Journal Club

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How to Reach: Movement Planning in the Posterior Parietal Cortex

Frederike H. Petzschner[1,2,3]* **and Melanie Krüger**[1,2,4]*

[1]Graduate School of Systemic Neurosciences, Ludwig-Maximilians-University, 82152 Planegg-Martinried, Germany, [2]University Hospital Munich Grosshadern, Department of Neurology, 81377 Munich, Germany, [3]Bernstein Center for Computational Neurosciences, 82152 Planegg-Martinried, Germany, and [4]Research Training Group 1091 "Orientation and motion in space", 81377 Munich, Germany

Review of Cui and Andersen

The planning and control of complex movements is one of the most impressive abilities of the brain. Recent neurophysiological evidence suggests that motor planning is mediated, in part, by a reciprocally connected parietofrontal neural circuit. An interesting property of this circuit is that it can represent, in parallel, multiple potential actions, even though ultimately only one can be executed (Cisek and Kalaska, 2010). The simultaneous preparation of multiple potential actions, which then compete for instantiation, is thought to offer an ecological advantage because it may reduce reaction times in a continuously changing environment (Cisek and Kalaska, 2010).

Neural activity related to potential spatial goal-directed action plans has been found in the posterior parietal cortex (PPC) for reaching (Scherberger and Andersen, 2007), grasping (Baumann et al., 2009), and eye movements (Glimcher, 2003). In addition to specifying the part of space to which actions should be directed, action planning in areas such as the parietal reach region (PRR), the dorsal area 5

(area 5d), and lateral intraparietal area (LIP) seems to also be linked to the effector (arm/eye) that will be used to acquire that goal. Thus, task-related neural activity in PPC could have several roles (Calton et al., 2002). In particular, it could represent the preferred effector, the spatial goal location independent of the effector, or both the effector and the spatial goal either in parallel or serially.

A recent paper by Cui and Andersen (2011), published in *The Journal of Neuroscience*, sheds new light on this issue. The authors investigated the functional involvement of the reach-related areas PRR and area 5d in effector selection and spatial goal-directed planning of reaching movements by separating the two processes in a forced-delay task. They recorded from PRR and area 5d cells while rhesus monkeys performed three different effector-selection tasks. Each trial started with a fixation period followed by a spatial cue that indicated the goal location. After a short delay period, monkeys could either freely choose the effector (arm or eye) with which they wanted to acquire the goal (effector-choice task) or they received a second cue specifying the effector they should use (effector-instructed task). In the third experimental task, monkeys received the effector cue together with the spatial cue after the fixation period, so they knew both the spatial goal location and the effector during the subsequent delay period (memory task).

Immediately after the spatial cue appeared, activity in PRR rose congruently in the effector-instructed and effector-choice tasks, followed by either maintenance of this elevated activity when the effector was specified as the arm or by a strong decrease in activity when the effector was specified as the eye. The persistent activity was slightly lower when the arm modality was freely chosen compared with when it was instructed (Cui and Andersen, 2011, their Fig. 2 A, B).

Remarkably, area 5d exhibited a different time course of activation. In particular, neurons in area 5d did not show any significant response until the effector was fully specified as the arm in both the effector-choice and effector-instructed tasks. Not surprisingly, when the cue simultaneously indicated both the spatial goal as well as the use of the arm (memory task), firing increased shortly after the onset of the cue (Cui and Andersen, 2011, their Fig. 2C).

From this set of results, Cui and Andersen (2011) suggest that the persistent PRR activity encodes potential reach plans while the effector is still ambiguous and the selected reach plan when the effector is specified as the arm. They speculate that activity in area 5d reflects only the selected reach plan, as there was no activity present when the arm was merely a potential effector. With respect to the recent finding of simultaneous early activity in PRR and LIP (Cui and Andersen, 2007) that is supposed to reflect mutual compe-

tition in the decision process on reach or saccade, or at least the parallel representation of both potential movements, the increase in neural activity in area 5d only after the effector decision could be interpreted as downstream to that decision process representing spatial plan selection. Hence, Cui and Andersen (2011) suggest a more serial processing stream for nonspatial effector decisions, in contrast to a more integrated processing stream for spatial goal selection.

