Making Choices between Rules or between Actions

Alexandre Pastor-Bernier[1] and Paul Cisek[1,*]
[1]Department of Physiology, Université de Montréal, C.P. 6128 Succursale Centreville, Montréal, QC H3C 3J7, Canada
*Correspondence: paul.cisek@umontreal.ca
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A new study by Klaes et al. in this issue of *Neuron* shows that the brain can simultaneously apply two rules to the same sensory information in order to specify two parallel potential action goals, which then compete for execution in the sensorimotor system.

Our lives are filled with decisions. Some of these are complex choices, such as whether to enroll in one university course or another. Some decisions are much simpler, such as selecting whether to reach toward a cup of coffee or a muffin. Still other kinds of choices involve the application of abstract rules to specific actions, such as whether to push the brake or the accelerator at a yellow light. What are the mechanisms by which the brain makes such decisions? Do we select between rules (stop versus go) or actions (press one pedal versus another)? In what form does the brain represent these situations? In recent years, many studies have addressed such questions by recording neural activity from animals while they make decisions. A large body of literature on saccade-selection tasks has shown that factors relevant for decisions modulate neural activity within the circuit that controls eye movements, including parietal cortex (Platt and Glimcher, 1999) and superior colliculus (Basso and Wurtz, 1998). Recordings in the sensorimotor circuits that control the arm have shown that before a decision between actions is made, neural activity represents the potential actions in dorsal premotor cortex (PMd) (Cisek and Kalaska, 2005) and the parietal reach region (PRR) (Scherberger and Andersen, 2007). However, the mechanisms involved are still far from understood. In this issue of *Neuron*, Klaes et al. (2011) provide important pieces of the puzzle by addressing two questions: (1) do we select between abstract *rules* (e.g., stop versus go at a yellow light), or concrete action *goals* (e.g., press the accelerator or brake pedal), when making decisions? (2) Does the brain make decisions by encoding all available movement *options* or the subjective *preferences* of the subject?

Klaes et al. trained monkeys to make reaching movements either toward the location where a stimulus appeared ("direct goal"), or toward a location in the opposite direction ("inferred goal"). This stimulus appeared 800–2000 ms before a GO signal, which sometimes indicated the correct rule with a color cue (green for direct, blue for inferred), and sometimes the monkey was allowed to choose freely. Because the monkeys did not know ahead of time whether their choice would be free, Klaes et al. could examine the pre-GO activity to get a glimpse of the strategies the monkeys used to make their choices. One possibility is that they first selected their preferred rule and then prepared the action associated with it, as illustrated in Figure 1A. An alternative possibility is that they instead applied both rules and prepared both actions simultaneously, allowing the actions to compete against each other, as in Figure 1B. Neural recordings in PRR and PMd revealed simultaneous preparation of both actions in parallel, supporting the latter scheme (or alternatively, the scheme shown in Figure 1C, in which competition occurs between rules as well as actions). Parallel action preparation has previously been shown in PMd (Cisek and Kalaska, 2005) and PRR (Scherberger and Andersen, 2007), but in those studies the actions were specified by distinct stimulus cues. Here, Klaes et al. show that a single stimulus can specify two actions, revealing the simultaneous application of two different transformation rules in parallel.

Interestingly, the direct goal engaged neural activity earlier than the inferred, consistent with prior studies showing that responses oriented directly toward stimuli are processed more quickly than responses requiring remapping (Crammond

and Kalaska, 1994). This suggests that the information for specifying the direct goal may be processed along a simple parietal-to-frontal route, while information for specifying the inferred goal may need to pass through prefrontal cortex and then be sent back to premotor and parietal regions. Indeed, an earlier study from the same lab showed that unlike direct goals, inferred goals were represented in PMd before appearing in PRR (Westendorff et al., 2010).

