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RESEARCH ARTICLE

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# FMRI evidence for a 'parietal reach region' in the human brain

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**Abstract** Event-related functional magnetic resonance imaging was used to examine activation in the posterior parietal cortex when subjects made pointing movements or saccades to the same spatial location. One region, well positioned to be homologous to the monkey parietal reach region (PRR), responded preferentially during memory-delay trials in which the subject planned to point to a specific location as compared to trials in which the subject planned to make a saccade to that same location. We therefore conclude that activation in this region is related to specific motor intent; i.e. it encodes information related to the subject's intention to make a specific movement to a particular spatial location.

**Keywords** fMRI · Intention-related activity · Posterior parietal cortex · Reaching

## Introduction

The posterior parietal cortex is the platform where the early computations for visually guided movements are mounted, with the transformations required for different actions being coded in different anatomical areas within this region (Mountcastle et al. 1975; Gnadt and Andersen 1998; Snyder et al. 1997, 1998; Batista et al. 1999; Buneo et al. 2002). The parietal reach region (PRR) in monkeys, for example, is specialized for planning target-directed limb movements. Moreover, neurons in this region show activity that is correlated with the direction of the movement the animal intends to make (for review, see Snyder et al. 2000; Andersen and Buneo 2002). Using event-related functional MRI, we have located what we believe is the human homologue of the monkey PRR—an area in the medial aspect of the posterior parietal cortex that is selectively activated when a subject plans to make a pointing movement to a remembered location but not when the subject plans to make a saccade to this same location.

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## Materials and methods

### Experimental procedures

While they were being scanned, subjects "held in mind" the location of a peripheral visual target over the course of a delay interval and pointed (or made a saccade) to its remembered location. The activation during this delay interval was compared with that seen in a control interval during which the subject knew a target would appear following the interval and the type of movement to be made, but had no a priori knowledge of the target's location. Ten subjects were scanned. A single event consisted of a delay trial followed by a control trial (Fig. 1). The delay and control conditions consisted of an equal number of pointing and saccade trials, half of which were pro-movements and half of which were anti-movements (pro-movements were made toward the peripheral target whereas anti-movements were made in the opposite direction but with equal amplitude). There were 16 trials in each functional run: 2 repetitions × 2 conditions (control vs. delay) × 2 effectors (saccade vs. pointing) × 2 movement types (pro- vs. anti-movement). Each subject was given six functional runs.

On saccade trials, subjects were instructed to make a pro- or anti-saccade while keeping their finger in a central position. On pointing trials, they were instructed to make a pro-pointing movement or an anti-pointing movement, while maintaining central fixation. On pointing trials, they were instructed to direct their index finger toward the target without being required to touch it. The use of this small movement prevented excessive head movement during scanning. In earlier experiments, we have found that this type of movement reliably recruits frontoparietal areas involved in reaching but not saccade tasks (Connolly et al. 2000). The motivation for using both pro- and anti-movements was to examine whether or not delay activation in the parietal cortex was further modulated by different effector-consistent intentional demands. In other words, would the delay signals

