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Neural underpinnings of the evidence accumulator

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Gradual accumulation of evidence favoring one or another choice is considered a core component of many different types of decisions, and has been the subject of many neurophysiological studies in non-human primates. But its neural circuit mechanisms remain mysterious. Investigating it in rodents has recently become possible, facilitating perturbation experiments to delineate the relevant causal circuit, as well as the application of other tools more readily available in rodents. In addition, advances in stimulus design and analysis have aided studying the relevant neural encoding. In complement to ongoing non-human primate studies, these newly available model systems and tools place the field at an exciting time that suggests that the dynamical circuit mechanisms underlying accumulation of evidence could soon be revealed.

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Introduction

When we face a difficult decision, and are therefore uncertain as to what the best choice is, we are slow to make up our minds; but when faced with an easy decision, we are fast. This experience from daily life is one of the most common behavioral observations in decision-making, and applies in a remarkably wide array of different types of decisions, ranging from perceptual decisions [1], to numerical comparison decisions [2], to social decisions [3], to visual search decisions [4,5], to gambling decisions [6], to memory retrieval decisions [7], to lexical retrieval decisions [8], to social decisions [3], to value-based decisions [9–15]. A conceptually simple model, introduced many decades ago in the behavioral literature [7,16–19] has been able to account very well for the observation across all the above decision-making domains. As a result, this model, known as the 'evidence accumulation' or 'evidence integration' model, has become widely adopted as a succinct yet powerful behavioral-level description of core decision-making processes.

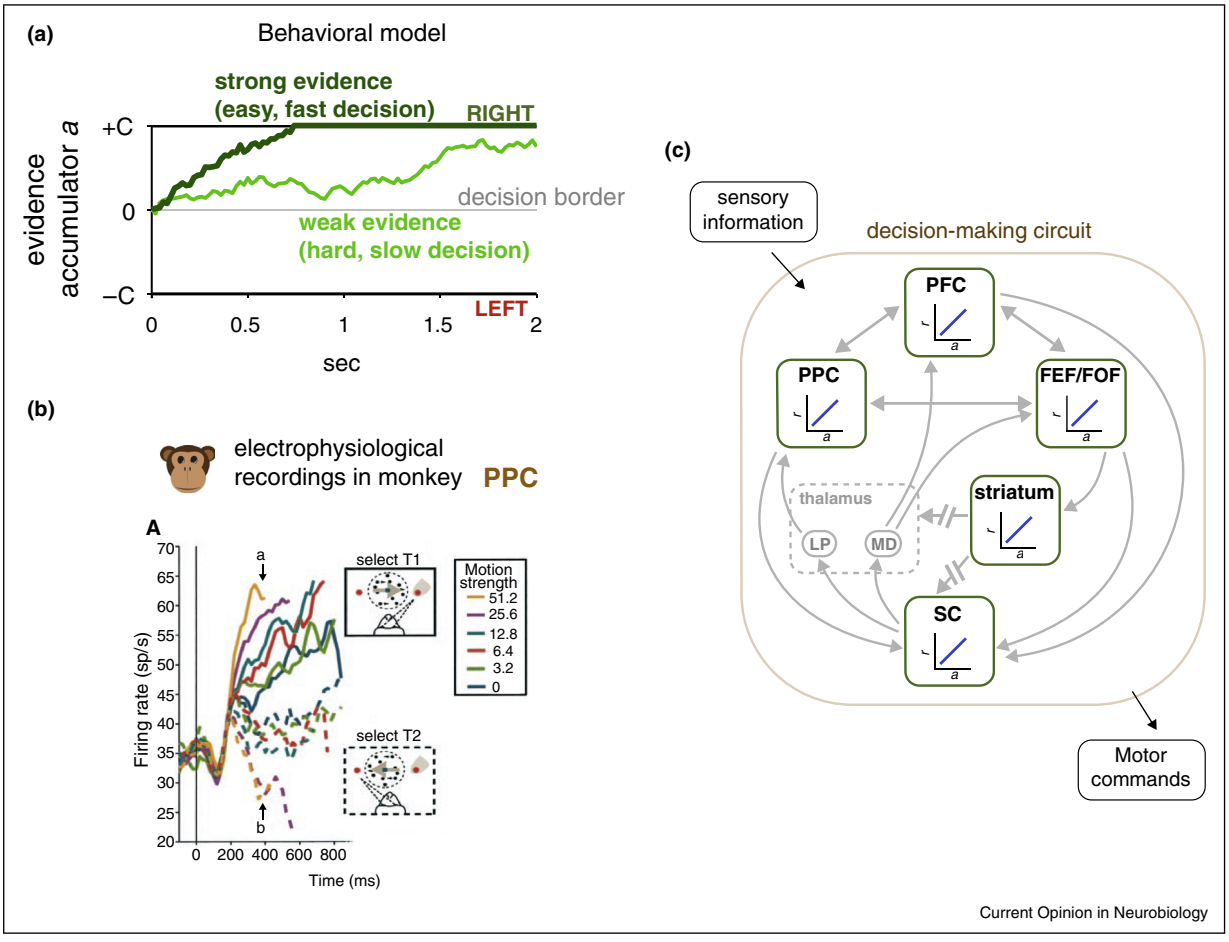
The central idea of the model is that as a subject is forming a decision, evidence for or against different possible choices is gradually accumulating in the subject's mind; the final value of this accumulated evidence then drives the decision itself — for example, committing to a particular choice by asking whether the accumulated evidence lies to one side or another of a reference value which we will label as the 'decision boundary' (see Figure 1a). In this model, when the evidence is strong, the accumulator's value quickly diverges away from the decision boundary, and it rapidly becomes easy to say on which side of the decision boundary it is. Whereas when the evidence is weak, the value of the evidence accumulator meanders away from the decision boundary only very gradually, leading to slower, more difficult decisions.

