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Dissociable contributions of ventromedial prefrontal and posterior parietal cortex to value-guided choice

Gerhard Jocham [a,g,*], P. Michael Furlong [d], Inga L. Kröger [e], Martin C. Kahn [f], Laurence T. Hunt [a,b], Tim E.J. Behrens [a,c]

[a] FMRIB Centre, University of Oxford, John Radcliffe Hospital, Oxford OX3 9DU, United Kingdom
[b] Department of Experimental Psychology, University of Oxford, South Parks Road, Oxford OX1 3UD, United Kingdom
[c] Wellcome Trust Centre for Neuroimaging, University College London, 12 Queen Square, London WC1N 3BG, United Kingdom
[d] The Robotics Institute, Carnegie Mellon University, Pittsburgh, PA, USA
[e] Department of Systems Neuroscience, University of Hamburg, UKE, Martinistrasse 52, 20246 Hamburg, Germany
[f] Graduate Programme in Neuroscience, University of Oxford, United Kingdom
[g] Center for Behavioral Brain Sciences, Otto-von-Guericke-Universität Magdeburg, Germany

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ABSTRACT

Two long-standing traditions have highlighted cortical decision mechanisms in the parietal and prefrontal cortices of primates, but it has not been clear how these processes differ, or when each cortical region may influence behaviour. Recent data from ventromedial prefrontal cortex (vmPFC) and posterior parietal cortex (PPC) have suggested one possible axis on which the two decision processes might be delineated. Fast decisions may be resolved primarily by parietal mechanisms, whereas decisions made without time pressure may rely on prefrontal mechanisms. Here, we report direct evidence for such dissociation. During decisions under time pressure, a value comparison process was evident in PPC, but not in vmPFC. Value-related activity was still found in vmPFC under time pressure. However, vmPFC represented overall input value rather than compared output value. In contrast, when decisions were made without time pressure, vmPFC transitioned to encode a value comparison while value-related parameters were entirely absent from PPC. Furthermore, under time pressure, decision performance was primarily governed by PPC, while it was dominated by vmPFC at longer decision times. These data demonstrate that parallel cortical mechanisms may resolve the same choices in differing circumstances, and offer an explanation of the diverse neural signals reported in vmPFC and PPC during value-guided choice.

Introduction

The ability to decide on appropriate courses of action amongst competing alternatives is central to adaptive success. Whilst neural signals representing the potential value of different courses of action are widespread throughout the brain (Cai et al., 2011; Dorris and Glimcher, 2004; Hernandez et al., 2002; Kable and Glimcher, 2007; Kim et al., 2008; Padoa-Schioppa and Assad, 2006; Platt and Glimcher, 1999; Serences, 2008; Sugrue et al., 2004; Wunderlich et al., 2009), two cortical regions, the ventromedial prefrontal cortex (vmPFC) and the posterior parietal cortex (PPC), have attracted particular attention for their likely roles in the selection process. Evidence for central roles in choice for these two brain regions comes from two independent and largely separate traditions. Extensive single unit recordings in the lateral intraparietal sulcus (LIP) of macaque monkeys during saccadic decisions have revealed activity that integrates sensory information to solve ambiguous sensory decisions (Gold and Shadlen, 2007); that tracks the relative value of competing actions (Platt and Glimcher, 1999; Sugrue et al., 2004) and the Bayesian evidence for different value-guided choices (Yang and Shadlen, 2007). By contrast, vmPFC's importance for value-guided choice has been established largely in the human literature. Patients with lesions to vmPFC become indecisive about even trivial decisions (Barrash et al., 2000); choices that *are* made are often made poorly (Bechara et al., 1994, 2000) and according to unusual strategies (Fellows, 2006). In human imaging experiments, neural activity in this region often contains value representations consistent with a decision (Basten et al., 2010; Boorman et al., 2009; Jocham et al., 2012; Kolling et al., 2012); and the balance of excitatory and inhibitory neurotransmitters in vmPFC impacts both on this neural signature and on behaviour in a fashion consistent with competitive models of choice (Jocham et al., 2012).

These findings suggest analogous roles in choice for PPC and vmPFC. Such similarities are further strengthened by the finding

* Corresponding author at: Center for Behavioral Brain Sciences, Faculty of Economics, Otto-von-Guericke-Universität Magdeburg, Gebäude 22, Universitätsplatz 2, D-39106 Magdeburg, Germany.
E-mail address: jocham@ovgu.de (G. Jocham).

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that vmPFC lesions also impair decision-making in macaques (Noonan et al., 2010); and that, in humans, the same signatures of categorical choice can be seen in magnetoencephalography (MEG) signals from these two cortical regions (Hunt et al., 2012). The existence of two such similar neural signatures in two brain regions so distinct in both their anatomical location and connectivity pattern (Öngür and Price, 2000; Sack, 2009) raises the question of what distinguishes neural processing in vmPFC and PPC, and in what situations either region might come to the fore to influence decision-making. One intriguing possibility comes from the aforementioned MEG study. Here vmPFC involvement was strongest in trials early in the experiment, and stronger in trials that required integration across choice dimensions. In both cases, more vmPFC activity was associated with longer reaction times, possibly as a result of more deliberate and less automated choices. These data provided a suggestive hint that vmPFC and PPC might be capable of performing the same computations, but do so under differing circumstances. We therefore designed an experiment to explicitly test the hypothesis that vmPFC and PPC would perform decision-related computations in choice situations without or with time pressure, respectively.