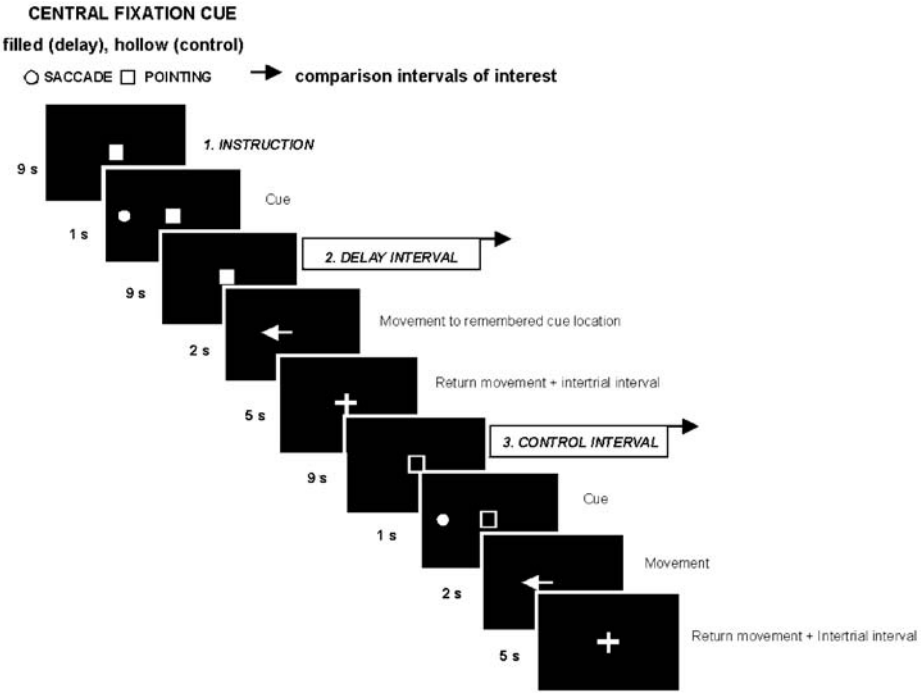


**Fig. 1** Paradigm used to examine delay interval modulation by the intended action. Subjects were instructed either to plan a saccade (but not a pointing movement) or to plan a pointing movement (but not a saccade). Subjects were first instructed as to the type of movement to be made (saccade or point) by the shape of the fixation point (*circle* or *square*). The direction of the movement (pro- or anti-movement) was indicated by its color (*white* or *red*). A delay or control trial was distinguished by having either a *filled* (delay) or *hollow* (control) *circle* or *square*. At the beginning of the delay interval, a peripheral target (a *filled white circle of 0.25° visual angle*) was presented between 9° and 12° to the left or right of center along the horizontal meridian. During the rest of the delay interval, the subject held in mind the location of the peripheral cue while maintaining fixation. At the end of the delay interval, the fixation point disappeared and the subject made either a saccade or pointed to the remembered location of the target. Following re-fixation, a control interval occurred during which the subject was again instructed as to the type and direction of movement to be made but did not know the location of the target. A target was flashed at the end of the control interval and the subject immediately made a saccade or pointed to its location

reflect the intention to move toward or away from a future target?

The target for saccades and pointing movements were presented in the same range of locations in the visual periphery, and there were an equal number of rightward and leftward movements. The upper arm was immobilized throughout to reduce head motion during scanning. The stimuli were projected off a mirror and onto the ceiling of the magnet bore. We used padding to tilt the subject's head and line of sight forward within the coil so that they could comfortably see beyond the bottom of the coil and view all stimuli directly. Since all subjects were right-handed, only the right hand was used to point.

In the data analysis, the levels of activation during the 9-s memory period of the delay trials were contrasted with the 9-s instructional interval of the control trials. [Note that the instructional cue for the type of movement was present on the screen during both intervals.] In the delay interval, the subject knew both the effector to be used and the target location, whereas in the control interval the subject knew what effector to use but not the target location. Comparing these two kinds of trials allowed us to determine whether or not there is a region within the parietal cortex that encodes metrical information over a delay interval to guide a particular target-directed action.

## Imaging and data analysis

Images were collected with a Varian Unity Inova whole body 4 Tesla MRI system (Varian, Palo Alto, CA; Siemens, Erlangen, Germany) to measure blood-oxygen level-dependent signal changes related to brain activation using a full head coil (Ogawa et al. 1992). Nine contiguous 6-mm thick functional slices were prescribed with an in-plane resolution of 3.4 × 3.4 mm (3.4 × 3.4 × 6 mm voxels). This axial slice volume included frontal and parietal cortices (64 × 64 resolution, 22.0 cm in-plane FOV, TE=15.0 ms, TR=0.5 s, FA=30°). Functional images were then superimposed on anatomical images that were obtained using a T1-weighted image set. All functional images were motion corrected using the Brain Voyager 4.3 software package (Brain Innovation, Maastricht, The Netherlands) and corrected for linear drift. Active clusters of 10 or more voxels that exceeded a statistical threshold corrected for multiple comparisons were considered significant foci of activation (ROI) (Forman et al. 1995).

