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Review Paper

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

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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.

Contents

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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).

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One prominent component of the sensory-evoked ERP, the centro-parietal 'P300' or 'P3', was specifically linked with making decisions: it was found to be evoked exclusively by task-relevant events requiring decisions (Sutton et al., 1965; Hillyard et al., 1971; Rohrbaugh et al., 1974); it was larger for a given sensory stimulus when detected than when missed (Hillyard et al., 1971; Parasuraman and Beatty, 1980); and its timing varied closely with RT (Ritter et al., 1972; Kutas et al., 1977; McCarthy and Donchin, 1981). These characteristics are in fact consistent with the theoretical decision variable from a bounded accumulation process. However, a direct connection was not made with the sequential sampling theories of decision making that were surfacing in mathematical psychology at that time (e.g. Link and Heath, 1975; Ratcliff, 1978), and thus the dynamical properties central to the function of a decision variable, such as evidence-dependent buildup rate and a threshold-crossing relationship with reaction time, went unexplored.

3.1. Functional imaging-based approaches

The more recent resurgence of interest in decision making in humans has occurred alongside major methodological advances. Most notably, functional magnetic resonance imaging (fMRI) approaches have been developed, which afford the ability to localize the discrete brain structures involved in decision making with millimeter-level precision. fMRI provides a systems-level vantage point over whole networks of active areas, and in this respect can be seen to have a significant advantage over single-unit recording techniques. Given their generality in human cognition, such mapping of decision making processes is important to understanding the functional organization of the brain more generally.

The initial fMRI studies that were based within the bounded evidence-accumulation framework conducted simple contrasts across stimulus categories in event-related designs (Josephs et al., 1997) in order to narrow in on structures representing the evidence, as distinct from those involved in decision formation (e.g. Heekeren et al., 2004; Binder et al., 2004; Pleger et al., 2006). Activations scaling with discrimination difficulty were seen in sensory areas appropriate to the modality of the discrimination in these studies. However, whether these signals definitively constitute "sensory evidence" is uncertain because an influence on the decision itself – as opposed to its correctness or difficulty – was not demonstrated independently of physical stimulus factors. Other imaging studies, which were primarily concerned with perceptual choice-predictive activity in sensory cortices rather than accumulation dynamics at higher levels, were able to identify true sensory evidence signals according to this stricter definition by examining perceptual error trials. For example, Ress and Heeger (2003) examined simple contrast detection within the framework of elementary signal detection theory, and demonstrated that near threshold, V1, V2 and V3 activation was greater for false alarms than misses, thereby correlating with the perceptual decision reported by the observer while fully opposing the physical reality. Similarly, activations in face-selective ventral occipital cortical areas have been shown to be relatively elevated not just for correctly identified faces compared to incorrectly identified ones, but also for stimuli of distinct categories that were misperceived as faces (Summerfield et al., 2006; McKeeff and Tong, 2007). In line with monkey neurophysiology studies (Britten et al., 1996), Serences and Boynton (2007) showed that perceptual reports of motion direction can be predicted from activation patterns in hMT+, the human homologue of area MT, even for stimuli containing no net motion in any particular direction, again representing a true sensory evidence signal that predicts perception independently of the physical evidence itself. The latter study is particularly significant for the current discussion, as it replicated previous work (Kamitani and Tong, 2006) in showing that a much wider set of visual areas, including V1, V2, V3, V3a, V4 and the intraparietal sulcus as well as hMT+, individually achieve robust classification accuracies in multi-voxel pattern analyses (MVPA) discriminating motion direction. Despite encoding significant motion information for physically strong stimuli, none of these areas could classify perceived direction in ambiguous displays at anywhere near the level achieved with unambiguous motion, except for area hMT+. This highlights the importance of distinguishing decoding operations from encoding in the definition of sensory evidence – not all neural signals that appear to vary as a function of task-relevant stimulus features are necessarily read out by downstream systems controlling behavior (see also Williams et al., 2007).

