Journal Club

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Attention and Intention, Decoded!

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Review of Quiroga et al. (<http://www.jneurosci.org/cgi/content/full/26/13/3615>)

Whether neural activity in the posterior parietal cortex (PPC) reflects attention and/or intention (i.e., motor plans) remains controversial. Some researchers emphasize the attentional properties of neural activity (Colby and Goldberg, 1999), whereas others argue that it is predominantly reflective of motor intention (Snyder et al., 2000). The recent paper by Quiroga et al. (2006) in the *Journal of Neuroscience* applies a novel analytic approach to the debate.

Specifically, the investigators used a combination of population analysis and decoding methods. Population analysis combines the activity of multiple cells into a multidimensional representation of the system. Once a multidimensional space is created for each condition, it can be used to generate predictions by correlating a given pattern of activation to the already established multidimensional space. Tight correlations suggest that a given pattern of activation reflects a particular state of the system. This method differs from traditional neurophysiological analysis in that functionality is determined by the predictive power of the aggregate neural activity rather than by tuning curves and receptive fields of single cells in each region. An obvious strength of this method is that it speaks to the most probable physiological reality: one in which activity from populations of neurons, rather

than from discrete single cells, generates behavior.

Quiroga et al. (2006) trained monkeys in delayed saccade and reach tasks. An array of eight possible target locations was presented with an illuminated central fixation. Then, one of eight peripheral light-emitting diodes (LEDs) signaled the target location. If it turned green, it indicated a saccade, and if it turned red, it indicated a reach (Fig. 1A). After a delay, fixation offset cued the monkey to initiate the appropriate movement to the location of the target. Saccade and reach trials were randomly interleaved. Single-cell activity was recorded from lateral intraparietal sulcus (LIP) and parietal reach region (PRR) [located in the medial intraparietal sulcus and extending dorsally into the parietal-occipital area, as described by Snyder et al. (2000)]. As in previous studies (Snyder et al., 2000), Quiroga et al. (2006) found activity consistent with effector specificity for LIP and PRR. Namely, after the effector cue (green or red LED), LIP cells showed sustained activity enhancement for trials in which saccades were cued and, conversely, PRR cells showed sustained activity enhancement for trials in which reaches were cued (Fig. 1B).

On a trial-by-trial basis, the authors aimed to decode either intention or attention from aggregated population activity. They tested two hypotheses: that population activity in LIP and PRR would best predict intention and that there would be effector-specific activity in the two PPC areas. Specifically, LIP activity would better predict saccade endpoint, and PRR activity would better predict reach end-

point. Framed in the attention versus intention context, if LIP or PRR cells code for attention only, then the effector should have no influence on activity. In other words, neither area should show modulation according to the movement plan, only according to target location. When LIP and PRR activity were grouped according to target location, the population activity was predictive of target location [Quiroga et al. (2006), their Fig. 3 (<http://www.jneurosci.org/cgi/content/full/26/13/3615/F3>)]. However, the activity from LIP also predicted saccade endpoint. Similarly, the activity in PRR strongly predicted reach endpoint but showed no lateralization. Despite this evidence for effector specificity, activity from both areas showed above-chance prediction of the other endpoint as well, providing evidence for both attentional (location-predictive) and intentional (action-predictive) signals [Quiroga et al. (2006), their Fig. 4 (<http://www.jneurosci.org/cgi/content/full/26/13/3615/F4>)]. Quiroga et al. (2006) emphasized that prediction of intention was greater than target location, concluding that the movement plan carries more weight than attention in the two PPC areas tested.

Quiroga et al. (2006) presented analyses on only a subset of their rich dataset. An additional line of inquiry could supplement the attention/intention debate, possibly in important ways. First, when comparing the activity in the PRR cell [Quiroga et al. (2006), their Fig. 2A (<http://www.jneurosci.org/cgi/content/full/26/13/3615/F2>)] with that of the LIP cell [Quiroga et al. (2006), their Fig. 2B

Received May 12, 2006; revised May 19, 2006; accepted May 19, 2006.

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DOI:10.1523/JNEUROSCI.2037-06.2006

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(<http://www.jneurosci.org/cgi/content/full/26/13/3615/F2>), the cells show different patterns of activation, if one assumes that the cells shown have typical response properties. Notably, they have discrepant temporal unfolding such that LIP showed early maximal modulation that resolved by 750 ms, whereas PRR showed sustained modulation over the entire time window (Fig. 1B). The initial peak in LIP activity suggests that there may be attention-related signals in the first 150 ms. As presented, the analysis was initiated 150 ms after the target location illuminated. Presumably, this was to avoid confounding intention activity and that attributable to the transient visual onset. However, it may be that the activity elicited from the transient visual onset is an attentional signal in LIP and PRR cells (Yantis and Jonides, 1984). This possibility remains untested in the report by Quiroga et al. (2006).

Additionally, a more demanding attentional task might be informative. As implemented by Quiroga et al. (2006), an abrupt visual onset serves to indicate the appropriate movement plan. However, if selection of a task-relevant location were more demanding, the design might provide a stronger test of attention. To achieve this, a condition in which a visual transient is irrelevant should be included. For example, adding irrelevant visual onsets (i.e., distracters) to the other seven nontarget locations would allow a differentiation between PPC attention-related activity attributable to visual onsets and that attributable to task-relevant selection (Fig. 1, compare A, C). It would also maintain all of the critical features for the intermixed delayed saccade and reach tasks. We argue that complementing the elegant intention design that Quiroga et al. (2006) used with a stronger attention

Figure 1. *A*, Schematic depiction of the stimuli appearing at the start of each trial (gray box in *B*); the effector cue, indicating which action to perform at fixation offset, was illuminated red or green. All eight peripheral locations were used in the experiment, and fixation (black central dot) was illuminated during the premovement delay. *B*, PPC single-cell responses to a preferred direction for different actions, adapted from Quiroga et al. (2006). The gray box (0–150 ms) indicates when the effector cue was present. The analysis window spanned 150–750 ms. The response of the PRR cell is shown in black: the solid line indicates when a reach was cued, and the dashed line indicates when a saccade was cued. Similarly, the response of the LIP cell is shown in gray: the solid line indicates when a reach was cued, and the dashed line indicates when a saccade was cued. Effector specificity is revealed by the difference between the solid and dashed lines. In the case of the PRR cell, reach trials show increased firing above saccade trials. The converse is true for the LIP cell. Note the different response profiles between PRR and LIP cells, assuming responses are typical of those areas. *C*, Schematic depiction of the suggested modification to the task. Here, transient visual onsets occur at all possible target locations. Comparing activity from trials containing task-relevant (red or green) cues to task-irrelevant cues would allow for a dissociation between attention drawn to the abrupt visual onset and attention deployed to a task-relevant location. The effects could be seen either early (during the cue stimulus period) or during the delay period before the go signal (fixation offset).

manipulation will help resolve the attention/intention debate.

In summary, Quiroga et al. (2006) have presented intriguing data. The findings are encouraging when considering the implications for rehabilitation. Specifically, neural population decoding in real time has implications for brain–machine interfacing and neuroprosthetics (Shenoy et al., 2003). Furthermore, the authors offer a novel approach to analyzing neural activity in PPC. Examination of a different temporal window and a slight task modification may provide even additional insight into the dynamics of PPC as a region involved in both attention and intention.

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