

# The road least taken

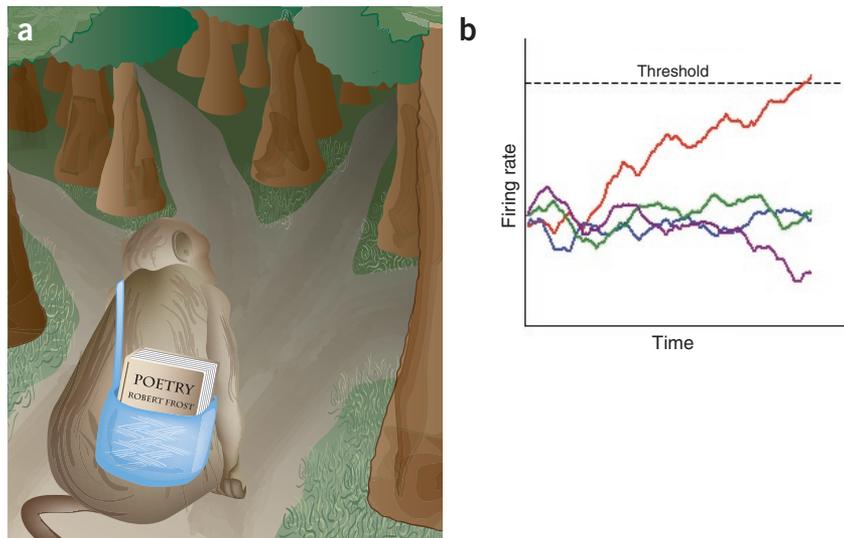
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**Decisions between two alternatives have been extensively studied and modeled. A study now reports that during choices among several options, the responses of neurons in the lateral intraparietal area are still well described by the integration-to-bound model, supporting the general applicability of this computational framework.**

When Robert Frost came to a fork in the road, he famously chose the road less traveled. How did he come to this important decision? He looked carefully at his two options, spent some time deliberating and bravely set forth along his chosen path. However, this account fails to specify some important details about the process. What are the relevant qualities that he should extract regarding the two paths? How does he compare those qualities? How long should he spend making his decision? Finally and most importantly, how and where is all of this information processed in his brain? Although these questions are beyond the scope of the poem, the neuroscience community has taken up this task and has begun to shed light on the neural mechanisms underlying decision-making.

Many current decision-making models have been inspired and supported by experiments where single-neuron activity is recorded while monkeys are making simple decisions about sensory stimuli. In a commonly used procedure, monkeys view a noisy display that is filled with independently moving dots and have to decide whether the predominant motion is to the left or to the right. One of the current models that is proposed to explain how monkeys, and presumably people, perform such a task is an integration-to-bound model, in which evidence for motion direction is accumulated for each alternative until one of them reaches a threshold<sup>1</sup>.

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**Figure 1** Four choices diverged in a yellow wood. (a) A monkey must choose between four possible actions. (b) Simplified schematic of the integration-to-bound mechanism for a four-choice task. As the monkey gathers sensory information, the cumulative evidence for each of the four choices is reflected in the firing rates of neural integrators, as shown by the four colored traces. Once one of the four firing rates exceeds the decision threshold, the monkey stops making observations and may report its choice. Note that the actual firing-rate magnitudes for the starting point, threshold and rate of rise may vary across neurons and across conditions.

However, the simplicity of the tasks in the supporting experiments limits the usefulness of the model<sup>2–4</sup>. In this issue, Churchland *et al.*<sup>5</sup> demonstrate that the integration-to-bound model applies equally well to more complex decision-making tasks.

The proposed integration-to-bound mechanism works as follows. As a subject observes a stimulus, task-relevant variables are encoded in early sensory areas. These variables, which are continuously updated as the stimulus changes and new evidence becomes available, are fed to integrators. The integrators sum up the available evidence

over time. There is a separate integrator for each possible choice. When the summed evidence in favor of any one choice exceeds a threshold, the subject stops gathering information and settles on that choice. Note that Frost did not deliberate indefinitely; he chose a path and moved on.