Of course, in many situations, we make decisions that are unrelated to any particular action. When choosing between university courses, one presumably is not planning routes for walking to class. Obviously the brain is capable of making abstract decisions that do not involve action, and many studies have examined the neural mechanisms which may be involved. For example, in a paradigm similar to that used in Klaes et al. (2011), Bennur and Gold (2011) compared how monkeys judged the direction of visual motion when they either did or did not know what saccadic response would be used to report their decision. It was found that even before a saccade plan could be made, some cells in parietal cortex were selective for the motion direction of the visual stimulus. In the reach-planning system, Nakayama et al. (2008) showed that premotor activity is selective even when monkeys are only given a "virtual" action plan, specifying whether the right-most or leftmost of two stimuli will be the target for movement but the locations of the stimuli themselves are still not known. In fact, the very same monkeys studied by Klaes et al. were very familiar with this kind of situation, having previously been trained on tasks in which the rule was indicated before the spatial target (Westendorff et al., 2010). In those cases,
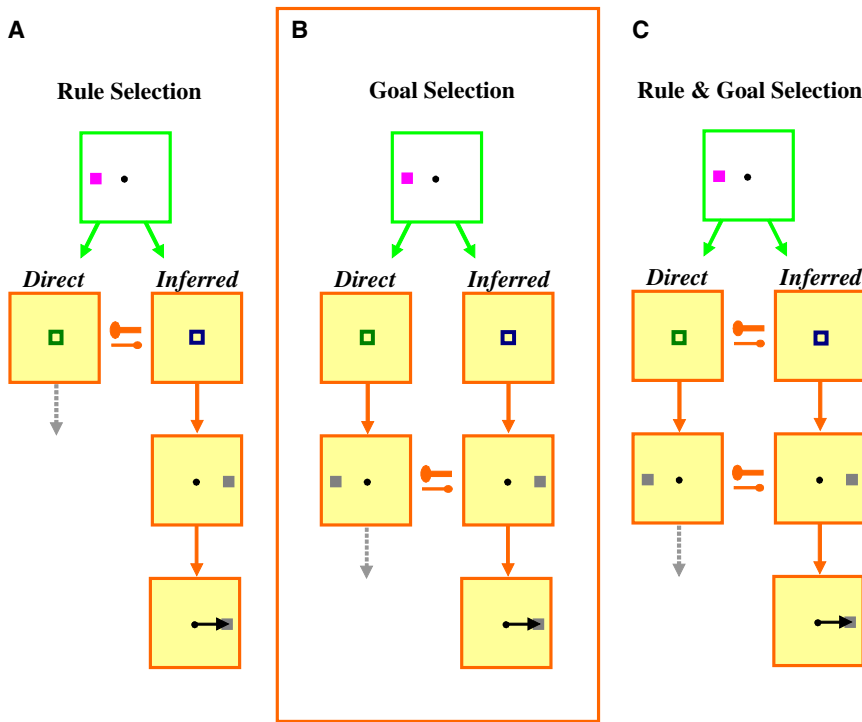
Figure 1. Three Possible Information-Processing Schemes under "Free-Choice" Conditions for Competition between Rules, Action Goals, or Both

Arrows indicate transformations of visual information (green box) through neural representations (orange boxes), and rounded arrows represent inhibitory interactions (thicker line indicates stronger inhibition). Rule selection in (A) implies that the competition is resolved first at an abstract level (green versus blue square cues), in this case favoring the "inferred rule" before any action goals are specified. Alternatively (B), both rules could be applied to generate two goals, which then compete, in this case with the "inferred goal" winning. In (C), both kinds of competition take place at the same time. Klaes et al. suggest the process shown in (B), although their data is not incompatible with the multilevel competition shown in (C).

one might imagine the competition took place between the rules, and then later, also between the actions (Figure 1C).

Since animals are clearly capable of making decisions between abstract rules, then why should they, in situations such as the experiment of Klaes et al., bother to simultaneously apply two rules to prepare two actions, only one of which can physically be performed? One answer, as Klaes et al. suggest, may be that doing so allows animals to make more informed choices. If one is able to define both actions, then one's decision can be influenced by factors related to the movements themselves, such as the energy required to produce them or their likelihood of success. For example, a tennis player should favor selecting strokes at which she is more proficient. In agreement with this, a recent study in our lab demonstrated that when humans are allowed to make free choices between equally valued targets, they prefer movements that

minimize biomechanical costs (Cos et al., 2011). In other words, if the brain can prepare multiple actions in parallel, then it can consider features of their execution and take these into account during selection. Furthermore, selecting actions may be more fundamental from an evolutionary perspective (Cisek and Kalaska, 2010). At the time the fundamental outline of our neural architecture was being established, animals were selecting between movement directions for escaping a predator, not between university courses.

