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Posterior Parietal Cortex Encodes Autonomously Selected Motor Plans

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SUMMARY

The posterior parietal cortex (PPC) of rhesus monkeys has been found to encode the behavioral meaning of categories of sensory stimuli. When animals are instructed with sensory cues to make either eye or hand movements to a target, PPC cells also show specificity depending on which effector (eye or hand) is instructed for the movement. To determine whether this selectivity retrospectively reflects the behavioral meaning of the cue or prospectively encodes the movement plan, we trained monkeys to autonomously choose to acquire a target in the absence of direct instructions specifying which effector to use. Activity in PPC showed strong specificity for effector choice, with cells in the lateral intraparietal area selective for saccades and cells in the parietal reach region selective for reaches. Such differential activity associated with effector choice under identical stimulus conditions provides definitive evidence that the PPC is prospectively involved in action selection and movement preparation.

INTRODUCTION

The posterior parietal cortex is an important sensory-motor interface and has been found to contain an intentional map (Andersen and Buneo, 2002). Two of its subdivisions, the lateral intraparietal (LIP) area and the parietal reach region (PRR), exhibit sustained activity when monkeys perform memory-guided delayed saccade and delayed reach tasks, respectively (Gnadt and Andersen, 1988; Snyder et al., 1997). Trial-by-trial decoding indicates that PPC activity predicts target locations less accurately than the movement plan for the same target locations (Quian Quiroga et al., 2006). LIP cells increase their firing rates after an instruction to prepare a saccade, whereas PRR activity increases after an instruction to prepare a reach, even before the spatial targets for the movements appear (Calton et al., 2002; Dickinson et al., 2003).

In the above studies, different color cues were used to instruct the effectors. Thus, it still remains unclear whether task-selective PPC activity is related to the impending movement or past sensory stimuli. Although the PPC was traditionally believed to be insensitive to color, it was recently found to respond selectively to cues for cognitive set regarding task rules (Stoet and Snyder, 2004) and to form experience-dependent categorical representations (Freedman and Assad, 2006; Toth and Assad, 2002). Thus, it is necessary to re-examine the role of the PPC in motor planning in a stricter behavioral context.

In order to test whether persistent delay activity in LIP and PRR retrospectively codes the behavioral meaning of the cue (saccade versus reach) or prospectively codes motor planning, we designed a saccade/reach plan selection paradigm in which monkeys chose to acquire a target by either a saccadic eye movement or a reaching arm movement in the absence of an instruction about the particular movement type. This is a nonspatial plan-selection task in which the monkey decides *how*—instead of *where*—to acquire a goal. The monkey's autonomous choice between a saccade and a reach under identical stimulus conditions eliminates the contribution of sensory-related retrospective coding of the category of the visual stimuli.

The results demonstrate that LIP cells respond more if a saccade is chosen, whereas PRR cells respond more if a reach is chosen. This differential activity indicates that the PPC is not only involved in assigning behavioral meaning to sensory stimuli, but also plays a prospective cognitive role related to plan selection and movement preparation.

RESULTS

Behavior Tasks

Figure 1A shows a schematic of the behavioral tasks. Monkeys were seated in front of a board with an array of buttons each containing a red and a green light-emitting diode (LED) placed next to one another. Each button had a diameter of 3.7 cm and was distributed 7.5 cm apart in a 3 × 3 matrix placed in a vertical board at 28 cm from the monkeys. At the beginning of the trial, both the green and red LEDs in the central button were turned on, and the monkey was required to fixate and touch it. Then both the red and green LEDs in a peripheral button were turned on simultaneously, and the monkey was required to continue fixating and touching the central fixation spot until it disappeared (GO signal). After 600 ms of cue duration, the

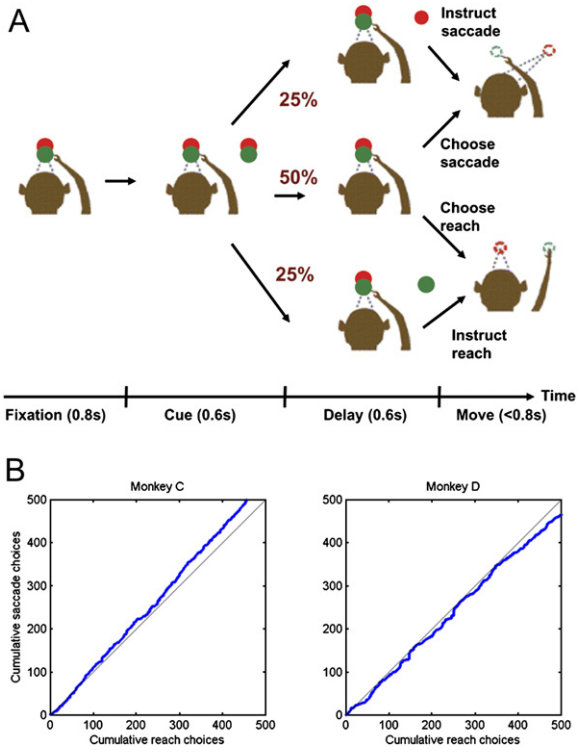

Figure 1. The Behavioral Tasks and Monkeys' Choice Sequences

(A) Diagram of interleaved effector delay-instructed saccade (top) and reach (bottom) and effector choice trials (middle).