Decision variable signals have been sought even more intensively, but are yet harder to identify using standard fMRI designs, as low temporal resolution precludes the direct observation of critical dynamic aspects such as threshold-crossing effects. In lieu of direct analyses of dynamics, comparisons across conditions based on qualitative predictions regarding the decision process have been conducted. Early fMRI studies relied on the assumption that the amplitude of the BOLD response in a decision making region should be greater for easy compared to hard discriminations because more evidence is available on such trials (Heekeren et al., 2004; 2006; Pleger et al., 2006). These studies have particularly highlighted the role of the left dorsolateral prefrontal cortex (DLPFC) which, unlike the effector-specific signals observed in monkeys, is activated independent of the particular sensory or motor requirements of the task (Heekeren et al., 2004; 2006;; Pleger et al., 2006). However, the assumption that stronger evidence – and hence steeper accumulation – leads to greater BOLD activation is of uncertain validity, and the exact opposite prediction has been employed by other investigators (Liu and Pleskac, 2011). The correct prediction critically depends on what the decision variable does once it has reached threshold – if it remains elevated after reaching threshold until some fixed post-stimulus time, then it would spend longer at a high level for earlier threshold crossings and hence BOLD activation would be higher for stronger evidence. In contrast, if the decision variable falls immediately to baseline upon reaching threshold, then stronger evidence would lead to shorter-duration ramps to threshold and hence smaller BOLD activation (Liu and Pleskac, 2011). While LIP activity is known to exhibit sustained elevation under conditions involving a delay before responding (Shadlen and Newsome, 2001), the generality of this effect for decision variable signals housed outside of LIP is unknown. Furthermore, it has been noted that even if decision regions do activate in proportion with evidence strength, similar relationships to task difficulty can be expected of other, non-decision regions, such as those falling within the default-mode network (Tosoni et al., 2008; Ho et al., 2009; Filimon et al., 2013). Consequently, a number of studies have applied alternative or additional criteria for classifying decision regions, such as earlier onset latency for stronger evidence (Ho et al., 2009), greater activation for correct versus incorrect trials or covariation with reaction time (Pleger et al., 2006; Binder et al., 2004), or significant effective connectivity with putative evidence regions (Filimon et al., 2013). Another innovative approach, designed to compensate for the poor temporal resolution of MRI, has been to use tasks in which the sensory evidence is gradually strengthened as the trial progresses and then to identify regions whose BOLD response scales with the evidence time course (Ploran et al., 2007; Ivanoff et al., 2008). As perhaps could be expected given such a variety of methodological approaches, there are broad inconsistencies in the literature in the number and locations of areas implicated in decision formation. For example, several of the more recent studies have failed to observe any significant decision-relevant activation in the left

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DLPFC region initially identified by Heekeren et al. (2004), instead implicating areas such as the posterior parietal cortex (Tosoni et al., 2008), intraparietal sulcus (Kayser et al., 2010; Liu and Pleskac, 2011), inferior frontal gyrus/sulcus (Filimon et al., 2013; Liu and Pleskac, 2011) and insula (Ho et al., 2009; Liu and Pleskac, 2011). A conclusive mapping of regions engaged in forging a decision variable would require empirical validation of the unique BOLD signal properties that they should exhibit. Methodological challenges notwithstanding, these fMRI studies have made a valuable contribution to the field by highlighting candidate structures whose role in decision making is now being investigated using complementary techniques (e.g. Philiastides et al., 2011).

A number of studies have sought to localize regions that specifically contribute to top-down, strategic adjustments of decision making behavior such as those required to emphasize speed versus accuracy (Bogacz et al., 2010). Three closely timed studies (van Veen et al., 2008; Ivanoff et al., 2008; Forstmann et al., 2008) used cues to encourage subjects to be variously fast or accurate in the upcoming perceptual decisions, and event-related analyses revealed several regions exhibiting greater sustained activation under speed emphasis than accuracy. While the studies differed in the number of regions thus localized, most areas were associated with motor planning or preparation, and changes in the pre-supplementary motor area (pre-SMA) and striatum were common to all three. The sustained nature of the observed activation changes has been interpreted as evidence that decision variables may shift to higher starting points rather than terminate at lower thresholds (Bogacz et al., 2010). However, caution is warranted given that slow, sustained changes are naturally more detectable than transient ones in the temporally broad BOLD response, and because build-to-threshold dynamics cannot be directly observed in these areas, it is difficult to say whether changes result from adjustment of a decision formation process as opposed to the encoding of abstract task instructions or more general task-set differences such as alertness. The general problem of evoked signal duration being confounded with signal amplitude in the BOLD response has been noted as a particular concern in studying the speed–accuracy tradeoff (van Veen et al., 2008; Bogacz et al., 2010). Again, direct observations in monkeys are critical to guiding the concrete predictions needed for fMRI experimental designs, and at the same time, the comprehensive mapping afforded by fMRI should guide the choice of homologous areas to record from in monkeys. Establishing, for example, what happens to decision variable signals in association and premotor areas after completion of the decision will be critical for constructing the appropropriate predictions and contrasts, and as we review later, this kind of information can potentially come from human electrophysiology as well.

A powerful general approach that is increasing in popularity is to leverage principled quantitative models, such as the drift diffusion model (DDM; Ratcliff, 1978; Bogacz et al., 2006) for two-choice discrimination decisions, to constrain the search for neural activations that play a role in the setting of important parameters for accumulation, such as the boundary, starting-point or drift rate (Forstmann et al., 2011; Turner et al., 2013). Such approaches not only borrow from the theoretical decision signal characterizations of mathematical psychology, but also employ quantitative cognitive modeling procedures developed in that field (e.g. Ratcliff and Tuerlinckx, 2002; Wagenmakers et al., 2007; Vandekerckhove and Tuerlinckx, 2008; Donkin et al., 2009). Forstmann et al. (2008) employed a straightforward version of this approach, whereby a linear ballistic accumulator (LBA; Brown and Heathcote, 2008) model was fit to behavioral data on an individual basis to measure changes in response caution (measured as the ratio between response criterion and the highest possible start point) in a condition emphasizing speed compared to one emphasizing accuracy, and this change in fitted criterion parameter correlated negatively across subjects with the difference in activation in the striatum and pre-SMA. Importantly, these correlations were only detectable for the LBA parameter of response caution and not for simpler measures of reaction time or accuracy considered individually, attesting to the value of the model-based approach.

