided saccade task was used to localize topographically organized areas in PPC (Konen and Kastner 2008a; Schluppeck et al. 2005; Sereno et al. 2001; Silver et al. 2005; Swisher et al. 2007). The detailed description of design, acquisition, and analysis of the data is given elsewhere (Kastner et al. 2007; Konen and Kastner 2008a). Briefly, subjects had to remember and attend to the location of a peripheral cue over a delay period while maintaining central fixation. After the delay period, the subject had to execute a saccade to the remembered location and then immediately back to central fixation. The target cue was systematically moved on subsequent trials either clockwise or counterclockwise among eight equally spaced locations. Subjects performed eight runs, each composed of eight 40-s cycles of the sequence of eight target positions.

**Data acquisition.** Data were acquired using the same sequence as described above for the movement experiment, except that 8 series of 140 volumes were acquired.

**Data analysis.** Fourier analysis was used to identify voxels that were sensitive to the spatial position of a peripheral cue during the task (Bandettini et al. 1993; Engel et al. 1997; Schneider et al. 2004). The phase of the harmonic at the stimulus frequency, which is the temporal delay relative to the stimulus onset, indicates the preferred spatial location in polar angle for each voxel.

**Topographic ROI definitions.** Each topographically organized area of the PPC contained a representation of the contralateral visual field and was separated from neighboring areas by reversals in the visual field orientation (for examples, see Konen and Kastner 2008a; Szczepanski et al. 2010). Anterior to visual area V7/IPS0, IPS1 and IPS2 were located in the posterior part of the IPS. IPS3 and IPS4 were located in the anterior-lateral branch of the IPS, whereas IPS5 extended into the intersection between the IPS and the postcentral sulcus. SPL1 branched off the most superior areas of the IPS and extended into the superior parietal lobule.

**Standard Space Coordinates**

For the purpose of reporting standard coordinates of hPGR and hPRR, we transformed each subject’s anatomic volume into Talairach space (Talairach and Tournoux 1988) using AFNI’s @auto_frc function. The resulting transformation matrix was used to convert the center-of-mass coordinates, determined from the cortical surface projection of the appropriate functional contrast of each ROI, into Talairach space. For subjects with multiple distinct clusters of activation, we report the coordinates for the largest cluster. The average
coordinates across subjects for hPGR and hPRR did not differ significantly when a weighted-average of the coordinates from all clusters was considered.

Meta-Analysis

To compare our reported coordinates with previous results, we performed a meta-analysis of 18 studies (in addition to the current study) reporting grasp- or reach-related activity in human PPC. Talairach coordinates (converted from MNI space where appropriate) were projected onto a cortical surface model of the N27 brain (transformed into Talairach space) provided in the AFNI/SUMA analysis package. To display the estimated borders of the topographic regions of the IPS (V7/IPS0, IPS1–IPS5, and SPL1), we created a probabilistic atlas of visual topography from 32 subjects (Wang et al. 2012). Briefly, after surface-based spatial normalization, corresponding ROIs from every subject were superimposed. A maximum probability map was generated by assigning each surface node to the ROI with the highest probability across all subjects. Given the variability in the underlying anatomy of the intraparietal sulcus and surrounding regions (Caspers et al. 2006; Konen and Kastner 2008a; Schepersjans et al. 2008), use of a standard anatomic volume and topographic ROI borders derived from a large population ensures that the resulting display is not biased by one of the individual subjects in our current study.

RESULTS

Previous fMRI studies have reported grasping- and reaching-related activation in a multitude of areas in human PPC, as well as somatosensory regions in anterior parietal cortex and motor regions in frontal cortex (e.g., Astafiev et al. 2003; Begliomini et al. 2007; Binkofski et al. 1998; Cavina-Pratesi et al. 2010; Connolly et al. 2000, 2003; Culham 2006; Culham et al. 2003; DeSouza et al. 2000; Fernandez-Ruiz et al. 2007; Filimon et al. 2009; Frey et al. 2005; Hagler et al. 2007; Levy et al. 2007; Pellijeff et al. 2006). Although we also observed activation of somatosensory and motor cortex related to movement type (see e.g., Culham 2004), the focus of the current investigation is the representation of movements in topographically organized areas along the IPS, as well as nontopographically organized areas in PPC. Because there were no consistent activation patterns across subjects for any of these analyses in the right hemisphere and subjects performed the movements with their right hands, we have focused our analysis and interpretation on the left hemisphere.