(B) Behavioral choice data from one day's session for each monkey plotting the cumulative number of trials in which the monkeys chose saccades and reaches. Both curves are very close to the diagonal line, indicating that monkeys selected saccades and reaches with virtually equal probability.

green LED was turned off, and only the red LED stayed on in 25% of trials, instructing a saccade after a delay (effector delay-instructed saccade, top of Figure 1A). In another 25% of trials, the red LED was turned off, and only the green LED stayed on, instructing a reach after a delay (effector delay-instructed reach, bottom of Figure 1A). In the remaining 50% of trials, both peripheral LEDs were extinguished. In these trials, the monkey chose to either shift gaze to the location of the peripheral target while continuing to touch the center spot or keep fixating the center spot but move the arm to reach the target (effector choice trials, the middle of Figure 1A).

In effector delay-instructed trials, the spatial target and movement effectors were cued asynchronously so that monkeys knew the target location, but not the instructed effector, during the first 600 ms from cue onset. The animal received liquid reward for all trials in which the instructed movement was correctly performed. It is noteworthy that those trials were introduced for a behavioral purpose only: to help to balance monkeys' behavioral choices, encourage monkey to work, and discourage anticipatory bias and too early decisions. Neural data collected during the instructed trials are included in the Supplemental Data available with this article online, but are not interpreted here to support any conclusion. First, those trials are similar to target-delay-cue tasks developed by Snyder and colleagues (Calton et al., 2002; Dickinson et al., 2003), so they are not novel paradigms. Second, they are not comparable with interleaved effector choice trials in many aspects, because the target stayed on during the delay period for instructed but not choice trials (Figure 1A), and there is also a difference in reward probabilities between the instructed and choice trials.

In effector choice trials, monkeys were only given a spatial cue and allowed to acquire a target either by saccading or reaching in the absence of direct instructions specifying the effectors. Since they were interleaved with effector delay-instructed trials, the monkey could not know whether he had to choose prior to cue offset. An algorithm was used to remove systematic biases by having the monkey play a competitive game with the computer (Barraclough et al., 2004). The monkey was rewarded only if his choice matched the computer's choice, and the computer biased its choice against the monkey's choice sequence during preceding effector choice trials (see Experimental Procedure). Such a competitive algorithm was found to be an effective method of balancing the monkey's bias in saccade/reach selection. After sufficient training (about 3–6 months), monkeys chose between saccades and reaches randomly and equally often (Figure 1B). This strategy maximizes reward and also balances reward expectation. Balanced reward expectation is an important factor because both LIP and PRR have previously been found to be modulated by reward expectation (Musallam et al., 2004; Platt and Glimcher, 1999).

Single-Cell Activity

Neuronal activity in effector choice trials for two example cells, one from LIP and one from PRR, is shown in Figure 2. The stimulus presented in the response field evoked a strong response, which was virtually identical during the entire cue period (600 ms). Because effector choice trials were randomly interleaved with effector delay-instructed trials, the trial type remained unknown so that the monkey was discouraged from making a decision until the cue offset. After the cue extinguished and the monkey realized he had to make his own decision, the LIP neuron in Figure 2A reduced its firing rate in the first 150 ms, similar to the reduction in activity after removal of a sensory stimulus. Then neuronal activity separated according to the effector chosen—it maintained a high firing rate for trials in which the monkey decided to initiate a saccade, but continued to decrease if the monkey decided to reach to the target (Figure 2A). Such a dramatic difference was maintained until the movement was completed. In contrast, the example PRR neuron showed a reversed response pattern during the delay/decision period and fired at a significantly higher rate for trials in which reaches were selected (Figure 2B).