Model-based analyses are now being extended further such that multiple decision model parameters are estimated on a single-trial basis from behavioral data and subsequently used to form regressors in general linear models of the fMRI data (van Maanen et al., 2011), an approach that was championed by investigators of reinforcement learning and value-based action selection (e.g. Daw et al., 2006; O'Doherty et al., 2007). These analysis approaches have become increasingly integrative in their handling of behavioral versus neural modeling, with recent hierarchical Bayesian modeling approaches allowing neural measures to be incorporated directly into trial-by-trial behavioral fitting procedures (Turner et al., 2013; Wiecki et al., 2013).

3.2. EEG/MEG-based approaches

Recent human neurophysiology (EEG and MEG) work has also been conducted within the same decision making framework based on sequential sampling of sensory evidence, and similar analytic approaches have also been applied. Despite having high temporal resolution, EEG- or MEG-based approaches are limited by the fact that temporally overlapping sensory, decision and motor signals – task-relevant or otherwise – overlap through global summation on the scalp and are thus hard to disentangle. This is especially problematic in traditional ERP/EEG paradigms that use discrete, sudden-onset stimuli since the time between sensation and action is short and includes non-task-specific sensory onset responses. Whereas blind source separation algorithms represent a popular solution in many areas of cognitive neuroscience (Makeig et al., 2004), the well-defined mechanistic framework of perceptual decision making has enabled the use of more task-specific, functionally-grounded data transformations. This is very well exemplified in a line of EEG studies centered on face-car discrimination, which employed a machine learning approach to derive a spatiotemporal profile of activity that strongly discriminates between the relevant stimulus categories (face versus car; Philiastides and Sajda, 2006) and between different difficulty levels (manipulated by image phase coherence; Philiastides et al., 2006). These authors identified both an early (170 ms) and a late (300 ms) ERP component that scaled monotonically between the extremes of an undistorted face and an undistorted car (Philiastides and Sajda, 2006). Although neither component was shown to predict decision outcome independently of physical evidence as required by the stricter definition of sensory evidence, it was later shown that trial bins with higher late component amplitudes within each stimulus coherence level were associated with higher drift rates in a diffusion model fit (Ratcliff et al., 2009). The latter study thus interpreted the late component as "postsensory processing that ultimately provides the decision-relevant evidence entering the diffusion decision process."

As in neuroimaging work, a variety of other model-based approaches have been applied to EEG/MEG data to identify neuroelectric/neuromagnetic components that relate to stages of the decision process. Van Vugt et al. (2012) extracted EEG signals bearing the theoretical dynamical signatures of the decision variable by constructing a set of stimulus-locked and response-locked regressors in accordance with decision model predictions and applying a general linear model in a similar way to event-related fMRI designs. This analysis revealed spectral changes primarily in the theta band as matching the dynamics of evidence accumulation. A similar regressor-based analysis was employed by Wyart et al.

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(2012), but rather than using stereotyped temporal profiles (e.g. ramp), these authors used regressors that distinguished between incremental decision updating and basic sensory changes in visual orientation across series of eight successive stimuli, in a task where subjects judged whether cardinal versus diagonal orientations dominated. They found that the weighting of each discrete stimulus in the series as an input to the accumulation process fluctuated in accordance with delta-band (1–3 Hz) oscillations. This is an important observation because it implies the presence of additional neural processes that influence the read-out of sensory evidence by the decision variable. Yet another model-based approach is exemplified in the study of Hunt et al. (2012), who used a biophysically plausible attractor network model of the emergence of a choice among competing action alternatives (Wang, 2002) to identify and localize source-reconstructed MEG activity that actively forges the choice, as distinct from that which merely correlates with relative value. Though the choices in that study were ultimately based on an integrated quantity of expected value (incorporating visually indicated magnitude and probability), the model process generalizes to, and indeed was originally rooted in, decisions based on simple sensations.

3.3. Models and observations

The foregoing discussion illustrates a growing trend to closely anchor noninvasive data analyses to principled quantitative models, an approach that is paramount to eventually achieving a concrete, mechanistic understanding of the processes by which decisions are forged in the brain. This being said, it is important to note that the usual caveats that have been continually acknowledged in computational/theoretical neuroscience more generally (Dayan and Abbott, 2001; O'Doherty et al., 2007; Heathcote et al., in press), apply to model-based cognitive neuroscience. Because model-based analytic approaches rely on specific models and their underlying assumptions, their validity is tied to that of the models, and establishing the latter is a nuanced enterprise. Even within the general class of sequential sampling models, a variety of mechanisms have been proposed, and there is an ongoing tension between parsimony (for economy of parameters) and comprehensiveness (for widely-achieved goodness of fit) among these alternatives (e.g. Reddi and Carpenter, 2000; Ratcliff, 2001, 2008; Wagenmakers et al., 2004; Palmer et al., 2005; Wagenmakers et al., 2007; Brown and Heathcote, 2008; Donkin et al., 2011; Heathcote and Hayes, 2012). A cognitive model's validity is typically assessed based on its ability to provide a good quantitative account of behavioral data, but how unique the model is in providing as good a fit, and whether a model captures the reality of underlying neural processes or remains an abstraction divorced from this ground-truth, can be hard to clarify. In most model-based analyses of noninvasive neural data, the data are essentially viewed through the lens of the model, and strong assumptions are implicitly imposed on the form, functional dependence and/or interrelationship of the signals under study. Therefore, in contrast to animal neurophysiology, the signals themselves are not directly observed in humans, and many core predictions of decision making models are *assumed* rather than *tested*.

