

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.

Neural Evidence for a Role of Urgency in the Speed-Accuracy Trade-off in Perceptual Decision-Making

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Review of Thura and Cisek

In the study of perceptual decision-making, the dominant theory holds that subjects accumulate evidence over time until a threshold level is reached and a response is executed (Gold and Shadlen, 2007; Forstmann et al., 2016). Formal evidence accumulation models have been exceptionally successful in explaining a variety of behavioral phenomena (e.g., Forstmann et al., 2016). Furthermore, neural studies show that single neurons appear to accumulate evidence (e.g., Gold and Shadlen, 2007), and thus also support the evidence accumulation theory. Both in behavioral and neural studies, researchers typically use the random-dot motion task (Ball and Sekuler, 1982), which requires subjects to decide the direction in which a cloud of dots appears to move.

Notwithstanding the general success of the evidence accumulation theory, several questions remain in the field. First, what is the neural mechanism underlying the ability of subjects to voluntarily increase accuracy at the cost of speed, and vice versa (e.g., Bogacz et al., 2010)? Evidence accumulation models typically account for the speed-accuracy trade-off by assuming that subjects alter their decision threshold: when accuracy is essential, subjects apply a higher threshold than when speed is paramount.

Although this mechanism accurately describes behavioral data, there is no full consensus on the neural implementation of the speed-accuracy trade-off (e.g., Standage et al., 2014). Notably, recent studies using single-cell recordings suggest that the rate of evidence accumulation increases under speed stress, without a decrease in threshold (Heitz and Schall, 2012; Hanks et al., 2014).

Another open question is whether there is a role for urgency in decision-making. The idea of urgency is that subjects become less patient as time passes, and therefore are willing to commit to a decision on the basis of less evidence. Urgency differs to speed stress in terms of the hypothesized mechanism that permits fast responding: speed stress is typically assumed to arise from a relatively low threshold that is constant within a trial; urgency is typically assumed to arise from a dynamically changing threshold or accumulation rate within a trial. The idea of urgency sparked wide interest but remains controversial (Hawkins et al., 2015). The Urgency-Gating model (Cisek et al., 2009; Thura et al., 2012) takes the idea of urgency a step further and assumes that an urgency signal grows over time, whereas the sensory evidence is tracked but not integrated/accumulated. When the urgency signal reaches a threshold level, a choice is made favoring the momentary sensory evidence.

In a recent study, Thura and Cisek (2016) address both the neural implementation of the speed-accuracy trade-off and urgency. They recorded single-cell activity in the dorsal premotor and primary motor areas in macaque monkeys performing a

decision-making task. In this task, 15 tokens sequentially move from a center position toward either the left or the right. Monkeys were trained to decide during a trial, whenever they feel confident enough, which position (left or right) they believe will ultimately contain the most tokens. After a decision is made, the remainder of the tokens sequentially move toward their final positions before a new trial starts.

The authors manipulated the speed-accuracy trade-off by changing the speed at which the remaining tokens move after a decision has been made. The idea is that, if the tokens move quickly toward their final positions after the monkey made a decision, there is little cost associated with making an error: the monkey may not get a reward for the current trial, but a new trial starts quickly. If the tokens move slowly after a decision, the costs of making an error are higher because more time passes before there is a new chance of reward. Thus, if monkeys aim to maximize the reward rate, the optimal policy is to respond more accurately in slow compared with fast trials. Summary statistics of the behavioral data indicated that this manipulation worked: in fast blocks, the monkeys made faster decisions with more errors than in slow blocks.

In the token task, the amount of evidence presented can be quantified at each point in time as a measure of the number of tokens for each choice option and the number of remaining tokens. This is not possible in tasks with a continuous stream of information, such as the random-dot motion task. By comparing the amount of evidence presented at the decision time between trials

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with different decision durations, it was shown that the monkeys used less evidence to inform their decisions as decision duration increased. The behavioral data therefore supports the idea of urgency.

