Journal of Physiology - Paris 109 (2015) 27–37

Contents lists available at ScienceDirect

Journal of Physiology - Paris

journal homepage: www.elsevier.com/locate/jphysparis

Review Paper

The neural processes underlying perceptual decision making in humans: Recent progress and future directions

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ARTICLE INFO

Article history:
Available online 7 September 2014

Keywords:
Perceptual decision making
Evidence accumulation
Noninvasive recording
Neurophysiology
Event-related potential
Functional imaging
Cognitive model

ABSTRACT

In the last two decades, animal neurophysiology research has made great strides towards explaining how the brain can enable adaptive action in the face of noisy sensory information. In particular, this work has identified neural signals that perform the role of a 'decision variable' which integrates sensory information in favor of a particular outcome up to an action-triggering threshold, consistent with long-standing predictions from mathematical psychology. This has provoked an intensive search for similar neural processes at work in the human brain. In this paper we review the progress that has been made in tracing the dynamics of perceptual decision formation in humans using functional imaging and electrophysiology. We highlight some of the limitations that non-invasive recording techniques place on our ability to make definitive judgments regarding the role that specific signals play in decision making. Finally, we provide an overview of our own work in this area which has focussed on two perceptual tasks – intensity change detection and motion discrimination – performed under continuous-monitoring conditions, and highlight the insights gained thus far. We show that through simple paradigm design features such as avoiding sudden intensity transients at evidence onset, a neural instantiation of the theoretical decision variable can be directly traced in the form of a centro-parietal positivity (CPP) in the standard event-related potential (ERP). We recapitulate evidence for the domain-general nature of the CPP process, being divorced from the sensory and motor requirements of the task, and re-plot data of both tasks highlighting this aspect as well as its relationship to decision outcome and reaction time. We discuss the implications of these findings for mechanistically principled research on normal and abnormal decision making in humans.

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http://dx.doi.org/10.1016/j.jphysparis.2014.08.003
0928-4257/

1. Introduction

Exposing the mechanisms underpinning simple sensorimotor transformations is critical to our understanding of how information is processed by the brain in general, including at higher cognitive levels (Shadlen and Kiani, 2013). Simple perceptual decisions can generally be broken down into three main processing stages: sensory encoding, decision formation and motor execution (Sternberg, 1969). The intermediate, and arguably most enigmatic, stage of decision formation has seen a significant escalation in interest recently, owing to a line of monkey neurophysiology studies (Gold and Shadlen, 2007) that has provided strong empirical support for a powerful theoretical framework based on sequential sampling (Smith and Ratcliff, 2004). The core principle of sequential sampling models is that a 'decision variable' builds with the integrated evidence in favor of a particular outcome and triggers action upon reaching a threshold (Link and Heath, 1975; Smith and Ratcliff, 2004; Usher and McClelland, 2001). This framework is appealing because, over and above signal detection theory (Green and Swets, 1966), it describes a neural computation through which adaptive actions can be selected on the basis of sensory information that, at any one moment in time, may be unreliable or weak. Moreover, it can comprehensively explain reaction time as well as decision outcome probabilities on a variety of different cognitive tasks (Ratcliff and McKoon, 2008). With this theoretical framework as a strong guide, signals exhibiting build-to-threshold dynamics have been found in several areas of the monkey brain, including parietal (e.g. Roitman and Shadlen, 2002; Hanks et al., 2006), frontal (Hanes and Schall, 1996; Kim and Shadlen, 1999) and subcortical (Ratcliff et al., 2007; Ding and Gold, 2010) oculomotor areas. This work has paved the way for a broad program of mechanistically principled research into how neural decision signals are constructed and are adapted to account for changing environmental contingencies (e.g. prior information, value, speed pressure) and internal brain states (e.g. sensory noise, attention). These investigations span multiple species, including monkeys (Gold and Shadlen, 2007; Shadlen and Kiani, 2013), rodents (Carandini and Churchland, 2013) and humans (Heekeren et al., 2008), and employ a variety of techniques.