An illustrative example is provided in recent work on the speed–accuracy tradeoff (SAT). The DDM and other sequential sampling models give elegant accounts of the SAT in terms of strategic shifting of decision boundaries (Ratcliff and Rouder, 1998; Ratcliff and McKoon, 2008; mathematically equivalent to shifting baselines in race models, see Bogacz et al., 2010). Modeling studies indeed show that allowing only boundary separation, or an equivalent distance-to-threshold parameter, to vary across speed/accuracy emphasis conditions provides a good quantitative fit to behavioral data (e.g. Ratcliff and McKoon, 2008) and this principle has been exploited in model-based fMRI analyses that estimate correlations between brain activations and model parameters (Forstmann et al., 2008; van Maanen et al., 2011). However, it remains to be determined what such correlations actually mean – as O'Reilly and Mars (2011) have pointed out, the "latent" or abstract parameters of cognitive models are invoked with the primary purpose of accounting for behavior, but it is not necessarily the case that they reflect quantities or mechanisms that are directly implemented in the brain. For example, a region whose activation co-varies with a threshold parameter may relate to the implementation of threshold adjustments in several possible ways: by simply encoding it as an abstract task-relevant quantity; by imposing a modulatory influence directly on the decision process; by itself forging the decision variable and in doing so expressing the adjustment; or through an indirect relationship involving supporting processes that may happen to be either coextensive in time or correlated in amplitude with the decision process.

Recently, intracranial single-unit recordings have provided a more direct picture by examining how decision variable-encoding neurons in the frontal eye fields (FEF) respond to varying levels of speed pressure (Heitz and Schall, 2012). Contrary to the simple boundary-lowering predicted by models like the DDM, the authors observed that the level of neural activity reached at the decision termination time actually *increased* with speed pressure, directly opposite to the prediction of decreased decision threshold from sequential sampling models. Moreover, these effects were accompanied by several additional adjustments, including a steeper build-up rate of FEF neurons as well as lower-level changes in the encoding of sensory evidence. Another recent study based on recordings in LIP (Hanks et al., 2014) found evidence for not only a shift in baseline activity but also a distinct evidence-independent urgency signal that plays out dynamically during the decision process. These findings serve to underline the fact that while behavioral data can be comprehensively explained with minimalistic computations, the neural implementation is likely far more complex. They also highlight the fact that there is a growing bolus of electrophysiological evidence that can and should be exploited in fMRI analyses. At the same time, the findings in monkey studies raise the important question of how parameter adjustments might be made in humans who can receive explicit instructions on speed–accuracy requirements through verbal instruction, and whose decision process is adjusted in immediate response to changing contingencies or instructions, rather than shaped through extended conditioning.

The foregoing paints a somewhat uneasy picture of the situation concerning models, model-based analyses and direct observations. The very nature of noninvasive recording modalities prevents direct observation in paradigms that invoke decisions of the level of complexity associated with naturalistic human behavior – which is one of the core motivating factors in doing human research. But it is commonly overlooked that the degree to which processes can be directly observed noninvasively does depend inversely on the complexity of the task, and that certain very simple decisions, though perhaps not the most interesting in their own right, can through their simplicity provide the means to observe and test the elementary processes that form the core for a diverse range of more complex behaviors.

4. Direct tracing of sensory evidence and decision signals

The success of studies using the random dot motion task of Newsome and colleagues (Newsome et al., 1989; Britten et al., 1992; Shadlen et al., 1996) is a strong example of how very simple, computationally tractable perceptual decisions can form a powerful test-bed for investigating the root mechanisms of decision

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formation. Recent MEG work using versions of this task has demonstrated that it is possible to observe build-up activity associated with the formation of a decision relatively directly in humans, by tracking the temporal evolution of noninvasively recorded signals related to motor preparation (Donner et al., 2009; De Lange et al., 2013). In a ground-breaking study of motion detection decisions (Donner et al., 2009), it was found that the lateralization of beta-band (12–36 Hz) activity over central scalp reflected the emerging motor plan associated with a decision, and that it correlated with the temporal integral of motion-induced gamma-band activity localized to region MT on the basis of MRI (Donner et al., 2009). De Lange et al. (2013) further demonstrated that pre-stimulus fluctuations in the hemispheric lateralization of choice-selective beta-band activity, whether spontaneous or evoked by informative cues, predicted an observer's eventual decision. The latter study also showed that the rate of buildup of the beta lateralization signal scaled with motion coherence when plotted as a function of time leading up to the response.