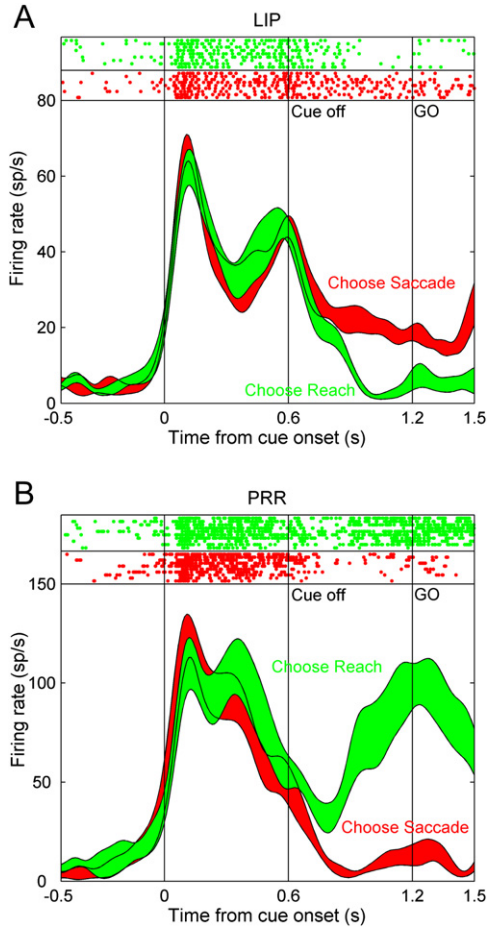

Figure 2. Single-Neuron Activity during the Effector Choice Task

Neural activity of example LIP (A) and PRR (B) cells during trials in which the monkey chose saccades (red) and reaches (green). Spike trains were aligned to the cue onset. The peristimulus time histograms (PSTH) were smoothed using a Gaussian kernel (SD = 50 ms), and its thickness represents the standard error (±SEM) calculated with the bootstrap method.

Population Analyses

The two neurons in Figure 2 were typical for the population of 100 LIP cells (67 from monkey C and 33 from monkey D) and 91 PRR cells (55 from monkey C and 36 from monkey D). The data from the populations are summarized in Figures 3–5.

Figure 3 compares paired mean firing rates of each cell in four consecutive time intervals (cue, early delay, late delay, post-GO) calculated for saccade and reach chosen trials. During the cue period, both LIP and PRR cells closely scattered along the diagonal line in a symmetric pattern (Figure 3A), indicating that they show similar responses and no bias in activity ($p > 0.5$ for both LIP and PRR populations, two-tailed Wilcoxon signed rank test). Because the effector choice trials were randomly interleaved with effector instructed trials, the monkeys could

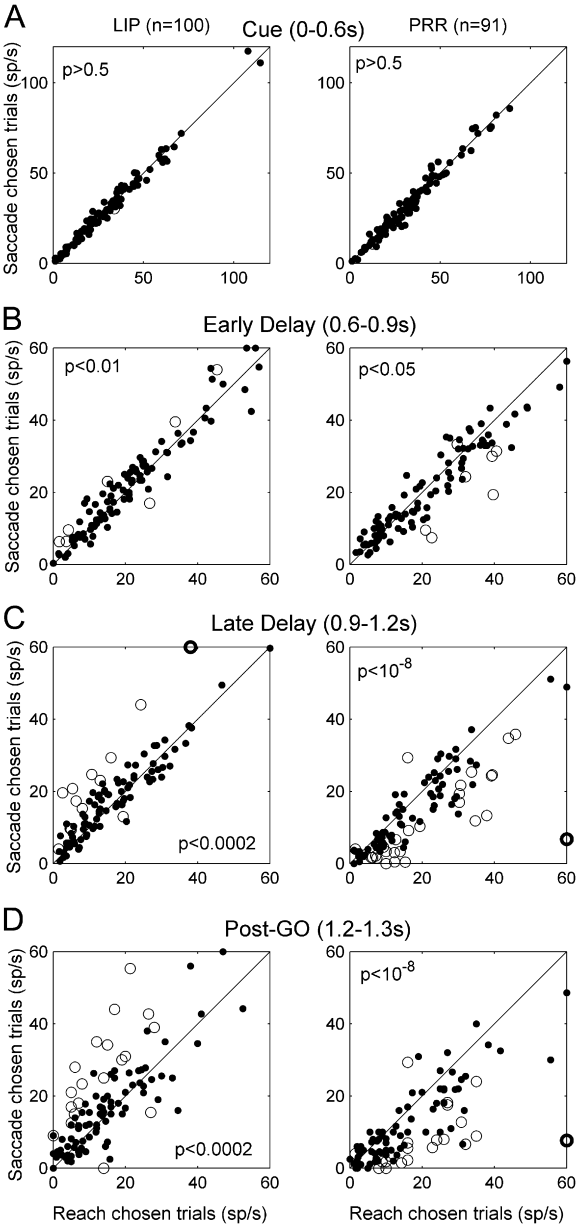

Figure 3. Comparison of Activity between Saccade Chosen and Reach Chosen Trials for the Entire Population

Left and right panels are corresponding to LIP and PRR cells, respectively. (A) to (D) represent four consecutive time intervals: cue duration (0–0.6 s after cue onset), early delay (0–0.3 s after cue off), late delay (0.3–0.6 s after cue off), and post-GO (0–0.1 s after GO signal - central fixation off). The p value in each panel represents statistical significance of differential activity between saccade and reach chosen trials for entire LIP or PRR population, measured by two-tailed Wilcoxon signed rank test. Open circles indicate neurons showing significantly different ($p < 0.05$, Kruskal-Wallis test) firing rates in saccade and reach chosen trials. Data points on the edge of plots represent normalized firing rates of few cells with activity far beyond the range of the plots (60 sp/s).

