that receive an increased attentional signal from the FEF on microstimulation trials. This model is convincing because it is consistent with the finding that subthreshold FEF stimulation leads to better visual discrimination in the movement field (Moore and Fallah, 2004) and the observation that FEF microstimulation enhances activity in visual area V4, which is reminiscent of an attentional effect (Moore and Armstrong, 2003). The authors' model further highlights the emerging view that microstimulation of a brain area does not simply modulate activity at the tip of the microelectrode, but also induces activity changes in distantly connected brain regions. Taken together, these data are exciting, because they demonstrate that attention and action interact more closely in the FEF than previously thought, and they suggest a mechanism by which attention can modulate saccade motor commands.

Of course, many interesting questions will have to await future investigations. For example, it may be that the position illusion alters the saccade command not in the FEF, but in an area downstream of the FEF. Such a dissociation between the motor signal and saccade metric has been found for saccades to remembered stimuli (Stanford and Sparks, 1994) and for saccades to moving targets in the superior colliculus (Keller et al., 1996). Another open question is whether this effect is specific to the FEF or whether attentional signals change saccade commands in other cortical or subcortical areas as well. An obvious candidate would be the superior colliculus, whose activity has been linked to both saccade generation and attention (Ignashchenkova et al., 2004). Schafer and Moore's study invites us to attend to and act on these questions.

REFERENCES

Bruce, C.J., Friedman, H.R., Kraus, M.S., and Stanton, G.B. (2004). In The Visual Neurosciences, L.M. Chalupa and J.S. Werner, eds. (Cambridge, MA: The MIT Press), pp. 1428–1448.

Corbetta, M., Akbudak, E., Conturo, T.E., Snyder, A.Z., Ollinger, J.M., Drury, H.A., Linenweber, M.R., Petersen, S.E., Raichle, M.E.,

Van Essen, D.C., and Shulman, G.L. (1998). Neuron 21, 761–773.

Ignashchenkova, A., Dicke, P.W., Haarmeier, T., and Thier, P. (2004). Nat. Neurosci. 7, 56–64.

Keller, E.L., Gandhi, N.J., and Weir, P.T. (1996). J. Neurophysiol. 76, 3573–3577.

Moore, T., and Armstrong, K.M. (2003). Nature 421, 370–373.

Moore, T., and Fallah, M. (2004). J. Neurophysiol. 91, 152–162.

Rizzolatti, G., Riggio, L., Dascola, I., and Umilta, C. (1987). Neuropsychologia 25, 31–40.

Sato, T.R., and Schall, J.D. (2003). Neuron 38, 637–648.

Schafer, R.J., and Moore, T. (2007). Neuron 56, this issue, 541–551.

Schiller, P.H., and Sandell, J.H. (1983). Exp. Brain Res. 49, 381–392.

Stanford, T.R., and Sparks, D.L. (1994). Vision Res. 34, 93–106.

Thompson, K.G., Biscoe, K.L., and Sato, T.R. (2005). J. Neurosci. 25, 9479–9487.

Whitney, D. (2002). Trends Cogn. Sci. 6, 211–216.

To Touch or Not to Touch: Posterior Parietal Cortex and Voluntary Behavior

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The primate posterior parietal cortex has been implicated in a large number of cognitive functions. In this issue of *Neuron*, Cui and Andersen show that neurons in this area maintain effector-specific coding of motor intentions without specific sensory instructions and therefore when behavior is chosen by the animal freely.

Spiking activity of retinal ganglion cells or receptor potentials of auditory hair cells clearly encode sensory information. We know this because the activity of such sensory neurons can be studied even in anesthetized animals and is not affected by the movements planned by the animal. Similarly, the functional relationship between the activity of muscles and motor neurons is relatively easy to study. In contrast, it is much more difficult to determine whether neurons in high-order association cortical areas, such as the posterior parietal cortex (Figure 1A),
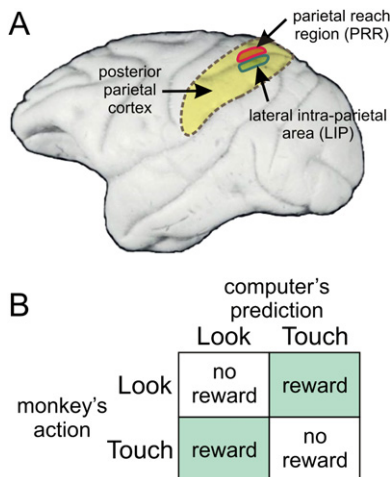
Figure 1. Posterior Parietal Cortex and Decision Making in a Competitive Game
(A) Lateral view of the rhesus monkey's brain, showing the posterior parietal cortex that contains the two areas studied by Cui and Andersen.
(B) Payoff matrix of the matching pennies game used in their study.