Figure 2 depicts left hemisphere activations evoked during grasping (red) or reaching (green) movements vs. baseline \((P < 0.001)\) or commonly activated during both types of movements (blue). The majority of topographically organized areas along the IPS (defined by an independent memory-guided saccade task; see METHODS) exhibited activation evoked by both grasping and reaching movements. This nonspecific activation was evenly distributed across V7/IPS0 and IPS1–IPS4, extending into IPS5 in four subjects (S2–S4 and S6), but did not extend into adjacent, nontopographic cortex. It should be noted that the nonspecific activation could be related to visual or attention-related aspects of the task that are not explicitly related to movement execution.

Although the overlapping activations were widely distributed across the IPS, a systematic pattern of activation regarding the preferential responses evoked by one or the other movement was found. In all six subjects, grasping-specific activation was found in IPS5 extending anteriorly and laterally into the postcentral sulcus. Three subjects (S2, S4, and S5) exhibited additional grasping-specific activation in IPS4. The location of this hPGR was confirmed by calculating the contrast grasping vs. reaching movements in individual subjects \((P < 0.01)\) as has been done in previous studies to localize a putative human homolog of macaque AIP (e.g., Begliomini et al. 2007; Cavina-Pratesi et al. 2007; Culham et al. 2003; Frey et al. 2005). The results showed partial activations within IPS5 extending outside this area into the postcentral sulcus that overlapped with the activation obtained from the comparison between grasping movements vs. baseline (data not shown). Overall, the location and functional characteristics make hPGR a good candidate for a functional homolog of AIP in macaques (Culham et al. 2006; Grefkes and Fink 2005).

Reaching-specific activation was found in all subjects in the medial part of PPC. In five subjects, reaching-specific activation overlapped with topographically organized IPS1/2 in the posterior IPS (S1–S5) as well as SPL1 (S1–S4 and S6). In two subjects (S1 and S3), reaching-specific activation extended into IPS3, whereas in another subject (S6), activation extended into area V7/IPS0. In all subjects, reaching-related activation extended medially from topographically organized areas of the IPS and/or SPL1 into the nontopographically organized precuneus and superior parieto-occipital sulcus. The location and functional characteristics make this hPRR a good candidate for a functional homologue of PRR in macaques (Culham et al. 2006; Grefkes and Fink 2005).

Taken together, the majority of topographically organized areas in PPC appeared to encode aspects of the task that were not related to the specific type of movement. However, within these regions, more posterior-medial and anterior-lateral portions were increasingly more specific for reaching and grasping movements, respectively. Additionally, posterior-medial and anterior-lateral non-topographically organized cortex in PPC exhibited strong movement preferences for reaching and grasping, respectively. From the posterior-medial to the anterior-lateral subdivisions of the PPC, the preference in responses gradually changed from reaching to grasping movements. In the majority of subjects, patches of activations that were related to the execution of reaching movements were most often found in IPS1/2 and SPL1. Specifically, preferential activation by reaching movements was found in the medial part of IPS1 and IPS2 and the posterior part of SPL1. In contrast, patches of activations that were mainly related to grasping movements were most often found in the anterior parts of IPS4 and IPS5.

To quantify the preferred responses evoked by grasping and reaching movements in and around topographically organized areas of PPC, we performed a number of additional analyses. It should be noted that the following analyses consider only the population response of an area as a whole, thereby discarding regional differences within an area.