not know the availability of choice prior to the cue offset. Consequently, they were discouraged to form biases toward either a saccade or reach choice, which was correspondingly reflected in the neuronal activity. During the delay period, the monkeys realized they were allowed to choose between a saccade and a reach. Accordingly, activity in the choice trials began to differentiate during the early delay period (Figure 3B, $p < 0.01$ for LIP and $p < 0.05$ for PRR) and separated further during the late delay period (Figure 3C, $p < 0.0002$ for LIP neurons and $p < 10^{-8}$ for PRR neurons). In the scatter plots, most LIP neurons were above the diagonal line, indicating stronger firing rates in trials in which the monkey decided to make a saccade. Conversely, most PRR neurons were below the unity line and fired stronger in trials in which the monkey decided to reach. Such effector-specific selectivity was most significant during the first 100 ms epoch after the GO signal and before 95% of movements were initiated (Figure 3D, $p < 0.0002$ for LIP and $p < 10^{-8}$ for PRR).

To quantitatively examine how reliably single-neuron activity predicts the monkeys' choices between saccades and reaches, we applied a receiver operating characteristic (ROC) analysis (Green and Swets, 1966). The choice probability (CP, area under the ROC curve) was calculated based on the number of spikes within a 200 ms interval centered on the GO signal for each cell. Figures 4A and 4B show the distributions of CPs for LIP and PRR cells, respectively. A CP larger than 0.5 (chance level) indicates selectivity for a saccade, while less than 0.5 indicates selectivity for a reach. The CPs of most LIP cells were larger than 0.5, with a mean of 0.5958 ($p < 10^{-6}$, two-tailed t test), while the CPs of most PRR cells were mostly less than 0.5, with a mean of 0.3577 ($p < 10^{-10}$, two-tailed t test). To show the time course of discriminability for effector choice, we performed the above ROC analysis using a sliding window. The center of a 200 ms interval was shifted in 20 ms steps. The dynamic evolution of the CPs of LIP and PRR neurons are shown in Figure 4C. During the pre- and early cue periods, CPs were around chance level for both LIP and PRR populations and exhibited no bias. The biases began to appear in the late cue period but were very small (e.g., single-neuron activity in Figure 2B), suggesting that monkeys still might anticipate a particular effector occasionally. The lack of a strong bias during this period is not surprising, since interleaved effector instructed trials discouraged the monkeys from making early decisions. Effector selectivity became much more significant after cue offset when the monkeys realized availability of choices.

To illustrate the time course of the raw population activity in detail, Figure 5 plots averaged activity across all the LIP and PRR neurons (bin = 20 ms). Both LIP and PRR populations showed similar responses during the cue period, and then activity began to diverge during the delay period. The LIP population was selective for saccades while the PRR population was selective for reaches, and differential activity was maintained to the end of the trials.

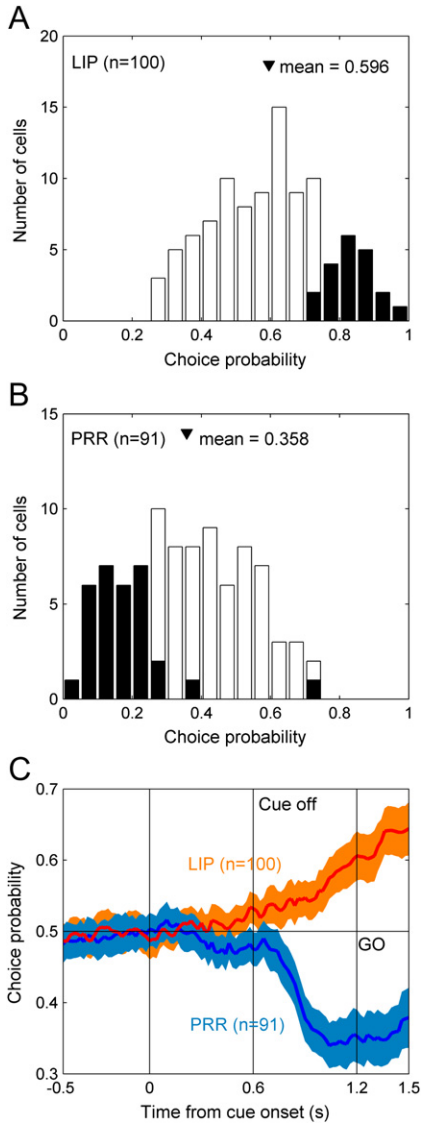

Figure 4. Distribution and Time Course of Choice Probabilities

(A) and (B) show the histograms of CPs calculated based on spiking activity within a 200 ms window centered on the GO signal for 100 LIP and 91 PRR neurons, respectively. The filled bars correspond to cells whose choice probability was significantly different from 0.5 measured by a permutation test. The triangle marker indicates the mean choice probability for each population.

