Journal Club

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Dorsolateral–Ventromedial Prefrontal Cortex Interactions during Value-Guided Choice: A Function of Context or Difficulty?

Ana Carolina Saraiva* and Louise Marshall*

Sobell Department of Motor Neuroscience and Movement Disorders, UCL Institute of Neurology, Queen Square, London, WC1N 3BG, United Kingdom

Review of Rudorf and Hare

Adaptation to complex, dynamic environments requires flexible, context-dependent valuation and choice. How does the brain manipulate value computations to maximize reward according to environmental context? Contemporary research into value-based decision-making has centered on regions of the prefrontal cortex, thought to constitute part of a frontostriatal decision network. One area of intense focus in human neuroscience is the ventromedial prefrontal cortex (vmPFC). fMRI studies have repeatedly demonstrated that human vmPFC activity correlates with the subjective reward value of a chosen option (Walton et al., 2015). Moreover, human lesion evidence suggests that the region plays a crucial role in value maximization during choice (Camille et al., 2011). While single-unit vmPFC studies are scarce, macaque vmPFC neurons have recently been shown to signal the value of a chosen offer during a two-option gambling task (Strait et al., 2014).

Because the environment is volatile, value computations must be modified according to the context in which we find ourselves. For instance, the relative values of an umbrella and a pair of sunglasses will vary according to whether there is rain or sunshine outside. The dorsolateral prefrontal cortex (dlPFC), linked to cognitive flexibility and working memory, has been proposed to play this modulatory role (Lee and Seo, 2007). Lesions to dlPFC impair the ability to identify context-dependent associations between sets of stimuli (Milner, 1963). Furthermore, transient disruption of human dlPFC induced by theta-burst transcranial magnetic stimulation hinders forward planning and flexible, outcome-specific decision behavior (Smittenaar et al., 2013).

Given their respective roles, it seems likely that the dlPFC and vmPFC interact during value-guided decision-making. Indeed, interactions between the two areas have previously been detected during value-based choice in the presence of conflicting desires requiring self-regulation, for instance in dieters assigning higher relative value to healthy rather than tasty food options (Hare et al., 2009). Extending earlier work, Rudorf and Hare recently published a study in *The Journal of Neuroscience* suggesting that dlPFC–vmPFC interactions in fact offer a general mechanism for context-dependent valuation that is nonspecific to self-regulation of conflicting reward types (Rudorf and Hare, 2014).

To assess this, the authors conducted an fMRI experiment in which human subjects made binary choices between stimuli whose values varied as a function of context. Importantly, all stimuli had three attributes (shape, pattern, and color) and the task goal remained constant (to maximize monetary reward by selecting the higher-value stimulus). In Default blocks (60% of trials), values were determined solely by each stimulus' shape, specifically, the number of sides; both color and pattern could be ignored. In Bonus blocks (40% of trials), a cue indicated that either the color or pattern of the stimuli increased or decreased the default values conveyed by the shape. Since monetary payment was the only reward type available, the task eliminated reward conflict while maintaining a requirement for context-dependent valuation.

Results showed that activity in the vmPFC, among other frontostriatal areas, reflected the value difference between chosen and unchosen stimuli in Bonus and Default trials, suggesting subjective value is encoded by vmPFC. A network of frontoparietal areas including dlPFC demonstrated context sensitivity, with increased activation occurring during choices in Bonus compared with Default trials. The dlPFC therefore appears well placed to modulate value encoding by vmPFC in a context-dependent manner. Indeed, connectivity analyses revealed that the presentation of cues signaling a switch from Default to Bonus blocks increased the correlation between dlPFC and vmPFC activity. Moreover, analysis of interindividual variability revealed that dlPFC–vmPFC interactions during Bonus choices correlated positively with encoding of relative bonus values in vmPFC. Based on this and previous work (Hare et al., 2009), Rudorf and Hare (2014) speculate that the dlPFC sig-

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*A.C.S. and L.M. contributed equally to this work.

Correspondence should be addressed to Ana C. Saraiva, 33 Queen Square, UCL Institute of Neurology, London, WC1N 3BG, UK. E-mail: a.saraiva@ucl.ac.uk.

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nals a context switch to the vmPFC, and initiates a reweighting of stimulus values necessary for context-dependent value maximization, even in situations that lack conflict between competing reward types.

The study's key findings rely on differences between the Default and Bonus blocks, the latter requiring a context-dependent reweighting of stimulus values. However, because Bonus trials necessitated an additional computation that the Default trials lacked, they were inherently more difficult and resource-demanding than Default trials. This was reflected by slower reaction times (RTs) and fewer optimal choices during Bonus trials. The authors considered this and conducted additional control analyses using RT and accuracy as covariates. Although results were not altered, switches in difficulty between Default and Bonus trials may still have contributed to the observed changes in brain activity. For instance, if RT is a nonlinear function of difficulty, residual differences between Default and Bonus conditions could remain, despite including RT as a covariate. Future work incorporating a detailed assessment of RT distributions in the Default and Bonus trials might offer clarification.