Following within-subject averaging, fMRI data were transformed into Talairach space (Talaraich and Tournoux 1988) and each averaged functional run was appended in time across subjects. Multiple regression analysis (as implemented in the general linear model: GLM) was then used to identify voxels with activity patterns that significantly correlated with the delay periods (Friston et al. 1991), following convolution with the hemodynamic response. The threshold for significantly active voxels was $F_{(4,3435)}$=43.60, $p$<0.01 (corrected).

Following the extraction of the GLM-determined ROI signal time-courses for each subject, linear deconvolution (Buckner 1998; Dale and Buckner 1997; Miezin et al. 2000) was used to correct for any decaying motor-related hemodynamic activity that extended into the subsequent control period. The motor peaks were clearly visible in the single subject time-courses. We fit a model hemodynamic response function, the gamma-variate function ($S(t)=At^{8.60}e^{-t/0.547}$), to the motor activity peak and subtracted out

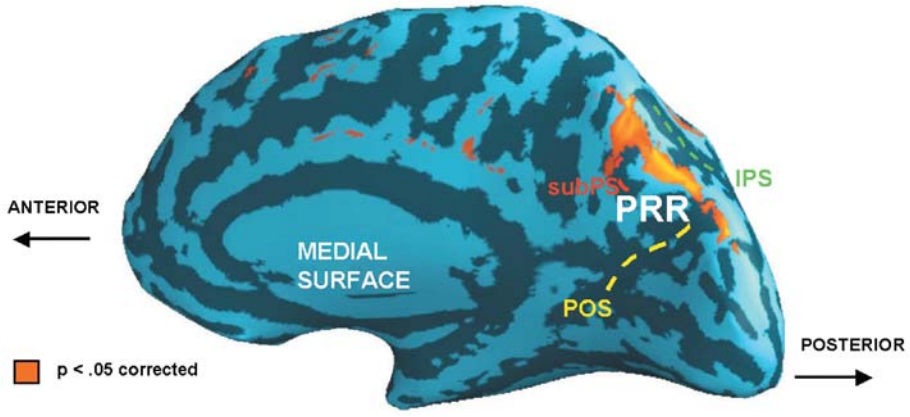


**Fig. 2** Medial view of an inflated cerebral cortex, showing unfolded sulci and gyri and the location of the fMRI delay interval activation, as determined using multiple regression analysis (ten subjects, $p<.05$). GLM signal time-courses that were subjected to further ANOVA analysis were situated anterior to the parieto-occipital sulcus, posterior to the sub-parietal sulcus, and medial to the intraparietal sulcus