Methods

Participants

31 healthy participants (11 females, aged 18 to 35 years) participated in the experiment. Written informed consent was obtained prior to the study. All experimental procedures were approved by the Central University Research Ethics Committee. Volunteers were paid between £ 20 and £ 30, depending on task performance. Three volunteers had to be excluded because of extreme head motion, leaving a final sample of 28 subjects (10 females).

Behavioural task

During fMRI, subjects performed a task that involved repeatedly choosing between a left and right option to obtain monetary reward (Fig. 1). Each option consisted of one rectangular horizontal bar and a percentage written underneath it. The bar width represented the reward magnitude and the percentage specified the probability with which this reward would be delivered. Reward probabilities were independent, such that on any given trial, either one of the two options, both or none of them could be rewarded. The task thus required subjects to integrate reward probability and magnitude into a value estimate to make the best possible choice. Subjects made choices by pressing a left or right button with the index or middle finger, respectively, of the right hand. When a reward was available for the chosen option, an amount proportional to the reward magnitude was added to a gray progress bar at the bottom of the screen. Subjects' goal was to move the progress bar across a gold target line to the right to win £ 2, at which time the progress war was reset to zero and subjects started over again. On a subset of trials, which we refer to as 'no brainer' trials, both the magnitude and probability of one option were higher than on the alternative option. The reward schedule was designed such that the correlation between chosen and unchosen value was as low as possible, thus allowing for largely separate portions of variance to be explained by those factors. The mean correlation of these two factors was $r = 0.18$.

In the *short* condition, options were presented on screen and subjects had to make a choice within one second. In the *middle* condition, options were presented on screen and subject could make a decision whenever they wanted, without any response deadline. In the *long* condition, options were first presented for a fixed viewing period of 3 s before a question mark appeared, from which time subjects had 1 s to respond. If subjects failed to respond within the 1 s response window in the *short* and *long* conditions, the following message appeared on the screen: "Please respond faster!". After a response was made, the selected option was highlighted by a grey frame around the chosen option, which remained on screen for 3.5 to 6 s until the outcome was revealed for 1 s. The outcome (reward or non-reward) was indicated by the bars turning green or red, respectively. On every trial, the outcomes of both options were revealed. The outcome was followed by an intertrial interval (blank screen) of 3.5 to 6 s. Short, middle and long trials were administered in alternating blocks of 10 trials. After 10 trials of one condition were completed, a precue with the message short, middle or long appeared on screen for 1 s. 70 trials of each condition were completed. Thus, trials in the three conditions were identical, except for the timing manipulation, which lead to different decision times (median decision time = 793, 1180 and 3366 ms, for the *short*, *middle* and *long* conditions, respectively).

In each condition, we searched for two possible neural signals, which are argued to represent different aspects of valuation and choice. An fMRI signal that correlates with the sum of available values is argued to represent a stimulus valuation stage that comes before a decision process (Hare et al., 2009, 2011a, 2011b; Hunt et al., 2012; Plassmann et al., 2007, 2010). By contrast, an fMRI signal that correlates with the difference between chosen and unchosen values is argued to reflect the outcome of the decision process itself (Basten et al., 2010; Boorman et al., 2009; FitzGerald et al., 2009; Hunt et al., 2012; Jocham et al., 2012; Kolling et al., 2012), as it requires the computation of which option has been chosen and which option remains unchosen. Indeed, if decision-related activity is imaged at millisecond resolution, a clear transition from value sum to value difference correlations can be seen as the decision unfolds (Cai et al., 2011; Hunt et al., 2012). Network models of decision making imply that this transition occurs because over time, the representation of the unchosen option changes. Thus, while initially, network activity correlates positively with the value of both options, it is the unchosen option which becomes suppressed, thereby resulting in a positive correlation between unchosen value and network activity. Our tests therefore focus on the effects of unchosen value.

Here, by simply manipulating the amount of time that subjects spend making decisions, we are able to change the types of value coding that can be seen in vmPFC and PPC. We find that under time pressure vmPFC encoded value sum, whereas PPC encoded value difference. Without time pressure, vmPFC encoded value difference, whereas coding of value-related parameters completely disappeared from PPC.

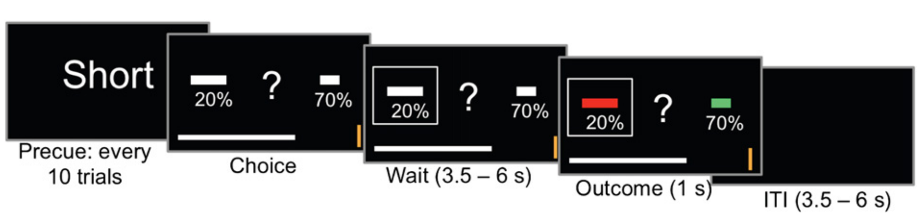

Fig. 1. Task schematic. Short, middle and long trials were grouped in alternating blocks of 10 trials. Every 10 trials, a precue signalled the condition for the next 10 trials. In the short and middle condition, subjects could respond as soon as the options were onscreen. In the long condition, there was a fixed viewing period of 3 s before the central question mark appeared, prompting them to respond within 1 s.