The most compelling results, however, come from the neural recordings. Generally, during a trial, neurons fired at baseline rates and then showed a ramping increase in firing rate, reaching a peak rate just before movement onset. Three factors contributed to this pattern. First, activity reflected the sensory evidence displayed. For example, the activity of a neuron tuned to the left position increased when a token moved leftward and decreased when a token moved rightward. Importantly, each token moving rightwards decreased activation of neurons tuned to the left, even when the total evidence still favored left. The authors argue that this indicates that evidence is not integrated, but tracked. Second, firing rates depended on the condition: in fast blocks, baseline firing rate was higher; and the rate of increase was higher than in the slow condition. Third, neuronal activity increased with decision duration. Importantly, this time-dependent rise is stronger in fast conditions than in slow conditions.

The three main neural results led Thura and Cisek to three conclusions. The first is that subjects track evidence without integration. Thus, the core assumption underlying evidence accumulation models is argued to be incompatible with the presented data. This is in contrast to previous studies (e.g., Gold and Shadlen, 2007; Purcell et al., 2010) in which two distinct subpopulations of cells were found: one tracking the sensory evidence and one integrating the evidence Purcell et al. (2010) even showed quantitatively that nonintegrator models could not account for their data.

This discrepancy can be explained by taking into account the tasks used. In the token task, all evidence shown remains visible throughout the trial (evidence accumulation is external). Thus, the “current” evidence equals the integral of all displayed evidence. Unlike the random-dot motion task, tracking the current sensory evidence in the tokens task is equal to integrating all evidence over time (Winkel et al., 2014). The presented neural activity patterns, showing that rightward moving tokens decrease activation of left-tuned neurons even when the total evidence remains favoring left, are also compatible with integrator models of decision-making because the integral of evidence for left decreases in such a case.

Thura and Cisek’s second conclusion is that there is an urgency signal. Indeed, the firing rates of neurons clearly increased over time, which is highly interesting in light of recent discussions about urgency. Hawkins et al. (2015) reviewed the behavioral evidence for urgency and showed that evidence is mixed: urgency is not necessary to account for most datasets, although it is necessary for some. Thura and Cisek’s neural data add to the case for urgency.

Future research is necessary to fully understand the role of urgency. Importantly, what underlies the differences between datasets showing evidence for and against urgency? One suggestion (Hawkins et al., 2015) is that the amount of training is crucial: highly trained subjects (including monkeys) are able to dynamically adjust thresholds or the rate of evidence accumulation. The current study falls in line with this proposal but did not directly test it. A second factor that might contribute to the appearance of urgency is the type of evidence accumulation: external or internal. With external evidence accumulation, subjects are continuously aware of the exact amount of accumulated evidence, and, in the tokens task, also the to-be-accumulated tokens. The presence of this information might lead subjects to use a time-dependent decision strategy (for a similar task and results, see Hawkins et al., 2012).

Third, Thura and Cisek make a new and interesting proposal on the neural mechanism underlying the speed-accuracy trade-off. Only two previous studies recorded single-cell activity with a speed-accuracy trade-off manipulation (Heitz and Schall, 2012; Hanks et al., 2014), and both suggested that, on a neural level, the manipulation did not influence the threshold, but rather the start point and rate of evidence accumulation. The present study replicates this finding and relates the start point and rate of evidence accumulation effects to the urgency signal. The authors propose that changes in urgency, not in threshold, underlie the speed-accuracy trade-off.

Some caution should apply here because the authors did not quantitatively fit formal models to the behavioral data. It is therefore not certain that the monkeys showed the same speed-accuracy trade-off behavior as humans. Nonetheless, this proposal is especially interesting in light of a recent study (Lo et al., 2015) showing that a behavioral change in threshold might be caused by a neural change in a control signal that modulates the gain of integrators in an attractor network model of decision-making. Al-

though the correlation between this control signal and an urgency gain signal was not studied, they play similar roles in the process. A new testable question emerges: Is it possible to fit behavioral speed-accuracy trade-off data with an urgency model in which only the urgency parameters change between conditions? It would be interesting to see whether models with urgency can outperform models with only a threshold by means of model comparison techniques.

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