Four additional extensions of this work may help to disentangle dlPFC's role in signaling a change in context and/or difficulty to the vmPFC. First, it would be useful to assess whether there were any changes in brain activity and/or dlPFC–vmPFC correlations during switches between the two Bonus contexts (pattern and color). In this situation, a context-dependent change in the reweighting rule must be detected to successfully determine the stimulus with the highest value, but importantly, the degree of difficulty between these two contexts is identical. Given dlPFC's role in working memory and mental manipulation (Lee and Seo, 2007), the region may signal a change in upcoming difficulty and prepare for a more resource-demanding process. Indeed, Rudorf and Hare (2014) suggest that engagement of dlPFC may reflect the recruitment of attentional resources during Bonus trials.

Second, difficulty could be manipulated further by including a third Bonus context in which shape, color, and pattern determine stimulus value. This would maintain a requirement for context-dependent value reweighting and introduce an additional computation compared with the other Bonus contexts. Equivalent increases in dlPFC–vmPFC connectivity following switches from Default to any one of the three Bonus contexts would add weight to the interpretation that dlPFC–vmPFC interactions underlie context-dependent stimulus valuation. However, increased dlPFC–vmPFC correlations during switches from Default to Bonus contexts requiring two computations compared with switches to Bonus contexts requiring one computation would indicate a difficulty effect.

Third, to further clarify whether dlPFC signals a difficulty-induced requirement for additional resources, one could examine whether RTs during Bonus trials correlated with dlPFC activity levels, and whether dlPFC–vmPFC connectivity was greater for trials on which RTs were slowest.

Fourth, the task could be modified to allow context switches within as well as between blocks. In the present study, the exact bonus associations remained constant within subjects. By randomizing the assignment of attributes and value during Bonus blocks such that no specific attribute is associated with a specific value, comparisons between trials within a particular context could be made. For example, within-context switches could be introduced by using the color blue to convey a reweighting of $+3$ in one trial and -1 in another.

Although alternative interpretations exist, Rudorf and Hare (2014) offer a key contribution to our understanding of brain interactions during context-dependent, value-based choices. Using psychophysiological interaction (PPI) analyses, it was possible to assess a statistical dependence between dlPFC and vmPFC activity while subjects performed the behavioral task. Although useful for whole-brain connectivity analysis, PPI is limited in that it can only inform us that the dlPFC and vmPFC showed functional coupling; it offers no clarification about the directionality or causality of their interactions. An alternative method, model-based dynamic causal modeling (DCM), holds the capacity to identify any effective dlPFC–vmPFC connectivity. Application of a DCM analysis to the neuroimaging data could offer a fruitful extension, establishing whether such functional interactions are indeed indicative of context-dependent modulation of vmPFC by dlPFC.

Interestingly, the current work supports recent findings that value comparison may exist not only between options, but also between attributes (Hunt et al., 2014). In Default trials, subjects were required to consider the value of just one attribute (shape), whereas in Bonus trials they had to consider two attributes (shape + color or shape + pattern) and integrate their value. Thus, comparison between attributes may have occurred in Bonus trials, requiring additional prefrontal resources and possibly adding to difficulty. Intriguingly, the contribution of shape value to vmPFC value encoding was reduced during Bonus trials, presumably due to the increased relative contribution of the relevant bonus attribute. This was supported by a decreased correlation between the relative shape value and BOLD signal during Bonus trials. Furthermore, the posterior parietal cortex, dorsal anterior cingulate cortex, and anterior insula were activated during encoding of additional stimulus attributes. Speculatively, these areas may interact with others, such as the intraparietal sulcus (Hunt et al., 2014), to perform between-attribute comparison and determine which attribute(s) are more relevant in making a value-based decision.

In summary, Rudorf and Hare (2014) provide additional evidence for proposed functions of vmPFC and dlPFC during decision-making. Crucially, they demonstrate that interactions between the dlPFC and vmPFC play a role in context-dependent, value-based choice, even in the absence of conflicting reward outcomes. It is likely that the dlPFC signals upcoming change to the vmPFC, but whether this signal relates to a change in context and/or a resource-demanding increase in difficulty remains uncertain. Further work considering conflict-independent switches between contexts of both equivalent and varying difficulty, and evaluating dlPFC–vmPFC effective connectivity during value-based choice behavior, will elucidate the roles played by these prefrontal areas more precisely.

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