primarily perform sensory or motor functions, and this has stirred intensive debate for many years. For example, does the activity of the neurons in the posterior parietal cortex reflect the animal's attention to a particular stimulus or the animal's intention to direct its movement toward the same stimulus (Andersen and Buneo, 2002; Colby and Goldberg, 1999)?

The study by Cui and Andersen (2007) published in this issue of *Neuron* shows that the activity in the posterior parietal cortex reflects the animal's intention to control its movements, even when the animals choose such movements voluntarily without specific sensory instructions. This study is significant for two related reasons. First, our natural movements are frequently directed toward or guided by sensory stimuli, and consequently, sensory stimuli and movements often vary together, raising the possibility that the brain structures and neurons processing the information about them may not be clearly segregated. Therefore, it is important to understand the extent to which the systems involved in the control of perceptual and motor processes can be distinguished. Second, it is extremely diffi-

cult to manipulate experimentally the animal's movements without changing sensory stimuli. Indeed, much of the progress in our understanding about the functions of the primate association cortex was due to the innovations in the behavioral techniques used to isolate specific components related to hidden mental operations in the brain.

It has been long known that many neurons in the posterior parietal cortex (Figure 1A) respond to sensory stimulus in a context-dependent manner, and their activity can be enhanced when the animal pays attention to a particular stimulus or plans a movement toward it (Mountcastle et al., 1975; Colby and Goldberg, 1999). For example, the experimenter may present a visual stimulus in a particular location and require the animal to reach or make an eye movement toward that stimulus. The animals are motivated to perform such tasks because successful behaviors are rewarded by food or water. During such experiments, neurons in many different parts of the brain, including the posterior parietal cortex, are activated, but since the end point of the movement coincides with the position of the stimulus, it is almost impossible to determine which of these two factors plays a more important role in shaping the pattern of neural activity. By presenting a separate trigger signal for the movement and forcing the animal to withhold its movement for a brief delay, researchers could separate the neural activity temporally related to the sensory stimulus and the subsequent movement (Hikosaka and Wurtz, 1983). However, neural activity time-locked to a particular sensory stimuli might still be related to an early process of movement planning, and similarly the activity time-locked to the movement could result from the reactivation of signals related to the previous sensory stimulus (di Pellegrino and Wise, 1993). Various approaches to dissociate the position of the visual stimulus and the metrics of the movements have been fruitful in characterizing the coordinate systems used by the neurons in the posterior parietal cortex (Zhang and Barash, 2000), but they do not completely resolve the question of

whether the neurons in the posterior parietal cortex encode the properties of sensory stimuli or planned movements. For example, if the activity of a neuron is determined by the vector of the second eye movement in a double-step saccade task, this could still be encoding the position of the visual target for the second eye movement in an oculomotor reference frame.

A more powerful approach has been used to dissociate the neural activity related to attention to a visual stimulus and intention to produce movements toward the same stimulus (Bushnell et al., 1981; Snyder et al., 1997). For example, monkeys were required to make an eye movement toward a red target and reach toward a green target (Snyder et al., 1997). During this task, neurons in the subdivision of the posterior parietal cortex known as the lateral intraparietal area (LIP) often responded according to the position of the target for eye movement, whereas those in the area referred to as the parietal reaching region (PRR) responded according to the position of the target for reaching (Figure 1A). Such effector-specific coding of motor intention seems unlikely to result from the color tuning properties of neurons in the posterior parietal cortex. Nevertheless, this possibility cannot be excluded completely, since it has been demonstrated that the neurons in the LIP can encode the stimulus color when it becomes behaviorally relevant (Toth and Assad, 2002). The new study by Cui and Andersen (2007) was designed to test more directly such effector-specific coding of intention in the LIP and PRR by requiring the animals to choose freely between the two different response modalities without any sensory instructions.