In two recent studies, we used simple paradigm innovations to enable parallel tracking of freely-evolving sensory evidence, decision variable and motor preparation signals (O'Connell et al., 2012a; Kelly and O'Connell, 2013). Our general strategy to enable such signal isolation was first and foremost to eliminate non-specific sensory responses typically elicited by sudden stimulus onsets, by avoiding discontinuous intensity transients and instead aligning evidence onset with a gradual or seamless transition in a continuously ongoing stimulus. Second, following the logic of previous studies (Donner et al., 2009; De Lange et al., 2013; Forstmann et al., 2008; Rinkenauer et al., 2004), we chose unimanual button presses as the decision-reporting actions so that we could exploit the well-characterized human neurophysiological signatures of lateralized motor preparation reflected in the lateralized readiness potential (LRP; see e.g. Coles et al., 1988) and spectral power changes in the mu (8–12 Hz) and beta bands (approximately 15–30 Hz; e.g. Pfurtscheller and Lopes da silva, 1999).

We applied these design principles in both a gradual-change detection task (O'Connell et al., 2012a) and a two-alternative motion discrimination task (Kelly and O'Connell, 2013). In both cases, we asked our subjects to perform the tasks under continuous monitoring conditions, where seamless transitions into target periods containing evidence occurred intermittently once every 5–13 s. This feature promotes long and variable reaction times by increasing the influence of trial-to-trial fluctuations, and thus enhances the ability to investigate the fluctuations themselves (Kelly and O'Connell, 2013), as well as to definitively identify signals as sensory evidence and decision variable signals simply by dividing trials by reaction time and decision outcome.

4.1. Continuous monitoring for gradual intensity changes

In the original version of our gradual-change detection task, subjects continuously monitored an annular visual pattern that flickered steadily at a fixed, relatively high frequency (20 or 21.25 Hz), indicating detection of intermittent, gradual, linear drops in contrast via a right-hand button press (Fig. 1; O'Connell et al., 2012a). The steady-state visual evoked potential (SSVEP; e.g. Di Russo et al., 2007) elicited by the flicker should represent the "sensory evidence" signal in this case, in that its amplitude directly reflects contrast representation, the very variable that the decision is based upon. Despite physically identical targets, we observed systematic differences in SSVEP amplitude during targets as a function of reaction time, thus identifying the SSVEP as a sensory evidence signal in the strictest sense described above (see Section 2).

With the sensory evidence thus spectrally contained in a discrete frequency, and motor preparation effectively cordoned-off in lateralized motor-specific signatures, we were able to finely trace the evolution of a relatively protracted decision process from onset to commitment in the event-related potential. Specifically, a centro-parietal positive potential ("CPP") exhibited a gradual build-up with a timecourse consistent with the temporal integral of the evidence – i.e., well-described by a quadratic function as compared to the linear evidence – and which built to an action-triggering criterion in a way that precisely predicts the timing and accuracy of decision reports (see Fig. 1a). As discussed above, these are the critical properties that identify a decision variable signal. Underlining its function as a dynamically-evolving accumulator process, we were able to induce systematic perturbations in its temporal trajectory mid-flight during decision formation by briefly interrupting the linearly decreasing trajectory of contrast during the target (Fig. 1b). Furthermore, when several target types of varying detectability were interleaved, subjects sometimes reported detection when in fact there was no physical evidence present, and these false alarms were associated with a significant build-up of the CPP (O'Connell et al., 2012a).

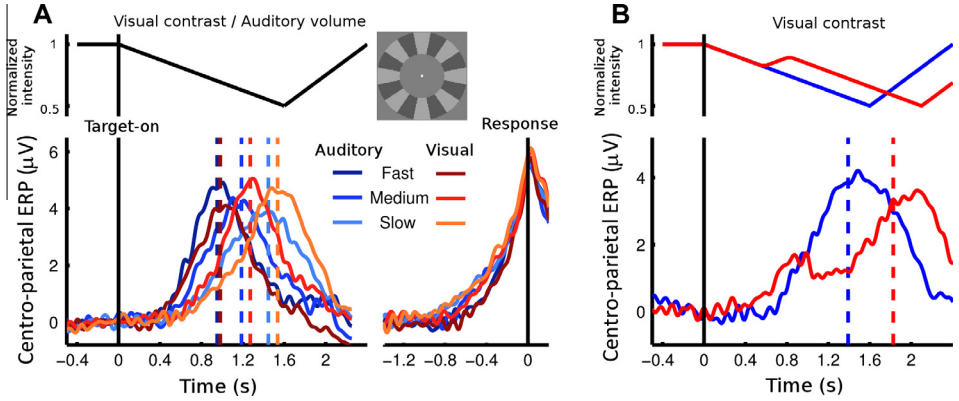

Fig. 1. The centro-parietal positivity ("CPP") exhibits the behavior of a theoretical "decision variable" in dynamically tracing cumulative visual and auditory evidence and in predicting reaction time for detection of gradual targets. (A) During continuous viewing of a flickering pattern (red) or alternatively, continuous listening to an auditory sinusoidally-modulated sound (blue), a target, defined by a fixed, slow linear intensity reduction to an eventual obviously decreased level at 1.6 s, was intermittently introduced. For both visual and auditory tasks, trials were sorted by RT and divided into three equal-sized bins. The centro-parietal ERP exhibited a gradual, accelerating buildup (CPP) consistent with integration of the physical intensity change reflected in the sensory evidence signal, evident in both the stimulus-aligned (left) and response aligned (right) waveforms. Vertical dashed lines denote mean RT. (B) CPP in response to gradually increasing contrast-change evidence with and without a mid-flight perturbation. These dynamics were also evident in motor-specific left-hemisphere beta-band activity, but whereas the pattern persisted for the CPP under conditions of covert counting, the beta-band pattern was abolished in this case (latter effect not shown; see O'Connell et al., 2012a, from which these data have been re-plotted).