(C) The time course of the mean CP (line) and its 95% confidence interval (shadow) calculated by ROC analysis with a 200 ms time window sliding with 20 ms steps.

The population activity basically followed similar dynamics to the single cells shown in Figure 2. Note that the whole populations of isolated LIP and PRR neurons were included regardless of selectivity for eye/hand effectors, and even whether or not they showed significant delay activity.

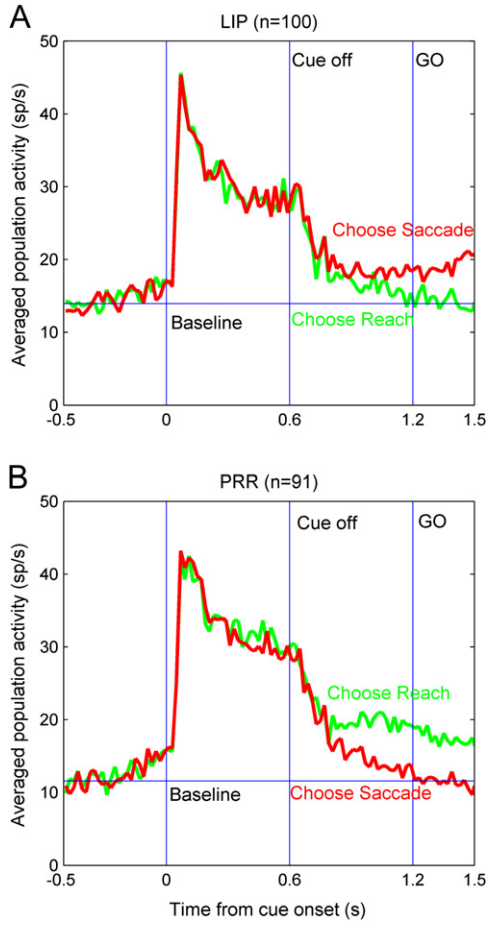

Figure 5. Time Course of Population Activity

Population histograms averaged across all isolated LIP (A) and PRR (B) neurons during saccade (red) and reach (green) chosen trials. The vertical thin lines indicate cue on, cue off, and central fixation off (GO signal), respectively. The horizontal thin line indicates baseline activity, which was defined by mean firing rate during the 300 ms interval beginning from 500 ms before cue onset for both saccade and reach chosen trials. Post-GO activity (0–100 ms interval after GO) of LIP population was significant higher than the baseline ($p < 0.005$) if the monkeys decided to saccade, but dropped to baseline ($p > 0.5$) if the monkeys decided to reach. On the other hand, post-GO activity of the PRR population was significantly higher than the baseline ($p < 0.0001$) in trials in which reaches were chosen, but dropped to baseline ($p > 0.8$) in trials in which saccades were chosen. Statistical significance was measured by a Kruskal-Wallis nonparametric ANOVA.

Instructed Trials

The instructed activity in PRR behaved similarly to that seen for the choice trials, with greater activity for instructed reaches than instructed saccades (results are shown in Figures S1B, S2, S3B, and S4B). This finding is also consistent with our previous study using instructed reaches and saccade (Snyder et al. 1997). In the case of LIP, we found that some cells behaved similarly to the choice trials, being more active for instructed saccades than reaches (Figures S1A, S2, and S3A). However, an approximately equal number of LIP cells showed the reverse behavior, being more selective for the instructed reaches (Figures S2 and S3A). As a result, the raw population activity did not distinguish between the two effectors (Figure S4A).

The finding of a group of LIP cells that prefer reaches is at first glance not consistent with our previous study showing that LIP cells usually are more selective for instructed saccades than instructed reaches. However, there are major differences between the tasks used in the two studies that complicate comparisons. Snyder et al. (1997) used a memory saccade task in which the target was extinguished during the delay period, whereas the targets remained visible in the current instructed trials during the delay. Thus, the additional sensory drive may be a factor. The reward schedule is completely different between the two tasks since the earlier study used only instructed delays resulting in a much higher success rate. Moreover, the overall design of the two tasks is very different, with the current one interleaving, in an unpredictable fashion, choice and instructed trials, whereas the earlier study used only instructed trials. Since we used the instructed trials here for behavioral purposes only, they were not designed to further probe LIP activity. However, this interesting observation may prove useful for the design of a future study.

DISCUSSION

In the absence of an instruction specifying effectors, LIP neurons exhibited strong activity during the delay period when the monkey chose a saccade, but little activity if a reach was chosen. PRR cells showed the opposite pattern of activity, being more active when reaches were chosen and less active when saccades were chosen. In this nonspatial decision paradigm, the monkeys performed action selection without distinguishing between stimuli. This enables us to dissociate prospective activity encoding selected plans from retrospective activity encoding sensory categories. This finding of differential activity associated with autonomously selected effectors suggests that the cognitive functions of the PPC include not only passively transforming sensory stimuli to behaviorally relevant representations, but also an active role in plan selection and movement preparation.

