Journal Club

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Target Selection: Choice or Response?

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Review of Scherberger and Andersen (http://www.jneurosci.org/cgi/content/full/27/8/2001)

The posterior parietal cortex (PPC) encodes information related to action (Desmurget et al., 1999). A subregion of the PPC, the parietal reach region (PRR), is involved in encoding the direction of volitional reaching movements to seen (Snyder et al., 1997) and unseen (Gail and Andersen, 2006) target locations. In their recent study in *The Journal of Neuroscience*, Scherberger and Andersen (2007) propose that the PRR plays an active role in the selection of targets for reaching movements.

The authors trained rhesus monkeys to make reaching movements to a target, chosen from two alternatives on opposite sides of a fixation point. The animals tended to have a strong bias toward one of the two potential targets because each target yielded a fixed reward. To overcome this bias, targets were presented sequentially, and the less preferred target always preceded the preferred target. The interval between these stimulus onsets, commonly referred to as the stimulus onset asynchrony (SOA), was varied using an adaptive procedure until the animals selected each of the two targets with equal frequency. Scherberger and Andersen (2007) recorded the activity of directionally tuned neurons in the PRR over the course of sequentially presented potential targets. Control manipulations included the performance of saccades to chosen targets and reaches and saccades on trials that did

not include the presentation of a second target.

One of the main findings was that the initial neural activity reflected the appearance of the stimulus but was modulated by selection preference. Cells that preferred the first target (T1) were compared with those that preferred the second target (T2). T1 cells became active shortly after presentation of the first target, but their activity decreased after a chosen second target was presented [Scherberger and Andersen (2007), their Fig. 5A, left (http://www.jneurosci.org/cgi/content/full/27/8/2001/F5)]. T2 cells became active shortly after the second target was presented and were more active when the animal moved to the second target than when the animal moved to the first target [Scherberger and Andersen (2007), their Fig. 5B (http://www.jneurosci.org/cgi/content/full/27/8/2001/F5)]. The firing rate of T1 cells at the moment the second target was presented appeared to be greater in trials in which the first target was chosen than when the second target was chosen, with this difference increasing as a function of SOA [Scherberger and Andersen (2007), their Fig. 5C (http://www.jneurosci.org/cgi/content/full/27/8/2001/F5)]. Scherberger and Andersen (2007) interpret these results in terms of a race or competition model between the two groups of cells. They argue that if the network is strongly active for the first target, the second target's representation by T2 cells is suppressed. Implicit in this model, selection is explained as the outcome of the race between the groups of cells responding to each target. If the net-

work is not strongly active for the first target, then the second target is encoded by the T2 cells, suppressing the T1 cells. The subsequently executed movement is represented by the population activity after this selection process.

However, there is a problem with this interpretation. The authors make clear that the monkeys tended to prefer one target in each pair. To offset this bias, the SOA was manipulated so that the monkeys were equally likely to move to each target. It is arguable whether this represents a "choice" on the part of the animal. An alternative interpretation of the data is that the observed neural activity reflects the formation of a reach plan to the target stimulus and that it is the variation in SOA alone that determines the eventual target selected. Once a target is presented, the neurons in PRR that are selective for that target begin firing. If another target is presented a short time later, and the response to the first target has not been sufficiently encoded, then the animal may move to the second target. However, with an extended SOA, the animal will move to the first target because it will be sufficiently encoded before the presentation of the second target. This situation varies greatly from what one might typically consider selection, in which both options have been considered and a choice is made according to some goal or desire.

How can we tell whether the actions animals take reflect a choice after consideration of the multiple options? Human subjects can be instructed not to select the same stimulus every trial, but it is very difficult to do this with animals. One strategy

for addressing this concern might be to train the monkey to expect differential rewards from each stimulus. The rewards can be random during training sessions, leading the animal toward picking the stimuli completely at random (and for the same amount of reward each time) during the testing sessions. Assuming that the extinction time for such learned behaviors can be limited, the monkey's original bias might well creep in before sufficient data can be accumulated. On a more abstract level, can any action produced to obtain an immediate reward simulate the more complex choice behaviors of humans?

It is important to consider whether animals can actually make choices or indeed have "free will." However, the concept of a "free choice" is a contentious one even for human behavior. Glimcher (2004) has shown that during a "work or shirk" paradigm, humans and rhesus monkeys are

able to select an action unpredictably to maximize their reward. This suggests that when exposed to a two-alternative selection task, monkeys can perform in an unpredictable or free-willed pattern. Glimcher believes that free will may simply be the name we give to the probabilistic behaviors that are mixed-strategy solutions, in which behavior is geared toward maximizing the goal or reward. In some circumstances when facing an uncertain situation, the maximal behavior is to be unpredictable. When this occurs, it might seem that the behavior is based on free will when in fact it is the probabilistic answer to an uncertain environment.

In summation, although Scherberger and Andersen (2007) replicated the specificity of the PRR for reaching movements, there are still questions as to whether this activity reflects a choice. Thus, it is more difficult to support the

authors' contention that the neural signals measured in the PRR are part of a target selection process rather than merely a function of the animal's response to the stimulus in front of it.

References

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