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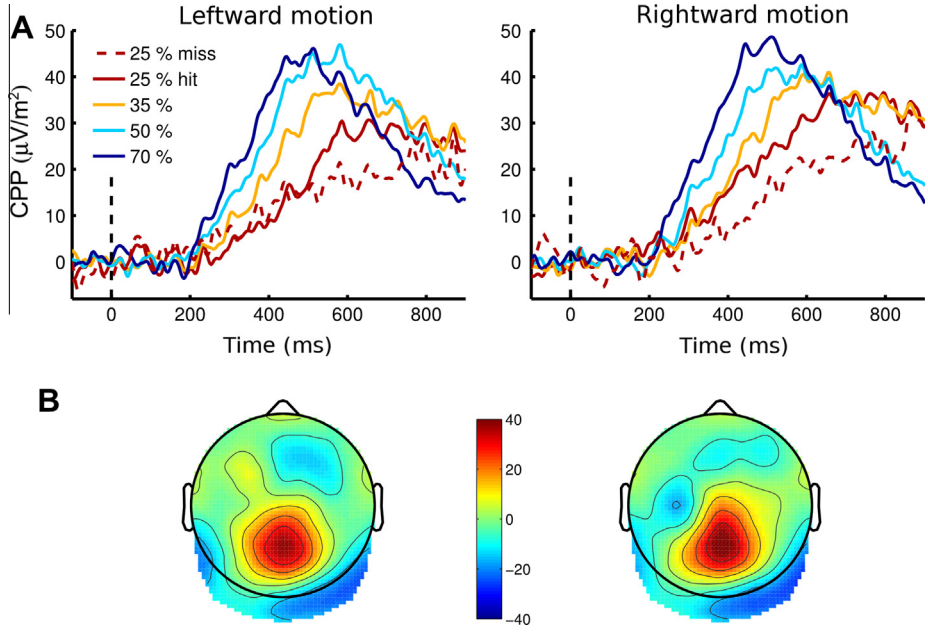

Fig. 2. (A) Stimulus-locked CPP waveforms in response to coherent motion targets toward the left and right, exhibiting a gradual build-up whose rate is proportional to the strength of coherent motion and which is invariant to the direction of motion. Misses (dashed) are clearly characterized by a failure of the decision signal to reach criterion. There were sufficient trials only for analysis of misses at the lowest coherence. When viewed in a response-aligned average, the CPP terminates at a stereotyped level, as it does in the contrast change task (Fig. 1; waveforms not shown here, but see Kelly and O'Connell, 2013). (B) Scalp topographies of the event-related amplitude between −150 and −50 ms relative to the manual response. The CPP clearly has an almost identical topography for the two directions of motion, although it is possible to see the smaller-amplitude lateralized readiness potential more frontally, shifting in laterality depending on the motion direction and hence hand of responding. Replotted from the data of Kelly and O'Connell (2013).

4.2. Continuous monitoring for coherent motion

In a follow-up study we employed a continuous-monitoring variant of the prototypical random dot motion discrimination task (RDM; Newsome et al., 1989; Britten et al., 1992), in which observers watch a set of randomly moving dots within a circular aperture, a subset of which coherently moves in one of two directions forming the choice alternatives. A key advantage of this paradigm is that sensory evidence can be finely manipulated by varying the percentage of coherently moving dots (i.e. "coherence"). In order to achieve the same isolation of decision formation processes as in the contrast-change detection task, we eliminated transient sensory evoked potentials at evidence onset by introducing coherent motion as a seamless transition from a preceding period of incoherent motion, rather than a sudden onset of coherently moving dots. In this two-alternative task, subjects had to press a button with their left hand upon detection of leftward motion, and with the right hand for rightward motion, allowing readout of the direction of the decision in lateralized motor preparation signals. Again, the CPP exhibited a build-to-threshold relationship to motion discrimination decisions and crucially, its build-up rate increased as a function of sensory evidence strength (see Fig. 2), thus establishing another key defining property of the theoretical 'decision variable' of sequential sampling models. Further, as we had previously shown for contrast change detection (O'Connell et al., 2012a), missed targets that occurred reasonably often for the lowest coherence level in this task were associated with a lower stimulus-locked CPP amplitude (Fig. 2). This is consistent with the idea that targets are missed when the decision variable fails to build all the way to threshold.