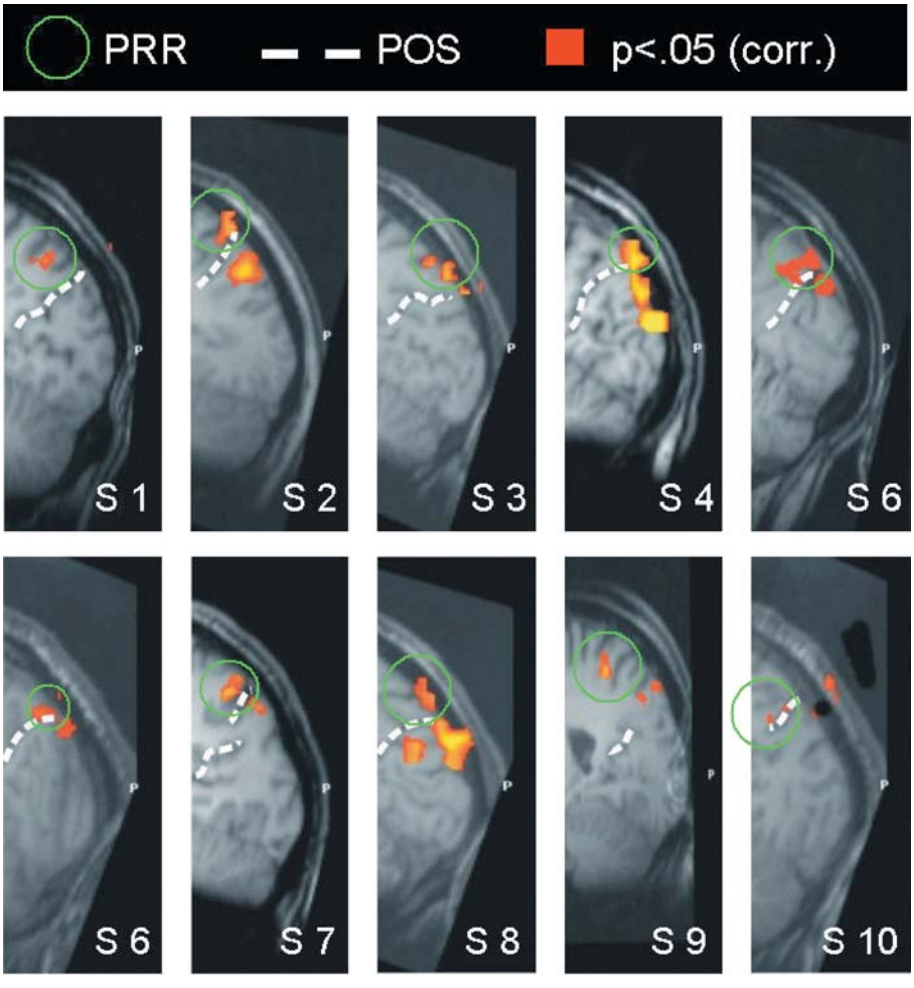


**Fig. 3** Single subject activation maps that show the degree of inter-subject variability in the location of the superior parietal ROI. The sagittal slices are medial to the intraparietal sulcus. All subjects showed activity just anterior to the parieto-occipital sulcus (*POS*). This activation is highlighted by the *green circles*. In some subjects, activation extended posterior to the POS

the decaying portion of the model response from the subsequent activity rise (for the control interval) for each single subject. When determining the delay and control values, a gamma variate function was fit to the preceding motor response and these values were subtracted out—leaving only the desired control values.

## Results

The single functional map shown in Fig. 2 represents data from all ten subjects, i.e. the results of the multiple regression analysis. The region of interest (ROI) that

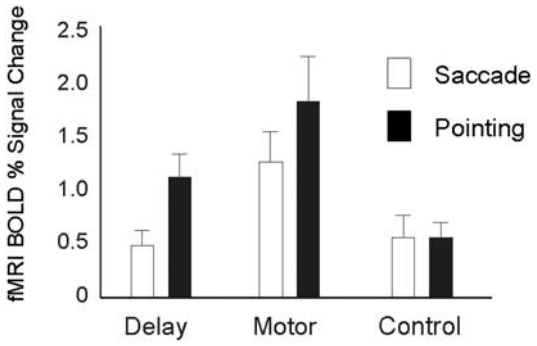


**Fig. 4** Peak percent signal changes averaged across subjects for the different pointing or saccade intervals. There was a significant motor response in the parietal ROI for the movement following the delay interval for both pointing and saccade trials. Delay interval activation was significantly higher than the corresponding control interval activation when the subject planned to point but not when the subject planned to make a saccade

showed activity correlated with the delay periods was situated along the medial surface of the parietal lobe, medial to the intraparietal sulcus, anterior to the parieto-occipital sulcus and posterior to the sub-parietal sulcus (Fig. 2). The activation was bilateral (although Fig. 2 shows only the right hemisphere). The cortical volume of the ROI was 6.35 $cm^3$. The Talaraich coordinates for the signal peak were $x = -1$ (negative value represents left hemisphere), $y = -74$, $z = +38$ ($x$ = medial/lateral, $y$ = anterior/posterior and $z$ = dorsal/ventral). These coordinates are consistent with a superior parietal locus reported in an earlier study in our laboratory ($x = -11$, $y = -73$, $z = 31$) that also showed activation during both pro- and anti-pointing and pro- and anti-saccade tasks (Connolly et al. 2000). Figure 3 shows the individual subject ROIs. As shown, each of the subjects showed significant superior parietal activation that correlated with the delay intervals. Each of the ROIs included active voxels just anterior to the parieto-occipital sulcus. All of the ROI slices shown (red circle) are medial to the intraparietal sulcus.

