Journal Club

Editor's Note: These short, critical reviews of recent papers in the *Journal*, written exclusively by graduate students or postdoctoral fellows, are intended to summarize the important findings of the paper and provide additional insight and commentary. For more information on the format and purpose of the Journal Club, please see http://www.jneurosci.org/misc/ifa_features.shtml.

Evidence for a Decision Variable in the Human Motor System

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Review of Selen et al.

Many traditional information-processing models assume that the processes underlying decision formation are neatly separable from, and causally antecedent to, those involved in action generation. According to these models, centralized cognitive processing results in the formation of a decision that is subsequently passed along to the motor system to be transformed into the desired action. Because the motor system is recruited only after the decision outcome is complete, these models leave little room for the motor system to play an ongoing role in the decision process itself.

Recent work on embodied cognition in cognitive science and robotics directly challenges these sequential models, suggesting instead that material properties of the body and aspects of motor behavior may be engaged in an ongoing fashion to augment and shape cognitive processing (Barsalou, 2008; Clark, 1999; Pfeifer and Bongard, 2006). Neuroscientists have also begun to uncover specific evidence that neural systems supporting action are more closely related to those supporting cognition than previously thought. For instance, signals that reflect accruing sensory evidence relevant to making perceptual decisions have been identified within the same oculomotor circuits that govern the planning of eye movements, indicating that decision formation and motor preparation may engage common neural systems (Gold and Shadlen, 2000, 2007).

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A recent paper by Selen et al. (2012), published in *The Journal of Neuroscience*, builds upon this emerging body of work. This study provides novel behavioral evidence for decision-related signals in the human motor system and advances the current state of the field in two major ways. First, one lingering criticism of earlier studies of perceptual decision making in nonhuman primates has been that the results might merely reflect the fact that monkeys were heavily trained to map perceptual decisions onto motor outputs. If true, discovering that accumulating sensory information is reflected in the oculomotor signals responsible for generating saccadic eye movements in an overtrained task would be an unsurprising and uninteresting result. Confirming the presence of similar effects in normal, untrained human subjects is therefore a critical step forward. Second, in moving from invasive recording and microstimulation paradigms involving monkeys (Gold and Shadlen, 2000, 2007) to human studies, Selen et al. (2012) were pressed to find a noninvasive method of obtaining a behavioral readout of evolving decision signals. Their recruitment of the elbow stretch reflex in this experiment thus represents an important achievement that potentially opens doors to other analogous, noninvasive methods for probing decision variables in humans.

In the experiment, subjects viewed moving random-dot stimuli that elicited the impression of motion in one of two opposing directions. Subjects were asked to report their decision about the direction of motion using either elbow flexion or extension to move a hand-held manipulandum in the same direction as the observed visual motion. The discrimination task is challenging because the strength of the motion signal can be experimentally controlled by varying the percentage of coherently moving dots in the stimulus. To make accurate decisions about motion direction, subjects typically need around several hundred milliseconds, depending on the strength of the motion stimulus. Consistent with previous findings, Selen et al. (2012) report that subject performance improved as a function of both increased motion coherence and viewing time.

The choices that subjects made in this decision task are well described by a drift-diffusion model. In this model, motion evidence is continuously integrated over time. This accumulated evidence is represented by a decision variable (DV), which compactly captures the information upon which subjects base their choices. By varying motion coherence and viewing duration, the authors obtained a continuum of DV values that ranged from small to large amounts of decision evidence regarding the direction of motion. Critically, while subjects were in the process of integrating this evidence, the stimulus was unpredictably turned off and, at the same time, the subject's arm was slightly deflected by a 60 ms pulse of external force delivered through a robotic manipulandum. This brief perturbation both cued the subject to rapidly make a choice and elicited a stretch reflex in muscles near the elbow joint. Selen et al. (2012) measured the magnitude or gain of this reflex through the difference in electromyographic (EMG) activity between the forearm flexor and extensor muscles. Intriguingly, the authors found that reflex gains evoked shortly after perturbation depended on both motion coherence and viewing duration. Importantly, these reflex gains are proportional to the modeled DV in this task, reflecting the amount of currently accumulated sensory evidence informing a subject's choice. This cognitive variable has been gated all the way into the muscles.