4.3. Separate supramodal and effector-selective decision variable signals

An intriguing aspect of the CPP is that it exhibits similar evidence-dependent buildup dynamics irrespective of the motor requirements (button press versus counting), sensory evidence modality (e.g. audition or vision, see Fig. 1a) or target defining feature (e.g. upward or downward intensity changes, and pitch changes; and intensity change versus dot-motion discrimination; see O'Connell et al., 2012a; Kelly and O'Connell, 2013). In other words, it is fully supramodal. Empirical observations of build-to-threshold decision signals in monkeys have been limited to premotor structures, which initially led to a view that decisions are made within an intentional framework where sensory evidence is directly incorporated into an evolving motor plan (Gold and Shadlen, 2007). How such a framework could support our general ability to forge decisions in a flexible way, abstracted from the specific parameters of sensation and action, has drawn an increasing theoretical focus, with many accounts positing that sensory evidence can be represented at multiple levels of abstraction in the brain (Cisek, 2012; Dehaene and Sigman, 2012; Freedman and Assad, 2011; Bennur and Gold, 2011; Shadlen et al., 2008). Indeed, fMRI studies have already highlighted specific brain regions that are activated in a domain-general fashion during decision making (Heekeren et al., 2008; Ho et al., 2009; Liu and Pleskac, 2011). The CPP opens up the possibility to trace the finer dynamics of such domain-general decision processes, and to access their critical parameters (e.g. buildup rate and threshold) via simple neural signal measurements.

Alongside the CPP we found that hand movement-selective motor preparation signals also exhibited many of the dynamical properties of the theoretical decision variable. Specifically, left-hemisphere beta-band activity decreased alongside the building CPP during the intensity-change detection tasks, reaching a threshold level immediately prior to response execution. Unsurprisingly for an effector-selective preparatory process, the beta decrease was abolished when there was no requirement to manually respond. In our study of the RDM task, we also investigated the relative timing of evidence accumulation dynamics in effector-selective and supramodal decision signals. In place of beta-band activity we analyzed the lateralized readiness potential (LRP) since it

provides a read-out of limb selective motor preparation with identical temporal resolution to the CPP (Gratton et al., 1988; Eimer, 1998). We found that the buildup of accrued evidence at the abstract level significantly leads the buildup at the motor preparatory level (Kelly and O'Connell, 2013). These data offer a unique insight into the temporal sequence of information processing during decision formation, and suggest that decision variables residing in effector-specific motor circuits such as those generating beta changes and the LRP may be driven by a more central accumulation process. A continuous flow of information from decision to motor regions likely serves to enable faster sensorimotor transformations, as well as the adjustment or countermanding of ongoing action (Selen et al., 2012).

Unlike the effector-specific motor preparation signals, the CPP did not differ as a function of the direction of motion in the RDM task. It rose over time with a positive polarity regardless of the direction, and also showed the same scalp topography (see left and right panels of Fig. 2). We hypothesize that supramodal accumulator neurons that favor the distinct alternatives co-inhabit the same region(s) in the brain and race against each other in the way posited in accumulator models (Usher and McClelland, 2001; Brown and Heathcote, 2008) and observed in LIP neurons (Roitman and Shadlen, 2002). Though distinct populations are activated for each of the two decision alternatives, their projection on the scalp would be identical because of this intermingled co-habitation. Other possible explanations include that the CPP may reflect the encoding of confidence rather than the decision variable itself (Urai and Pfeffer, 2014). Thus, even the underlying cortical signals generating the scalp-measured CPP may not hold any content regarding the impending decision outcome. However, the threshold-crossing effect demonstrated in both the contrast-change and dot motion tasks, where the CPP reaches a stereotyped level for all evidence strengths and reaction time bins, would seem inconsistent with this proposition since it is known that observers do not tend to be equally confident of their decisions across speeds and difficulty levels (Yeung and Summerfield, 2012). Further work will be required to establish the intracranial origins of the CPP, perhaps through the integration of simultaneous EEG and fMRI recordings (see e.g., Philiastides and Sajda, 2007; O'Connell et al., 2012b) or the combination of microelectrode recordings and electrocorticography (see e.g. Whittingstall and Logothetis, 2009; Cohen et al., 2009).

Taken together these data point the way to further human brain experiments that can probe multiple levels of the sensorimotor and decision architecture simultaneously, enabling interrelationships among signals at these levels to be examined on a millisecond time-scale. The ability to parse sensory, decision and motor stages also holds great promise for clinical research. Decision making deficits are seen in a range of psychiatric and neurological disorders. Given that the deficits may manifest in very similar ways (i.e. slower and more variable response times, diminished accuracy), a key challenge for researchers is to identify disease-specific aetiological pathways by pinpointing the precise information processing stages and computations that are impacted by specific disorders.