An interesting challenge that must have faced the authors of this study concerns how to keep the animals choosing the two targets equally often without using any sensory instructions. For example, if the animal is completely free to choose between making an eye movement and reaching toward a target to get the same reward, the animal might choose an eye movement exclusively. At first, why an

animal would ever need to randomize its choices in its natural environment may not be obvious. However, a random or stochastic behavior might become optimal when the animal faces other intelligent decision-making agents that also try to maximize their own self-interest. Take, for example, the game of rock-paper-scissors, where paper beats rock, scissors beat paper, and rock beats scissors. It is easy to see that an optimal strategy for this game is to choose all three options with the same probability of 1/3, because any other strategy, such as choosing rock exclusively, can be exploited by a rational opponent who wants to maximize the chance of winning. Such competitive interactions might be common among social animals, including humans and other primates (Lee and Seo, 2007).

In the study by Cui and Andersen (2007), monkeys were trained to choose freely between making an eye movement and reaching toward a particular visual target during a computer-simulated matching pennies game (Barraclough et al., 2004). Matching pennies is a two-person game, in which one wins if the two players choose the same option, such as the head of a coin, and the other wins otherwise. Therefore, both players constantly try to predict each other's choice. In this study, the computer opponent was programmed to predict and exploit the animal's choice, and the animal was rewarded only when the computer failed to predict the animal's choice correctly (Figure 1B). Consistent with the results from previous studies in which monkeys made their choices during competitive games (Barraclough et al., 2004; Dorris and

Glimcher, 2004), the animals in this study also successfully distributed their choices more or less equally between the two response modalities. In addition, the activity in the LIP and PRR reflected the animal's choice such that the LIP (PRR) neurons showed higher activity when the animal chose to make an eye (a hand) movement. Importantly, there was no difference in the sensory stimuli presented to the animal between the trials in which the animal chose to touch the target and those in which the animal chose to look at the target. Therefore, the difference between the LIP and PRR must reflect the voluntary choice of the animal rather than the properties of sensory stimuli.

This study demonstrates nicely that the free-choice task, such as the matching pennies game, can be adapted to probe the neural basis of voluntary behavior. Its focus, however, was not on the question of how the animal chooses to move its eyes or its hand at a particular moment, and this should be investigated further in future studies. Some of the factors that were not explicitly manipulated in this study might have influenced the animal's choice on a trial-by-trial basis. In this study, for example, the free-choice trials were interleaved with the instructed trials in which the animal was required to move its eyes or hand according to the sensory cue. Do the animal's behaviors in these instructed trials influence the choice in subsequent free-choice trials? In addition, when the animal fails to receive reward in a particular free-choice trial, does this influence the animal's subsequent choices systematically? Do the neurons in the LIP and PRR also carry signals related

to the expected value or utility of reward from different motor outputs, as seen in free-choice tasks involving only eye movements (Platt and Glimcher, 1999; Sugrue et al., 2004; Dorris and Glimcher, 2004)? Answers to these and other new questions generated by this study will further demystify the role of the posterior parietal cortex in the control of voluntary behavior.

REFERENCES

Andersen, R.A., and Buneo, C.A. (2002). Annu. Rev. Neurosci. *25*, 189–220.

Barraclough, D.J., Conroy, M.L., and Lee, D. (2004). Nat. Neurosci. *7*, 404–410.

Bushnell, M.C., Goldberg, M.E., and Robinson, D.L. (1981). J. Neurophysiol. *46*, 755–772.

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

Cui, H., and Andersen, R.A. (2007). Neuron *56*, this issue, 552–559.

di Pellegrino, G., and Wise, S.P. (1993). J. Neurosci. *13*, 1227–1243.

Dorris, M.C., and Glimcher, P.W. (2004). Neuron *44*, 365–378.

Hikosaka, O., and Wurtz, R.H. (1983). J. Neurophysiol. *49*, 1268–1284.

Lee, D., and Seo, H. (2007). Ann. N Y Acad. Sci. *1104*, 108–122.

Mountcastle, V.B., Lynch, J.C., Georgopoulos, A., Sakata, H., and Acuna, C. (1975). J. Neurophysiol. *38*, 871–908.

Platt, M.L., and Glimcher, P.W. (1999). Nature *400*, 233–238.

Snyder, L.H., Batista, A.P., and Andersen, R.A. (1997). Nature *386*, 167–170.

Sugrue, L.P., Corrado, G.S., and Newsome, W.T. (2004). Science *304*, 1782–1787.

Toth, L.J., and Assad, J.A. (2002). Nature *415*, 165–168.

Zhang, M., and Barash, S. (2000). Nature *408*, 971–975.