We also found delay activation in two other parietal regions. The first region was situated lateral to the intraparietal sulcus about mid-way between the parieto-occipital and postcentral sulci, an area that could be homologous with the lateral intraparietal area (LIP) in the monkey. The second was located just posterior to the post-central sulcus and was also just lateral to the intraparietal sulcus, in an area that could be homologous with the anterior intraparietal area (AIP) in the monkey. In other experiments, we have also found activation in these regions during saccade (Connolly et al. 2002) and pointing (Connolly et al. 2000) tasks, respectively. But because the observed signal changes in these regions were so weak (<0.25%) and unreliable in the present experiment, they are not discussed further.

Event-related changes in activation were tracked within the superior parietal ROI. Following linear deconvolution, repeated-measures mixed-effect ANOVAs, which treated subjects as a random effect (Kirchoff et al. 2000), were conducted to further examine the effects of Time (delay period, movement period, control period), Effector (saccade, pointing), and Direction (anti-or pro-movement) on the percent signal change relative to the minimum signal value within the identified ROI. The activation peaks were identified for the delay and control intervals (over each 9 s interval). The gamma-variate shaped motor peaks (movement period) were clearly visible in each of the event-related trials following the delay intervals and any overlapping delay activity was subtracted out via linear deconvolution from these signal rises. The peak percent signal change for each interval relative to the minimum value within the entire event was determined on a subject-by-subject basis and submitted to a mixed-effects ANOVA.

Figure 4 shows the peak signal changes that occurred in the ROI (averaged across subjects) during the different time intervals of a single trial (the delay interval, the motor response following the delay interval, the control interval that followed) collapsed across pro- and anti-trials for saccades and pointing. There are several noteworthy observations with regard to these peaks.

As Fig. 4 shows, there was a main effect of time interval (the delay interval, the motor response, and the control interval), $F_{(2,18)}=16.98$, $p<.0001$. There was also a significant interaction between time interval and effector (saccades or pointing), $F_{(2,18)}=5.62$, $p=.01$. No other main effects or interactions were significant. Thus, whether or not the subject was required to generate a pro- or an anti-movement did not affect the level of activation observed in any condition or for any movement type.

Post hoc t-tests revealed that there was a significant movement-related response within the ROI for both saccade and pointing trials (Fig. 4). In fact, the levels of activation associated with the production of a saccade or a pointing movement were significantly higher than their respective control intervals, $t_{(9)}=4.17$, $p<.01$ and $t_{(9)}=4.03$, $p<.01$.

Post hoc t-tests also revealed the nature of the interaction between time interval and effector in our experiment. The level of activation in PRR was greater during the delay interval for pointing than it was during the corresponding control interval in which no target location had been specified, $t_{(9)}=4.23$, $p<.01$ (Fig. 3). There was no difference in activation, however, between the delay interval for saccades and the control interval for saccades, $t_{(9)}=0.74$, n.s.. In other words, there was a significant increase in activity within the PRR when the subject planned to point to the target but not when the subject planned to make a saccade. Indeed, a direct comparison of the level of activation in the two delay intervals showed that mean level of activation for pointing was significantly higher than that for saccades, $t_{(9)}=3.08$, $p=.01$. In short, the level of delay activity in the ROI that we identified was modulated by the effector the subject planned to use to acquire the remembered target—with relatively greater activity occurring when the subject planned to point rather than saccade to the target.