Here we will first briefly describe studies with non-human primates into the neural basis of the evidence accumulator. Our main focus will then be on more recent work using rodents, proposed as a complementary model system with which to unravel the mechanistic circuit dynamics underlying the phenomenon. We limit ourselves to two-alternative decisions (for multi-alternative decisions, see [20]), and will not address work in humans (see [21]).

Seminal studies in non-human primates

Starting in 1996, Michael Shadlen, William Newsome and colleagues (in addition to related parallel work from Jeffrey Schall's group [22]), began a series of highly influential electrophysiological experiments that suggested a connection between neural responses and evidence accumulation. Using monkeys trained to perform a visual perceptual decision-making task in which the experimenters could titrate each trial's difficulty ('random dot motion discrimination' (RDM) task; [23,24]), Shadlen and Newsome found that during the process of decision formation, neurons in the lateral intraparietal (LIP) subregion of posterior parietal cortex (PPC) had firing rates that appeared to ramp up in time. Critically, when averaged across difficult trials, firing rates ramped slowly; but when averaged across easy trials, firing rates ramped much more sharply — precisely as expected of the evidence accumulator ([25–27]; Figure 1b). This was the first time anyone had observed a signal *inside the brain* that matched

Figure 1



Evidence accumulator models and associated circuits. **(a)** Schematic of evidence accumulation process, here illustrated for a case when the subject must decide between orienting left or right. As the decision process unfolds, noisy evidence favoring one choice (RIGHT) adds to the accumulator while evidence favoring the other choice (LEFT) subtracts from the accumulator. The sign of the accumulated evidence when the subject is asked to report their decision dictates the resulting decision choice. Trials with strong evidence that more consistently favors one choice over the other result in steeper slopes on average, and the accumulator will soon be far away from the decision boundary, so easy decisions can be made quickly. Weaker, less consistent evidence will result in meandering trajectories with shallower slopes on average, and even after lengthy accumulation periods, the accumulator may not be far from the decision boundary, leading to slow, more error-prone decisions. In tasks in which the subject determines the duration of the decision process, known as 'reaction time tasks,' the subject commits to a decision when the evidence reaches a bound (+C or −C in the figure); the reaction time is determined by when the bound is reached, and the decision choice is given by which bound was reached. **(b)** Average neural responses from monkey PPC (area LIP) during the period of decision formation in the random dot motion discrimination task [27]. After a delay, responses exhibit ramping response profiles with slopes that depend on stimulus strength. Stronger motion leads to sharper slopes and weaker motion to shallower slopes. This corresponds to the average trends predicted by the evidence accumulator model. **(c)** Diagram of interconnected brain regions that have been demonstrated to exhibit responses profiles correlated with accumulating evidence. These areas thus serve as candidates to be involved in the evidence accumulation process.

what had been predicted for many years by the widespread accumulator model. Their seminal finding led to the proposal that there may be a 1-to-1 relationship between PPC firing rates and the value of the evidence accumulator.

Work in several laboratories (e.g. [28]) has uncovered similar firing rate patterns in multiple brain regions, most prominently in the frontal eye fields (FEF) [4,29,30,31••], but also in other regions (dorsolateral prefrontal cortex [29]; superior colliculus [32–34]; and striatum [35]; Figure 1c). To date, causal perturbation studies of these areas with the primate RDM task have been limited, with only three existing published studies, all using only unilateral electrical microstimulation. Gold and Shadlen used microstimulation in the FEF to conclude that 'developing oculomotor commands may reflect the formation of the monkey's direction judgement,' but made no conclusions about the causal role of the FEF itself [36,37]. In the striatum, Ding and Gold found mixed