This study also presents an example of nonspatial decision making as contrasted to spatial target selection. In other words, the decision concerns *how* rather than *where*. As a crucial aspect of higher intelligence, decision making is an important topic of neuroscience investigation (Cohen and Blum, 2002; Glimcher, 2003; Romo and Salinas, 2001; Schall and Thompson, 1999). Nearly all previous studies of the neural mechanism of decision making have emphasized its spatial aspect, and many brain areas have shown activity related to target selection from multiple spatial alternatives (Barraclough et al., 2004; Cisek and Kalaska, 2005; Coe et al., 2002; Platt and Glimcher, 1999; Romo and Salinas, 2001; Shadlen and Newsome, 2001). However, animals also can choose among different

actions or strategies to achieve a unitary goal. The results indicate that the PPC encodes nonspatial decisions regarding effector choice in addition to spatial decisions regarding target selection.

As a highly cognitive area bridging perception and action, it has been a matter of debate whether the PPC encodes motor intention prospectively or sensory-related representation retrospectively (Andersen and Buneo, 2002; Colby and Goldberg, 1999; Curtis and D'Esposito, 2006). An argument has been made that LIP shows stronger saccade-related activity solely because the saccade target attracts more attention (Bisley and Goldberg, 2003). The use of identical stimuli and autonomously selected effectors eliminates the contribution of sensory-related retrospective coding. Thus, the effector-selective activity reported here is difficult to explain as merely a result of spatial attention. Even if saccades were to command the most attention, targets for reaching arm movements have been shown to attract considerable attention as well (Baldauf et al., 2006; Deubel et al., 1998). Nevertheless, the LIP activity virtually dropped to baseline if the monkey chose to reach (Figure 5A, $p > 0.5$) during the first 100 ms epoch right after the GO signal and did not exhibit any elevated activity related to attentional enhancement to the reach target.

Of course, the PPC activity certainly reflects highly cognitive sensory-related activity markedly modulated by attention and reward (Colby and Goldberg, 1999; Musallam et al., 2004; Platt and Glimcher, 1999). It might be argued that sustained delay activity during the effector choice task also reflects top-down attention linked to a particular motor plan. If so, such attention is linked to the forthcoming movement as defined in a framework of the premotor theory of attention (Rizzolatti et al., 1987), in which case attention and intention are equivalent, and the debate becomes entirely semantic.

Given the competitive gaming algorithm that was adopted to balance the monkey's saccade/reach effector choice, it might be argued that differential activity between saccade and reach effector choice trials is an artifact caused by the algorithm. During competitive gaming, the monkey's behavioral choice usually is not arbitrary and may depend on the previous sequence history. As a consequence, activity in the current trial may be modulated by time-varying expectation or uncertainty of reward similar to the recent finding by McCoy and Platt (McCoy and Platt, 2005). However, converging evidence suggests that differential activity is difficult to explain by sequence-related modulation. First, the current paradigm with the competitive gaming algorithm worked effectively with the monkey choosing saccades and reaches equally often (Figure 1B). Thus, reward probabilities for saccade and reach choices should be similar. Second, because choice trials were randomly interleaved with instruction trials and the computer chose between saccade and reach based on an algorithm applied only in choice trials, two trials next to each other often were independent. Third, even if some uncertainty of reward or intertrial correlation existed, it cannot explain the fact that LIP and PRR areas exhibited opposite effector selectivity. Both areas show increased activity for larger reward expectation (Musallam et al., 2004; Platt and Glimcher, 1999), so it is hard to conceive how LIP and PRR activity would be modulated by risk, uncertainty, or sequence in opposite ways. Finally, if the differential activity was caused by some variable related to the previous history, the differential activity should appear from the trial beginning and be maintained to the end of trial. However, we found that the differential activity appeared only after the delay period (Figures 2–5) and thus is more likely related to motor planning.

Prospective coding of autonomously selected motor plans provides an additional scientific basis for cognitive neural prosthetics. It has been demonstrated that neural signals in the PPC can be decoded to position cursors on a computer screen without the animals emitting any behavior when they are instructed to plan reach movements (Andersen et al., 2004; Musallam et al., 2004). However, there is usually no cue to instruct particular effectors in natural conditions. The current results show that parietal-based cognitive neural prosthetics should also be able to decode autonomously selected movements.

As mentioned previously, PRR and LIP cells exhibited vigorous responses during the cue period (Figures 2, 3A, and 5). Such activity independent of effector choice might reflect the monkey's default planning before a particular effector was specified, spatial attention to the target, or solely a sensory response. It has been proposed that motor planning may be initiated before a final decision is made, and decision making is in fact a selection by competition between potential plans (Cisek, 2006). Further experiments are essential to determine if such a mechanism occurs in PPC.