A previous study suggested that the accumulation process for bounded integration is implemented in the lateral intraparietal area (LIP)<sup>2</sup>. In these experiments, a monkey identified the predominant direction of noisy stimulus motion and then indicated its choice with an

eye movement to one of two targets on either side of the stimulus. Neurons in area MT, an early sensory area, represent a moment-by-moment estimate of motion direction. These MT responses look approximately flat in time<sup>6</sup>. In contrast, neurons in LIP show a ramping up of firing when motion favors the choice whose target is in that neuron's receptive field<sup>2</sup>. This was interpreted as the accumulation of sensory evidence in favor of that choice. The monkey, who is free to indicate its decision at any time, initiates an eye movement shortly after the LIP firing rate reaches a particular level, suggestive of a decision bound.

Churchland *et al.*<sup>5</sup> explored the generality of this integration-to-bound model by conducting an analogous experiment with four, rather than just two, possible directions of motion. Even in this four-alternative forced choice task, LIP neurons behaved similar to bounded integrators (Fig. 1). In particular, the ramping activity reflected evidence accumulation in both the two- and four-choice tasks, and the firing rate reached approximately the same level before the monkey made its decision. One notable difference between the two tasks is that the initial firing rate before the motion starts was lower in the four-choice task than in the two-choice task; that is, the bound was effectively higher in the four-choice task. This agrees with the intuition that more evidence is required when there are more alternatives from which to choose and with the observation that reaction times increase with the number of alternatives<sup>7</sup>.

Accumulation of evidence was also recently demonstrated by using a very different task<sup>8</sup>. In the weather-prediction task, monkeys selected one of two targets on the basis of a sequence of abstract shapes, each shape providing probabilistic evidence that a saccade to one or the other target would be rewarded on that trial. The monkeys learned to combine the probabilities associated with each shape in the sequence and LIP activity quantitatively tracked this process. The results of both Churchland *et al.*<sup>5</sup> and the weather-prediction task<sup>8</sup> lend credence to the hypothesis that decisions in general are made by a bounded integration of evidence and that this process occurs in LIP.

Although these and other experiments<sup>2–5,8</sup> suggest that LIP neurons act as integrators, this function must be reconciled with other putative functions of LIP. For example, LIP activity has been linked with planned saccadic eye movements<sup>9</sup>. In fact, LIP neurons in the motion-discrimination experiments were identified on the basis of memory-period activity in a task where the monkey was required to remember the location of an eye-movement target. A natural question, which has yet to be addressed, is whether LIP's role in decision-making extends beyond tasks in which eye movements indicate the responses. For example, LIP might not integrate evidence for tasks where the decision is indicated by reaching to a target.

LIP may also have a role in directing spatial attention. Previous work has argued that LIP activity indicates the monkey's locus of attention in the visual field<sup>10,11</sup>. From that point of view, as evidence accumulates to make a particular target the more probable choice, spatial attention may shift toward that target<sup>12</sup>. If the ramping up of LIP activity reflects the gradual shifting of spatial attention, then we might see integration of evidence in LIP when the decision is indicated by reaching to one of several targets, but not when the decision is indicated by a nonspatial action such as a lever release. Although these predictions have not been tested, it should be noted that nonspatial features, including category identity<sup>13</sup> and numerosity<sup>14</sup>, can influence LIP activity in tasks where those features are relevant.

Still other studies have suggested that LIP contains a neural representation of expected value. In tasks where the monkey makes saccadic eye movements to a cued target, the size of the anticipated reward has been shown to modify the magnitude of the LIP response<sup>15</sup>. However, a representation of value need not be in conflict with a role in decision-making. If decisions arise from computations in LIP, then factors that influence a decision must also influence LIP activity. This predicts that any influence of the differential rewards on choice behavior should be accompanied by a corresponding change in LIP responses in a direction-discrimination task where the two targets

are assigned different reward values. Indeed, it makes ecological sense for decision mechanisms to maximize the reward that the animal receives. Given data suggesting a variety of roles for LIP, perhaps it makes sense to think about the changing LIP firing rate as an evolving estimate of the value of a target, integrating prior probabilities, cost functions and sensory evidence. This information can then be used to allocate spatial attention or to plan eye movements. The integration-to-bound model provides a neurally plausible framework for explaining how such a process might evolve and terminate.

There are many roads that we can take to learn more about the decision-making process. We might employ a wider variety of tasks, including more varied stimulus modalities and means of responding. We might consider how multiple neurons tuned to the same location interact with each other and how they are read out as a population. Or we might bridge the gap between monkeys and humans by designing tasks that are suitable for cross-species imaging. Each road will provide different insights to help us better understand how choices are made. And our choices, as Frost knows, can make all the difference.

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