The continuous evolution of a DV has typically been observed in the firing rates of neurons in the monkey oculomotor network (Gold and Shadlen, 2007). By contrast, Selen et al.'s (2012) study shows that the muscles do not track the formation of the DV before and without the assistance of the experimental perturbation (Selen et al., 2012, their Fig. 4*B*, column G1). Instead, only reflex gains following perturbation onset provide a useful window on the evolving DV (Selen et al., 2012, their Fig. 4*B*, columns G2, G3). One apparent limitation of this gain reflex-based measure is that each trial provides only a snapshot of the current state of the DV at the time of (or slightly after) the perturbation. This limitation is mitigated by aggregating across many trials in which the perturbation is applied at different times relative to stimulus onset. In this way, the authors arrive at a continuous proxy signal for the underlying dynamics of the evidence accumulation process in the motor system.

Another, more important, limitation of Selen et al.'s (2012) study is that it cannot test a key prediction of the drift-diffusion model. The model predicts that subjects make a choice and an associated movement when the accumulating evidence reaches a critical bound. However, in Selen et al. (2012), subjects were required to make a movement at the specific time of the perturbation, not necessarily at the time they have reached a decision. Consequently, it is not feasible to test whether the EMG signal reaches a decision bound before the movement is executed. Resolving this issue in the future will require different experimental designs not subject to this limitation.

Since reflex gains provide only a crude estimate of the early accumulation dynamics and cannot be used to test all key aspects of the drift-diffusion model, future work must characterize more precisely the formation of a perceptual DV in motor circuits. To our knowledge, no such study has been undertaken in either monkeys or humans. A more precise characterization can answer a number of important questions, including whether motor signals converge to a bound when a decision is made. Future research will also be critical in identifying the motor areas in the brain that represent this evolving decision process. Given that the DV is gated into the muscles through the induction of a spinal cord reflex, we tentatively propose that evidence accumulation for perceptual decisions might be represented in peripheral motor cortical regions, including M1 and PMd.

Finally, one might argue that the EMG signal identified in Selen et al. (2012) does not represent a cognitive variable at all, but instead reflects a purely motor variable such as force. While Selen et al. (2012) suggest a complex interplay between decision and motor processes, they do not provide the means to distinguish unambiguously between these possibilities. More radically, the study by Selen et al. (2012) may indicate that, in some cases, it is impossible to disentangle these possibilities experimentally because some measured decision and motor variables merely provide different viewpoints on a single, unitary process. Future experimental studies will be needed to shed more light on this issue.

In summary, the study of Selen et al. (2012) extends the results of previous studies in nonhuman primates demonstrating the presence of a decision variable in the oculomotor network. The study shows that during perceptual decision making, the currently accumulated sensory evidence informing the decision to make an arm movement is continuously represented in the human motor system. This finding paves the way for future studies to characterize the dynamics and motor regions involved in the process of evidence accumulation during perceptual decision-making. More generally, the study suggests that in circumstances where perceptual decisions result in impending movements, such as when riding a bicycle or returning an approaching tennis ball, our cognitive deliberation is likely to be continuously reflected in many aspects of the motor system, including our ongoing movements. Such direct links between cognition and action might be advantageous not only for contending with the immediate concerns in everyday behavioral contexts, but might also reflect a long history of evolutionary pressure to bind the two systems together. To date, the rationale behind this proposition has been far from obvious. However, recent findings, such as those reported by Selen et al. (2012), successfully chip away at these potentially misleading intuitions and enable a deeper appreciation of the complex interplay between cognitive and motor processing in the brain.

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