The second question addressed by Klaes et al. is whether the neural activity they observed in PRR and PMd objectively reflects the options that were presented, or whether it reflects the monkeys' own subjective preferences. To examine the role of subjective preference, if any, in decision making, the authors exploited the monkeys' spontaneously adopted strategy in the absence of external biases: when given a free choice, both monkeys

tended to preferentially select the inferred goal over the direct goal. This might appear counterintuitive, since the direct action is clearly easier. However, the monkeys perforce required more training to learn the inferred goal than the easier direct goal. Furthermore, favoring the inferred target may also be strategic, since it is easy to switch to the direct action if so instructed. Nevertheless, whatever the reason for the monkeys' preference, it provided Klaes et al. the opportunity to examine whether neural activity was related to the objective options or to subjective preferences and strategies. For these experiments, the monkeys were trained on two different reward schedules. In the "balanced set" schedule, the probability of reward for repeated choices was reduced, encouraging balanced choice behavior. In the "biased set" schedule, the monkeys were not penalized for any strategy, and both spontaneously adopted a bias in favor of the inferred action. Recordings in the two conditions showed that, in both PRR and PMd, neural activity reflected the current strategy: during the balanced set, when monkeys' choices were approximately equal between direct and inferred targets, both movement goals were approximately equally represented in neural activity. In contrast, during the biased set, activity related to the inferred goal was much stronger than activity related to the direct goal, reflecting the monkeys' preference.

This finding supports the hypothesis that the brain prepares multiple actions in parallel and selects between them through biased competition in the sensorimotor system (Cisek, 2006; Shadlen et al., 2008). This competition can be biased by many factors, such as expected gain (Platt and Glimcher, 1999), subjective strategies (Dorris and Glimcher, 2004), or indeed any factor relevant to the choice. Dorris and Glimcher (2004) proposed the term "relative subjective desirability" to imply that what modulates neural activity during decision tasks is a subjective variable that depends upon the relative desirability of one option versus another. Klaes et al. show that the modulation of neural activity is indeed related to subjective desirability. A recent study in our lab (Pastor-Bernier and Cisek, 2011) shows that this neural modulation is related to relative, rather than absolute, desirability. In our study,

monkeys made decisions between two targets whose stimulus features indicated how many drops of juice each was worth, and we examined whether neural activity in PMd reflected a competition between the two potential reaching actions. As expected, we found that neural activity increased as the value of the preferred target increased while the other target's value was constant. We also found that if we kept the preferred target's value constant and increased the other target's value, neural activity decreased, suggesting a competitive interaction. Most importantly, if only a single target was presented then neural activity was completely insensitive to its value—strongly suggesting that in all cases, activity specifying potential actions is modulated by the subjective desirability of those actions relative to other options. This further strengthens the proposal made by Klaes et al. that the modulation of activity in PMd and PRR reflects subjective preferences for one action goal over another.

The question of how the brain makes decisions is the topic of many recent and ongoing studies. Klaes et al. provide a critical piece of the puzzle by showing that the brain is capable of simultaneously applying two rules to the same sensory information in order to specify two parallel potential action goals in the sensorimotor regions of frontal and parietal cortex. They show that these activities do not simply reflect sensory information, nor do they simply reflect the motor options, but that they reveal the animals' strategies and subjective preferences. Taken together with other studies cited here and in Klaes et al., these findings support an "intentional" framework for sensorimotor behavior (Shadlen et al., 2008), whereby the brain makes decisions about actions through a biased competition taking place within the same system that guides the execution of those actions (Cisek, 2006). Although the brain can also make purely perceptual decisions in situations where no response has yet been specified (e.g., Bennur and Gold, 2011), the strategy of specifying multiple potential actions appears to be adopted in all situations in which it is possible. Given that for many millions of years, decisions were almost exclusively related to the selection of actions (fight versus flight, rest versus forage, turn left versus turn right), it makes sense that the architecture for making decisions has evolved to be so strongly integrated with sensorimotor control (Cisek and Kalaska, 2010).

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