First, for each subject and area, we determined the number of voxels that were activated during the execution of grasping only or reaching only or commonly activated during both types of movements \((P < 0.001)\) in the topographically organized areas. The resulting volumes were normalized to the overall volume of each topographically defined area and then averaged across subjects (Fig. 3). Note that outside topographic cortex, hPGR and hPRR, which were functionally defined by the comparison between grasping or reaching movements vs. base-
line, were excluded from this analysis. The results revealed that all topographically organized areas contained a significant percentage of voxels that were activated during the performance of both movement types ($P < 0.01$). The comparison between the volume that was activated during the performance of one movement or the other, however, revealed that the two types of movements were differentially represented across areas. Area V7/IPS0 only contained voxels that were activated during both movement types, IPS1–IPS3 in the posterior part of the IPS and SPL1, branching medially into the superior parietal lobe, are only labeled for S5. Movement-related activity was thresholded at $P < 0.001$. Red regions denote voxels that showed significantly greater activations during the execution of grasping relative to baseline, green regions denote voxels that were more strongly activated during the execution of reaching relative to baseline, and blue regions denote voxels that were activated during both types of movements, without any preference for either movement type. From posterior-medial to anterior-lateral PPC, the preferential responses changed from reaching to grasping movements. A, anterior; M, Medial; P, posterior; L, lateral.

The activated volume analysis was complemented by an analysis of the mean time course of signal changes across all activated voxels in a given area during the execution of grasping or reaching movements. We included hPGR and hPRR in this analysis for comparison with the topographic regions, although hPGR and hPRR were functionally defined using the same movement task data set. Figure 4 shows the time courses of fMRI signals in all ROIs. For each area, we extracted mean signal changes from the first four time points of each movement condition and compared the results across subjects. Area V7/IPS0 and IPS1–IPS4 showed no significant differences in mean signal changes between grasping and reaching movements (paired $t$-test, $P > 0.05$). IPS5 and hPGR showed significantly stronger responses during the performance of grasping compared with reaching movements ($P < 0.001$). The reversed pattern of responses was observed in SPL1 and hPRR; both areas showed significantly stronger responses during reaching compared with grasping movements ($P < 0.01$).

To compare the preferences in responses evoked by grasping and reaching movements across areas, we computed an MPI.
expected reach-related bias in the medial portions of the PPC, extending from the parieto-occipital sulcus to the anterior portions of the SPL, and the expected grasp-related bias in the anterior-lateral portions of the PPC, near the junction of the IPS and the postcentral sulcus. These results are consistent with the single-subject analyses presented above (Fig. 2).

**DISCUSSION**

We determined the relationship between grasping- and reaching-related activation and topographically organized areas of the human PPC mapped in individual subjects. Grasping-specific activation was localized in the left anterior IPS, partially overlapping with IPS5, and extending into the postcentral sulcus. Reaching-specific activation was localized in the left precuneus and SPL, partially overlapping with SPL1 and SPL1. The majority of activation within the left topographic regions V7/IPS0 and IPS1–IPS4 was nonspecific with respect to movement type. The quantitative analysis of the population response in and around topographic cortex revealed a gradient of movement type specificity in the human PPC, with a posterior-medial preference for reaching and an anterior-lateral preference for grasping.

![Fig. 3. Volumetric analysis of grasping- and reaching-related activity in topographically organized areas of PPC. Values are percentages of activated voxels, relative to the absolute size of an area as defined by topographic mapping, showing greater responses evoked by both types of movements (white), grasping movements (black), or reaching movements (gray), averaged across subjects (n = 6). For each ROI, bars for conditions in which no subject showed any activated voxels are not shown. *P < 0.05, volumetric differences that are significantly greater than zero. Error bars indicate SE.](http://jn.physiology.org/)

![Fig. 4. Time courses of functional MRI (fMRI) signals during grasping and reaching movements. Time course signals were averaged for each area and movement task (black, grasping movements; gray, reaching movements) and across subjects (n = 6). IPS5 and human parietal grasp region (hPGR), located in the anterior part of the IPS and posterior part of the postcentral sulcus, showed significantly stronger responses during grasping movements, whereas SPL1 (superior parietal lobe) and human parietal reach region (hPRR), located medially to the IPS, showed stronger responses during reaching movements. The other areas showed similar responses during both types of movements. Error bars indicate SE.](http://jn.physiology.org/)
TABLE 1. Talairach coordinates for hPGR and hPRR