## Discussion

We have identified a region located along the medial surface of the superior aspect of the posterior parietal cortex that responds preferentially when the subject plans to point rather than to make a saccade to a remembered location. Based on similarity in anatomical location relative to sulcal landmarks, this locus may be homologous with the monkey PRR, a region which shows activity related to arm movements (Snyder et al. 1997, 1998; Batista et al. 2000; Buneo et al. 2002; Ferraina et al. 1997; Galleti et al. 1997) and projects to a region of the dorsal premotor cortex that also codes reaching movements (Tanne et al. 1995; Shipp et al. 1998). Monkey PRR is located at the posterior end of the superior parietal lobule, medial to the intraparietal sulcus, and includes portions of medial intraparietal area (MIP) and area V6A (Snyder et al. 2000). The apparent homology between the human and macaque PRR is paralleled by other homologies that have been observed in the organization of the visuomotor areas within the posterior parietal cortex in human and macaque, including a 'grasping' area in AIP and a 'saccade' areas in LIP (for review, see Culham and Kanwisher 2001). The emergence of these different areas in the primate brain presumably reflects the need to orchestrate the movements of the fingers, hands, limbs, head, and eyes in different ways to support a range of skilled visually guided behavior (Goodale and Milner 1992; Milner and Goodale 1995; Andersen and Buneo 2002).

Although we found greater activity in the delay interval for pointing as opposed to saccade trials, we did not find greater activity for pointing during the control intervals, when the action was specified but the location of the target was unknown. These findings contrast with the electrophysiological data of Calton et al. (2002), who reported finding relatively greater preparatory activity when monkeys were instructed via a colour cue to prepare to reach (as compared to when they were instructed to prepare to make a saccade) when the target location was not yet known. Although it is certainly possible that the small changes in unit activity that were reported by Calton et al. may be below the sensitivity of the BOLD response, it should also be noted that we used far longer delays (9 s) than those used in the monkey study (600, 800, or 1200 ms). In other words, it is not clear whether or not in the monkey, preparatory activity for reaching would be maintained for as long as 9 s when no target had been specified. In any case, pointing-related activation in our study was greater during the memory-delay interval (when both the target and the action had been specified) than it was during the control interval (when only the action had been specified). This result parallels a recent finding in our laboratory showing that an eye-movement related region in the intraparietal sulcus (probably homologous with area LIP in the monkey) shows delay activation for saccades but does not show any evidence for preparatory set during a gap task similar to the control task that was used in the present study (Connolly et al. 2002). It should also be noted that anti-pointing movements showed the same level of activation as pro-pointing movements during the delay condition, a result that also parallels our earlier observations in putative LIP (Connolly et al. 2002).

In summary, this is the first neuroimaging study to show greater delay activity during pointing as compared to saccade trials in a region of the human posterior parietal cortex that appears homologous with monkey PRR. In other words, the coding of visuomotor intention (the intention to make an arm movement to a particular location) appears to be one of the primary functions of this region. It is worth noting that multi-site recordings are currently being tested in monkey area MIP (corresponding to a portion of monkey PRR) with the hope of developing a neural prosthesis that makes use of visuomotor coding in this region (Shenoy et al. 1999; Pesaran et al. 2002; Andersen and Buneo 2002). The present data represent a step forward in localizing and characterizing the function of a putative human homologue from which signals related to motor planning could perhaps one day be extracted.

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## References

Andersen RA, Buneo CA (2002) Intentional maps in posterior parietal cortex. Ann Rev Neurosci 25:189–220

Batista AP, Buneo CA, Snyder LH, Andersen RA (1999) Reach plans in eye-centered coordinates. Science 285:257–260

Buckner R (1998) Event-related fMRI and the haemodynamic response. Hum Brain Mapp 6:373–377

Buneo CA, Jarvis MR, Batista AP, Andersen RA (2002) Direct visuomotor transformations for reaching. Nature 416:632–636

Calton JL, Dickenson AR, Snyder LH (2002) Non-spatial, motor-specific activation in posterior parietal cortex. Nature Neurosci 5:580–588

Connolly JD, Goodale MA, DeSouza JFX, Menon RS, Vilis T (2000) A comparison of frontoparietal fMRI activation during anti-saccades and anti-pointing. J Neurophys 84:1645–1655

Connolly JD, Goodale MA, Menon RS, Munoz DP (2002) Human fMRI evidence for the neural correlates of preparatory set. Nature Neurosci 5:1345–1352