5. The functional significance of the P300

An exciting additional aspect of the CPP is that it bears many similarities to the classic P300 (alternatively labeled 'P3' or 'P3b') component of the human ERP, including polarity, temporal coincidence with response execution and contingency on task relevance, and we showed that its topography and amplitude correlates with that of the P300 across subjects (O'Connell et al., 2012a). The P300 has been the most intensively studied EEG signal across five decades, attracting huge interest due to its apparent ubiquity across cognitive paradigms and its sensitivity to a diverse range of clinical conditions including Alzheimer's disease, dementia, Parkinson's disease, depression, attention-deficit hyperactivity disorder, obsessive compulsive disorder and narcolepsy (Polich and Criado, 2006; Rossini et al., 2007). Although early studies established the sensitivity of P300 amplitude to factors such as decision confidence (Squires et al., 1975) and peak latency to stimulus evaluation time (Magliero et al., 1984), the mechanistic nature of these links remained unclear and in the intervening years, a consensus regarding the P300's precise functional role in decision making has not been reached. Current theories disagree even on the question of whether the P300 emerges before or after the decision process has been completed (Donchin and Coles, 1988; Kok, 2001; Nieuwenhuis et al., 2005; Verleger et al., 2005; Polich, 2007). This uncertainty likely stems partly from the signal overlap problem in typical discrete ERP paradigms, as well as the classical view of each component as the culmination of a unitary event (peak measurement) rather than as a dynamic process that actively evolves from onset to peak.

If the CPP can be equated with the P300, then our findings point to a mechanistic account of the P300's role in decision formation. Such a view also calls for a re-consideration of past findings pertaining to the P300 and should guide future approaches to its measurement. Traditionally the P300 has been measured in terms of the latency and amplitude of its peak in a stimulus-aligned average waveform. However, given that a decision variable signal should under most circumstances be more tightly locked to the response than to stimulus onset, stimulus-aligned peak amplitude and latency will increase in inverse proportion to reaction time variability. In other words, as can be seen in Fig. 2, differences between conditions or groups in stimulus-aligned P300 amplitude can arise purely from differences in reaction time dispersion in the absence of any change in threshold. This is an issue that only a few studies have directly addressed (e.g. Poli et al., 2010; Saville et al., 2011; Verleger et al., 2013). In addition, the problem of signal overlap in discrete stimulus designs means that amplitude or latency differences cannot be unambiguously attributed to changes in the P300 process. Adopting paradigms that involve gradual evidence changes may offer a solution to this problem for future studies. Aside from potentially revealing the functional significance of the P300, our results also highlight that measuring it solely in terms of its stimulus-aligned peak amplitude and latency would provide only part of the picture. We have shown that the P300 signal bears a number of additional variable parameters that directly impact on the timing and accuracy of decisions: (A) the latency of its onset which marks the start of evidence accumulation, (B) its rate of rise, indexing the rate of evidence accumulation, (C) its amplitude at response execution, indexing the decision threshold and (D) its peak latency on a single trial, indexing the time at which that threshold is reached. The fact that each of these parameters can be directly related to performance means that this recasting of the P300 can contribute to a new and more precise understanding of how clinical brain disorders and experimental manipulations impact on decision making in humans.

The decision variable account of the P300 could also be informative in the ongoing investigation of the role of neuromodulatory systems such as the Locus Coeruleus-Norepinephrine (LC-NE) system in decision making. It has long been noted that the antecedent conditions for eliciting phasic LC responses are highly similar to those modulating the amplitude of two positive ERP components occurring at approximately 300 ms following discrete stimuli (e.g. Pineda et al., 1989; reviewed in Nieuwenhuis et al., 2005). One of these components, the centro-parietal "P3b" equates to the P300 we refer to above and thus may also equate to the CPP. The other, "P3a," is a more frontally distributed, earlier component

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elicited by salient oddball stimuli that are not necessarily task-relevant but are novel. Although the CPP decision process bears a clear relationship to only one of these two processes (it is absent for irrelevant stimuli; O'Connell et al., 2012a), this link poses interesting questions regarding the involvement of the LC-NE system, whose importance for general attentional focus on tasks is well known, in decision formation.

6. Summary and conclusions

In this review we have sought to highlight the many challenges that researchers face when attempting to untangle the neural mechanisms underpinning human decision making using non-invasive recording techniques. A walk through the recent literature reveals that through the combination of careful paradigm design and the integration of data from multiple imaging modalities, substantial progress has already been made to overcome many of these challenges and to close long-standing gaps between human and animal research. Mathematical models have provided a vital foundation for the field by generating hypotheses regarding the mechanisms that are necessary for optimal decision making and the parameter adjustments that are required to deal with changing external and internal contingencies. However, much work is yet required to establish the extent to which these models accurately represent the underlying neural dynamics. A key lesson from recent animal and human neurophysiology is that although behavioral data can be comprehensively explained with minimalistic computations including, for example, a single "decision variable" process, the practical implementation may be more complex and distributed, with multiple neural signals interacting within and across brain areas to play the role of the theoretical decision variable, its inputs, its outputs and its modulators (Gold and Shadlen, 2007; Ding and Gold, 2013). This underlines the value in reciprocal interactions between cognitive modeling and neural activity measurements, as recently pointed out by some authors (Forstmann et al., 2011). Neural waveforms measured in the context of paradigms such as we have described can guide more specific, neurally based specification of integrator mechanisms and evidence time-courses compared to what is possible when dealing with the theoretical abstractions implicit in behavioral model fitting procedures. The signals and techniques are now in place to enable experiments that comprehensively probe the human brain's perceptual decision making network and that illuminate the precise site and nature of influence of major factors such as prior information, speed/accuracy emphasis, value, attention, and practice.

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