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<td>50</td>
<td>44</td>
<td>3,756</td>
<td>17</td>
<td>78</td>
<td>38</td>
<td>9,868</td>
</tr>
<tr>
<td>S5</td>
<td>37</td>
<td>37</td>
<td>50</td>
<td>2,403</td>
<td>4</td>
<td>71</td>
<td>37</td>
<td>6,534</td>
</tr>
<tr>
<td>S6</td>
<td>31</td>
<td>51</td>
<td>50</td>
<td>3,953</td>
<td>24</td>
<td>79</td>
<td>33</td>
<td>8,967</td>
</tr>
<tr>
<td>Mean ± SE</td>
<td>31 ± 2.3</td>
<td>44 ± 3.4</td>
<td>50 ± 1.6</td>
<td>3,544 ± 472</td>
<td>13 ± 3.3</td>
<td>73 ± 3.0</td>
<td>37 ± 3.8</td>
<td>8,422 ± 478</td>
</tr>
</tbody>
</table>

Reported coordinates reflect the center of mass of the largest cluster of activity for human parietal grasp region (hPGR) and human parietal reach region (hPRR). The average coordinates did not change appreciably when the center of mass was considered across all clusters (i.e., a weighted average).

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The parietal cortex contains multiple functional subdivisions (Filimon et al. 2009; Grefkes et al. 2004) and the other in the superior parieto-occipital cortex (SPOC; Cavina-Pratesi et al. 2010; Connolly et al. 2003), have most often been identified as putative functional homologs of macaque PRR. One possibility is that human PRR contains multiple functional subdivisions (Filimon et al. 2009; Prado et al. 2005). Reaching-related activity in SPOC has been associated with visually guided reaching (Filimon et al. 2009), only for peripheral (i.e., nonfixated) targets (Prado et al. 2005). A more anterior region in the medial IPS extending into the precuneus has been associated with both visually and nonvisually guided reaching (Filimon et al. 2009), as well as reaching toward both fixated and peripheral targets (Prado et al. 2005). Evidence from neuropsychology is consistent with these results, as well as the activation foci of the current study. Patients with optic ataxia (Balint 1909) show inaccurate reaches when visual targets are viewed in peripheral vision. Karnath and Pererin (2005) identified specific parietal foci associated with optic ataxia by contrasting parietal lesions in patients with and without the disorder. They found that optic ataxia is commonly associated with several lesion foci in the parietal cortex: one in the precuneus, one in the superior occipital gyrus near the parieto-occipital junction (SPOC), and one in the SPL. Thus it is likely that the reach-related activation, referred to here as hPRR, comprises multiple distinct functional subregions. However, the current study did not incorporate the appropriate conditions to disentangle these regions.

It should be noted that in our experimental design, all grasping movements contained a reaching movement. This may limit the utility of the reaching-related activity we observed in the medial PPC. Recently, Cavina-Pratesi et al. (2010) independently manipulated the inclusion of grasping and reaching components in a prehension task. They identified reaching-specific regions in the SPOC and anterior SPL. In addition to these results, our meta-analysis (Fig. 6) confirms that our reported posterior-medial preference for reaching and anterior-lateral preference for grasping is consistent with a variety of previous studies. Although the distinction between cortical regions involved in the grasping and reaching components of movement discussed above serves as a useful way to delineate the dorsolateral and dorsomedial networks, it is important to note that these networks are not strictly independent. During normal activity, reaching and grasping almost always co-occur and thus require intimate coordination. Indeed, grasping deficits often accompany reaching deficits after cortical lesions of medial-posterior PPC in humans (Pererin and Vighetto 1988) and monkeys (Battaglini et al. 2002). Transcranial magnetic stimulation...
applied to PPC, near the middle of the IPS, has been shown to disrupt reaching movements (Desmurget et al. 1999). Additionally, electrophysiological recordings have shown that reaching neurons in V6A are sensitive to orientation and shape of a target object (Fattori et al. 2009, 2012), as well as the hand shape necessary to grasp different objects (Fattori et al. 2010). In humans, the SPOC, in the dorsomedial stream, is also sensitive to hand orientation during grasping movements (Monaco et al. 2010). Likewise, a recent neuroimaging study (Gallivan et al. 2011) showed that grasping movements to differently sized targets could be decoded from multivoxel patterns of activity throughout a network of parietal and frontal regions, including the posterior IPS. Our results are indicative of the necessary interactions between reaching and grasping networks in that they show a gradient of specificity moving from posterior-medial to anterior-lateral regions of PPC. Finally, the contributions of the dorsomedial and dorsolateral networks may not reflect reaching and grasping, per se, but rather different underlying task demands, such as movement planning (Glover et al. 2012), online control (Glover et al. 2012; Grol et al. 2007), or the integration of perceptual information (Verhagen et al. 2008).