2. Neural decision signals: defining properties

One of the major goals of decision making research has been to identify and dissociate "sensory evidence" and "decision variable" signals (Gold and Shadlen, 2007). These signals represent two fundamental ingredients of a powerful theoretical framework for understanding the organization of decision making systems in the brain. Each has critical characteristics by which it can be strictly identified. At the sensory level, any given stimulus will elicit a range of sensory signals of which several may be irrelevant to the task at hand. The key defining characteristic that distinguishes a *bona fide* sensory evidence signal from other sensory activity is that it forms the input to the decision process (i.e. the evidence accumulator). Co-variation of a signal with a relevant physical stimulus variable (e.g. contrast, pitch, resemblance to a face), while clearly a necessary condition, is not by itself sufficient to definitively identify it as the input to the decision process; the signal must further be shown to systematically influence reaction time and/or choice independent from physical stimulus factors. This criterion has been successfully met by signals isolated in non-human primate neurophysiology work. For example, when monkeys perform a motion discrimination task, the firing rates of direction-tuned neurons in the middle temporal area (MT) exhibit significant levels of "choice probability," i.e. they significantly predict a monkey's direction decisions, even when there is physically no net motion in any particular direction (Britten et al., 1996; Parker and Newsome, 1998). Perhaps most compellingly, microstimulation near sensory neurons tuned to one of the two alternative directions induces a systematic bias in a monkey's perceptual reports in that very direction (e.g. Salzman et al., 1990).

Identifying a decision variable signal is equally challenging because in theory, the decision variable represents the temporal integral of the evidence and should therefore be highly correlated with the evidence itself. This makes sense logically for the chain of processing stages forging a decision, but means that signals representing the momentary encoding versus the temporally-extended accumulation of sensory evidence can be difficult to disentangle, especially when using neural measurements that lack fine-grained temporal resolution. Through direct recordings in monkeys, scientists have been able to isolate neuronal firing-rate signals that exhibit the two cardinal properties that distinguish a decision variable signal from sensory evidence: (1) a rate of buildup – as opposed to momentary level – that scales with evidence strength and (2) the triggering of action upon reaching a stereotyped threshold level or bound (e.g. Roitman and Shadlen, 2002; Huk and Shadlen, 2005; Churchland et al., 2008). While much of the initial progress in establishing the neural dynamics underpinning decision formation has been achieved through direct recordings in animals, this work has sparked a considerable effort to probe decision making in the human brain, which we review next.

3. Non-invasive assays of decision making in humans

A look over the decision neuroscience literature from the last two decades provides an excellent illustration of the necessity for and benefits of reciprocal interaction between studies of human and animal subjects. Direct recordings in animals have enabled the characterization of neural signal dynamics underpinning perceptual decision making at a level of detail that is impossible with non-invasive recording techniques. This intracranial work has strongly influenced and guided investigations in humans, as predictions for noninvasive signals can be derived from the aggregate behavior of neuronal populations involved in decision formation (Heekeren et al., 2008), even when diverse response dynamics are seen on the individual neuron level (Meister et al., 2013). At the same time, noninvasive assays are informative in their own unique ways; the global view of brain function that is offered by electroencephalography (EEG), magnetoencephalography (MEG) and functional magnetic resonance imaging (fMRI) makes it possible to study decision making at a systems level, to simultaneously probe distinct levels of the sensorimotor hierarchy, and to examine interactions with other systems that play a supporting role, such as neuromodulatory and attention systems (e.g. de Gee et al., 2014; Cheadle et al., 2014; Kelly and O'Connell, 2013). More practically, studying decision making in humans is important because its neural underpinnings may differ between humans and over-trained animals, because more elaborate decision making behaviors and environmental contingencies can be examined more feasibly in humans, and because in general, the advances made in primate neurophysiology and theoretical neuroscience need to be bridged to the basic study and diagnosis of psychiatric and neurological disorders.

Human neurophysiological research on perceptual decision making actually began in the 1960s, even before sequential sampling models gained a wide foothold in the community. The event-related potential (ERP) technique in particular, which offers high temporal resolution, was recognized as holding promise in isolating distinct processing stages intervening between stimulus and response, and disentangling their individual contributions to reaction time (RT; Woodworth, 1938; Hillyard and Kutas, 1983).