Like previous studies of spatial decision making, our results demonstrate that the PPC encodes nonspatial decisions by reflecting an impending effector-specific motor intention. However, it still remains unclear how the decision is computed and whether the PPC merely reflects the outcome of decision made by higher cortical areas or indeed plays a causal role in deliberation as a necessary part of the decision network. Although the PPC seems unlikely to be the "central executive" in charge of effector-specific decisions, it may be involved in the deliberation through intrinsic reciprocal loops in addition to projections to/from frontal cortex and other areas. Determining whether there is a causal role of the PPC in decision making will require more direct examination with lesions, stimulation, or other experimental interventions.

EXPERIMENTAL PROCEDURES

Two male macaque monkeys (*Macaca mulatta*, 12–15 kg) were studied in this experiment. Under isofluorane anesthetic, a head holder and search-coil monitoring eye position were implanted. During training sessions, the head-fixed monkeys were seated in front of a touch-board displaying visual stimuli. They were trained to fixate the red spot with their eyes and to touch the green spot with their hands. Next they were trained to perform memory-guided delayed saccades and reaches (Snyder et al., 1997). The animals were then trained in the effector

delay-instructed and effector choice paradigms. Note that once so trained, each animal was able to perform all paradigms.

Once a trial was initiated, eye and hand movements were restricted by a real-time behavioral control program written in LabVIEW (National Instruments, TX) and running on a real-time PXI platform. After their performance became satisfactory, a second surgery was performed to implant a recording cylinder over the PPC centered at 6 mm posterior to the interaural line and 12 mm from the midline to cover the intraparietal sulcus (IPS). All procedures were in accordance with guidelines of NIH and were approved by the Caltech Institutional Animal Care and Use Committee.

During recording sessions, microelectrodes were lowered into area LIP or PRR, as determined by physiological criteria (Snyder et al., 1997) with the help of previously collected magnetic resonance images. PRR was located on the medial bank of the IPS, and roughly 4–6 mm subsurface as shown in Figure 1 of Scherberger et al. (2003). The LIP cells were recorded from an anatomically segregated area, about 3–4 mm lateral and 1–2 mm anterior to the PRR on the lateral bank of the IPS, typically 5–7 mm subsurface.

Once a neuron was isolated, its response field was mapped with center-out delayed reach and delayed saccade tasks (Snyder et al. 1997). If there was a significant response and directional tuning to either task, then the recording proceeded to the effector choice and delay-instructed paradigms. The target position was randomly selected from the cell's preferred location and a nonpreferred location. Choice and instruction trials were randomly interleaved with equal (50%) probability. For each combination of target location and trial type (chosen saccade and reach, instructed saccade and reach), there were 7 to 15 trials (mean = 10) recorded for each neuron. In the effector delay-instructed trials, the monkey received liquid reward for every trial in which the instructed movement was correctly performed. In effector choice trials, an algorithm (algorithm 1 of Barraclough et al., 2004) was used to minimize systematic biases by having the monkey play a competitive game with the computer. The monkey was rewarded only if his choice matched the computer's choice, and the computer biased its choice against the monkey's choice sequence during five preceding effector choice trials with the same peripheral target location.

Single-neuron activity was recorded with microelectrodes using either an FHC drive (Frederick Haer & Co, ME, USA) or a multiple-electrode microdrive (5-channel "mini-matrix," Thomas Recordings, Germany). The raw signal from each electrode was preamplified through a headstage (20×), then band-passed and amplified by a Plexon recording system (Plexon Inc, TX, USA). Data on the time of action potentials, eye and hand positions, and the displayed stimuli were automatically stored on a computer disc drive.

Data were analyzed using Matlab 6.5 (MathWorks). The baseline activity was defined as the 300 ms interval starting 500 ms before cue onset. The early delay period was defined as the first half (0–300 ms after cue offset) of the delay period, while the late delay period was defined as the second half (300–600 ms after cue offset) of the delay period. The post-GO period was defined as the first 100 ms after the GO signal (the central LEDs were extinguished). Ninety-five percent of movements were initiated after this first 100 ms. Reaction times of autonomously chosen saccades and reaches were 163 ± 45 ms and 269 ± 76 ms, respectively. Latencies of effector delay-instructed saccades and reaches were 167 ± 57 ms and 269 ± 73 ms, respectively. There were no significant differences in latencies between choice and instruction trials or between monkeys.

Supplemental Data

The Supplemental Data for this article can be found online at http://www.neuron.org/cgi/content/full/56/3/552/DC1/.

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REFERENCES

Andersen, R.A., and Buneo, C.A. (2002). Intentional maps in posterior parietal cortex. Annu. Rev. Neurosci. *25*, 189–220.

Andersen, R.A., Burdick, J.W., Musallam, S., Pesaran, B., and Cham, J.G. (2004). Cognitive neural prosthetics. Trends Cogn. Sci. *8*, 486–493.

Baldauf, D., Wolf, M., and Deubel, H. (2006). Deployment of visual attention before sequences of goal-directed hand movements. Vision Res. *46*, 4355–4374.