The experimental set-up allowed Cui and Andersen (2011) to partially discriminate the functional role and temporal structure of neural activity within and between PRR and area 5d. In particular, the spectrum of possible contributions of area 5d to spatial goal selection and effector decision has been narrowed. In previous studies in which the arm was predefined as the effector, area 5d cells were found to be responsive to spatial goal information before and during movement execution, as well as during memory periods between goal localization and movement execution (Crammond and Kalaska, 1989; Snyder et al., 1997). Cui and Andersen (2011), however, show that, regardless of the presence of a spatial goal, area 5d is not active as long as the movement is not specified as being a reach. Thus, area 5d seems not to be involved in effector-independent planning itself, but strongly depends on the outcome of the effector decision.

These results raise a few questions. First, the meaning of neural activity observed in PRR remains somewhat unclear. The increase in firing of PRR cells after the spatial cue and before the subsequent effector decision might be explained by considering a finding by Calton and colleagues (2002). They reported selectivity of PRR neurons for spatial and effector cues, with a subgroup of neurons being responsive to both. However, the majority of neurons showed selectivity for only one of the two cues (spatial/effector). Therefore, PRR activity before the effector decision might reflect (1) an involvement in the effector decision process itself independent of the potential spatial movement goal or (2) the encoding of multiple effector- and spatial goal-dependent movement plans in parallel. How the changes in neural activity relate to these different processes cannot be disentangled with the setup used in Cui and Andersen (2011). In addition, the role of activity in area 5d is unclear. It could be related to a single selected reach plan, which will be executed subsequently, or it might

represent the next step in the process of movement planning, at which multiple potential spatial reach plans still exist and are represented in parallel.

A slight modification to the experiment that allows independent manipulation of effector-dependent and spatial goal-dependent movement planning could help clarify the role of PRR and area 5d. The latter manipulation was used in a recent study by Klaes and colleagues (2011). They recorded from primate PRR and dorsal premotor cortex and investigated whether, in the presence of an uncertain mapping rule between spatial target location and movement goal, primates either compute multiple movement goals simultaneously before choosing an action or represent a single movement goal after selecting a rule. A potential spatial target location was presented at the beginning of each trial and, after a delay period, monkeys either had to freely choose a spatial goal (reach or anti-reach, no-context-instructed condition) or had to reach toward a prescribed goal if instructed (context-instructed condition). Thus, in comparison to the study by Cui and Andersen (2011), the effector mapping with prespecified spatial goal was replaced by a spatial goal mapping with prespecified effector. This setup allowed Klaes and colleagues (2011) to show that PRR, in the presence of an uncertain mapping rule, simultaneously represents multiple potential spatial goal-dependent movement plans in parallel and not one single selected plan.

In principle, representing a potential movement independent of the spatial goal is similar to representing it independent of the effector. One way to experimentally disentangle the two representations is by introducing an additional stage into the effector decision task used by Cui and Andersen (2011) that specifies the spatial goal only after the effector decision has been made. By doing so, effector-dependent and spatial goal-dependent activity could be separated in PRR and area 5d. The resulting task would then consist of three stages. First, a spatial target location would be cued, but the effector (eye or arm), as well as the final spatial goal (reach-to-target or anti-reach) would remain unknown. In a delayed, second stage, the effector would be instructed or left unspecified for free choice. The delayed, third stage would specify the spatial goal, or also leave it open for free choice. This setup would address the question of whether area 5d is also involved in the decision process of spatial goal selection after the

effector decision is made. In other words, one could differentiate whether neural activity in area 5d represents multiple potential spatial goals, or instead reflects one selected movement plan. Further, it would be possible to investigate whether PRR activity before the effector decision shows only effector-dependent activity or reflects multiple potential effector- and spatial goal-dependent action plans as described by Klaes et al. (2011).

To summarize, in a natural movement, the effector choice and the spatial movement goal are usually linked to each other, and once the effector is chosen, the goal is specified by that choice. Consequently, to be able to describe the functional roles of PPC subregions in movement planning, one has to use independent experimental manipulations of both spatial goal mapping and effector choices. The recent work by Cui and Andersen (2011) has been a good step in that direction, although further work will be needed to fully understand the different processes underlying the planning of reaching movements in the PPC.

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