The location of hPGR and hPRR relative to topographically organized cortex indicates that over the course of evolution, functionally similar areas located in the IPS in monkeys were partially relocated outside of the IPS in humans, possibly to accommodate human-specific areas in PPC. The macaque IPS contains areas LIP (lateral), VIP (ventral), MIP, and AIP. Previous studies have indicated functional similarities between human IPS5 and area VIP in monkeys. Both contain a coregistered, multimodal representation of tactile and visual space, especially near the face (Duhamel et al. 1998; Sereno and Huang 2006). Additionally, both show a preference for smooth-pursuit eye movements compared with saccades (Konen and Kastner 2008a; Schlack et al. 2003) and selectivity for motion-inducing optic flow patterns (Konen and Kastner 2008a; Schaafsma et al. 1997). In monkeys, area AIP is located anterior to VIP. Thus our data suggest that the spatial relationship between AIP and VIP seems to be preserved in humans. However, hPGR seems to be located outside of the IPS, at the junction of the IPS and the postcentral sulcus. Previous studies have also suggested a functional correspondence between macaque LIP and human IPS1/2. Both regions show activity related to spatial attention (Colby and Goldberg 1999; Lauritzen et al. 2009; Silver et al. 2005; Szczepanski et al. 2010), saccadic eye movements (Konen and Kastner 2008a; Snyder et al. 2000), working memory (Gnadt and Andersen 1988; Schluppeck et al. 2005; Sheremata et al. 2010), reaching (current results; Levy et al. 2007; Snyder et al. 1997), and object representations (Jansen et al. 2008; Konen and Kastner 2008b; Mruczek et al. 2013; Sereno and Maunsell 1998). Additionally, human IPS2 and the ventral portion of macaque LIP show similar topographic representations of visual space relative to more posterior regions (Arcaro et al. 2011; Ben Hamed et al. 2001). In humans, IPS1/2 is mainly on the medial bank of the IPS, whereas LIP is confined to the lateral bank of the IPS (see also Koyama et al. 2004). In monkeys, area MIP and V6A form the functionally defined PRR and are located posterior and medial to LIP. Our results indicate that the relative position of PRR to LIP is preserved in humans but that it has been relocated outside of the IPS proper and into the SPL. Consequently, hPRR, similar to hPGR, appears to be relatively distinct from the topographic regions in the IPS.

The comparison of macaque and human IPS suggests that IPS3/4 may be candidate areas that contribute to the large increase in human parietal cortex relative to the macaque (Brodmann 1909; Van Essen et al. 2001) and are presumably involved in human-specific functions such as calculation and language functions. Simon et al. (2002) found that calculation and language-related tasks activated the lateral bank of the IPS and that this activation was independent from that observed for grasping, pointing, saccades, or attentional shifts. On the basis of their description, these activations do not necessarily overlap with the topographic maps, leaving open the possibility that IPS3/4 are newly evolved areas or that, during evolution, other regions of the macaque split into multiple subregions with different functions. Our results are consistent with their data and show that, over the course of evolution, posterior-medial (LIP, MIP, V6A) and anterior-lateral (AIP, VIP) areas in the macaque have become spatially separated, presumably to accommodate expanses in parietal cortex that support human-specific functions.

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Grasping and Reaching Activity in Human Topographic PPC


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