Barraclough, D.J., Conroy, M.L., and Lee, D. (2004). Prefrontal cortex and decision making in a mixed-strategy game. Nat. Neurosci. *7*, 404–410.

Bisley, J.W., and Goldberg, M.E. (2003). Neuronal activity in the lateral intraparietal area and spatial attention. Science *299*, 81–86.

Calton, J.L., Dickinson, A.R., and Snyder, L.H. (2002). Non-spatial, motor-specific activation in posterior parietal cortex. Nat. Neurosci. *5*, 580–588.

Cisek, P. (2006). Integrated neural processes for defining potential actions and deciding between them: a computational model. J. Neurosci. *26*, 9761–9770.

Cisek, P., and Kalaska, J.F. (2005). Neural correlates of reaching decisions in dorsal premotor cortex: Specification of multiple direction choices and final selection of action. Neuron *45*, 801–814.

Coe, B., Tomihara, K., Matsuzawa, M., and Hikosaka, O. (2002). Visual and anticipatory bias in three cortical eye fields of the monkey during an adaptive decision-making task. J. Neurosci. *22*, 5081–5090.

Cohen, J.D., and Blum, K.I. (2002). Reward and decision. Neuron *36*, 193–198.

Colby, C.L., and Goldberg, M.E. (1999). Space and attention in parietal cortex. Annu. Rev. Neurosci. *22*, 319–349.

Curtis, C.E., and D'Esposito, M. (2006). Selection and maintenance of saccade goals in the human frontal eye fields. J. Neurophysiol. *95*, 3923–3927.

Deubel, H., Schneider, W.X., and Paprotta, I. (1998). Selective dorsal and ventral processing: Evidence for a common attentional mechanism in reaching and perception. Vis. Cogn. *5*, 81–107.

Dickinson, A.R., Calton, J.L., and Snyder, L.H. (2003). Nonspatial saccade-specific activation in area LIP of monkey parietal cortex. J. Neurophysiol. *90*, 2460–2464.

Freedman, D.J., and Assad, J.A. (2006). Experience-dependent representation of visual categories in parietal cortex. Nature *443*, 85–88.

Glimcher, P.W. (2003). The neurobiology of visual-saccadic decision making. Annu. Rev. Neurosci. *26*, 133–179.

Gnadt, J.W., and Andersen, R.A. (1988). Memory related motor planning activity in posterior parietal cortex of macaque. Exp. Brain Res. *70*, 216–220.

Green, D.M., and Swets, J.A. (1966). Signal Detection Theory and Psychophysics (New York: Wiley).

McCoy, A.N., and Platt, M.L. (2005). Risk-sensitive neurons in macaque posterior cingulate cortex. Nat. Neurosci. *8*, 1220–1227.

Musallam, S., Corneil, B.D., Greger, B., Scherberger, H., and Andersen, R.A. (2004). Cognitive control signals for neural prosthetics. Science *305*, 258–262.

Platt, M.L., and Glimcher, P.W. (1999). Neural correlates of decision variables in parietal cortex. Nature *400*, 233–238.

Quian Quiroga, R., Snyder, L.H., Batista, A.P., Cui, H., and Andersen, R.A. (2006). Movement intention is better predicted than attention in the posterior parietal cortex. J. Neurosci. *26*, 3615–3620.

Rizzolatti, G., Riggio, L., Dascola, I., and Umilta, C. (1987). Reorienting attention across the horizontal and vertical meridians: evidence in favor of a premotor theory of attention. Neuropsychologia *25*, 31–40.

Romo, R., and Salinas, E. (2001). Touch and go: decision-making mechanisms in somatosensation. Annu. Rev. Neurosci. *24*, 107–137.

Schall, J.D., and Thompson, K.G. (1999). Neural selection and control of visually guided eye movements. Annu. Rev. Neurosci. *22*, 241–259.

Scherberger, H., Fineman, I., Musallam, S., Dubowitz, D.J., Bernheim, K.A., Pesaran, B., Corneil, B.D., Gilliken, B., and Andersen, R.A. (2003). Magnetic resonance image-guided implantation of chronic recording electrodes in the macaque intraparietal sulcus. J. Neurosci. Methods *130*, 1–8.

Shadlen, M.N., and Newsome, W.T. (2001). Neural basis of a perceptual decision in the parietal cortex (area LIP) of the rhesus monkey. J. Neurophysiol. *86*, 1916–1936.

Snyder, L.H., Batista, A.P., and Andersen, R.A. (1997). Coding of intention in the posterior parietal cortex. Nature *386*, 167–170.

Stoet, G., and Snyder, L.H. (2004). Single neurons in posterior parietal cortex of monkeys encode cognitive set. Neuron *42*, 1003–1012.

Toth, L.J., and Assad, J.A. (2002). Dynamic coding of behaviourally relevant stimuli in parietal cortex. Nature *415*, 165–168.