Culham JC, Kanwisher NG (2001) Neuroimaging of cognitive functions in human parietal cortex. Curr Opin Neurobiol 11:157–163

Dale AM, Buckner RL (1997) Selective averaging of rapidly presented individual trials using fMRI. Hum Brain Mapp 5:329–340

Ferraina S, Johnson PB, Garasto MR, Battaglia-Mayer A, Ercolani L, Bianchi L, Glover GH (1999) Deconvolution of impulse response in event-related BOLD fMRI. Neuroimage 9:416–429

Forman SD, Cohen JD, Fitzgerald M, Eddy WF, Mintun MA, Noll DC (1995) Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): use of a cluster-size threshold. Magn Reson Med 33:636–647

Friston KJ, Frith CD, Liddle PF, Frackowiak RS (1991) Comparing functional (PET) images: the assessment of significant change. J Cereb Blood Flow Metab 11:690–699

Galletti C, Fattori P, Kutz DF, Battaglini PP (1997) Arm movement-related neurons in the visual area V6A of the macaque superior parietal lobule. Eur J Neurosci 9:410–413

Gnadt JW, Andersen RA (1988) Memory related motor planning activity in posterior parietal cortex of macaque. Exp Brain Res 70:216–220

Goodale MA, Milner AD (1992) Separate visual pathways for perception and action. Trends Neurosci 15:20–25

Kirchoff BA, Wagner AD, Maril A, Stern C (2000) Pre-frontal temporal circuitry for episodic encoding and subsequent memory. J Neurosci 20:6173–6180

Lacquaniti F, Caminiti RJ (1997) Combination of hand and gaze signals during reaching: activity in parietal area 7 m of the monkey. J Neurophysiol 77:1034–1038

Miezin FM, Maccotta L, Ollinger JM, Petersen SE, Buckner RL (2000) Characterizing the haemodynamic response: Effects of presentation rate, sampling procedure, and the possibility of ordering brain activity based on relative timing. Neuroimage 11:735–759

Milner AD, Goodale MA (1995) The visual brain in action. Oxford University Press, Oxford

Mountcastle VB, Lynch JC, Georgopoulos A, Sakata H, Acuna C (1975) Posterior parietal association cortex of the monkey: command functions for operations within extrapersonal space. J Neurophysiol 38:871–908

Ogawa S, Tank D, Menon R, Ellermann JM, Kim SG, Merkle H, Ugurbil K (1992) Intrinsic signal changes accompanying sensory stimulation: functional brain mapping with magnetic resonance imaging. Proc Natl Acad Sci U S A 89:5951–5955

Pesaran B, Pezaris J, Sahani M, Mitra PM, Andersen RA (2002) Temporal structure in neuronal activity during working memory in macaque parietal cortex. Nature Neurosci 5:805–811

Shenoy KV, Kureshi SA, Meeker D, Gillikin BL, Dubowitz DJ, Batista AP, Buneo CA, Cao S, Burdick JW, Andersen RA (1999) Soc for Neurosci 25:152.19

Shipp S, Blanton M, Zeki S (1998) A visuo-somatomotor pathway through superior parietal cortex in the macaque monkey: cortical connections of areas V6 and V6A. Eur J Neurosci 10:3171–3193

Snyder LH, Batista AP, Andersen RA (1997) Coding of intention in the posterior parietal cortex. Nature 386:167–170

Snyder LH, Batista AP, Andersen RA (1998) Change in motor plan, without a change in the spatial locus of attention, modulates activity in posterior parietal cortex. J Neurophysiol 79:2814–2819

Snyder LH, Batista AP, Andersen RA (2000) Intention-related activity in the posterior parietal cortex: a review. Vision Res 40:1433–1441

Talaraich J, Tournoux P (1988) Co-planar stereotaxic atlas of the human brain. Thieme, New York

Tanne J, Boussaoud D, Boyer-Zeller N, Rouiller EM (1995) Direct visual pathways for reaching movements in the macaque monkey. Neuroreport 7:267–272