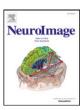
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## The influence of contextual reward statistics on risk preference

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#### ABSTRACT

Decision theories mandate that organisms should adjust their behaviour in the light of the contextual reward statistics. We tested this notion using a gambling choice task involving distinct contexts with different reward distributions. The best fitting model of subjects' behaviour indicated that the subjective values of options depended on several factors, including a baseline gambling propensity, a gambling preference dependent on reward amount, and a contextual reward adaptation factor. Combining this behavioural model with simultaneous functional magnetic resonance imaging we probed neural responses in three key regions linked to reward and value, namely ventral tegmental area/substantia nigra (VTA/SN), ventromedial prefrontal cortex (vmPFC) and ventral striatum (VST). We show that activity in the VTA/SN reflected contextual reward statistics to the extent that context affected behaviour, activity in the vmPFC represented a value difference between chosen and unchosen options while VST responses reflected a non-linear mapping between the actual objective rewards and their subjective value. The findings highlight a multifaceted basis for choice behaviour with distinct mappings between components of this behaviour and value sensitive brain regions.

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#### Introduction

Context dramatically affects value-based choice (e.g., Huber et al. 1982; Kahneman and Tversky 1979; Ludvig et al., 2013; Stewart et al. 2003; Tversky and Shafir 1992). A striking example is the so-called framing effect, in which risky options are preferred more when choices are framed in terms of losses rather than gains (Kahneman and Tversky 1979). Though contextual effects have been extensively described, we know little about the mechanisms through which contextual representations arise and contribute to decision making. One possibility is that prevailing contextual reward statistics influence the mapping from objective to subjective values and in this way affect choice. There are two competing hypotheses about how this might occur. One is that the contextual statistics of reward induce a reference point relative to which values are rescaled (Ludvig et al., 2013; Stewart et al. 2003, 2006). This predicts that, for example, the same dish is likely to be evaluated as being worse in a good restaurant than in a bad one. An alternative possibility derives from a Bayesian perspective that proposes objective reward values are integrated with prior subjective value expectations arising from a prevailing contextual reward distribution (Seymour and McClure 2008). Posterior subjective values would be hence estimated in such a way that they increase/decrease in contexts characterized by larger/smaller reward distributions. This makes an opposite prediction that the same dish will be evaluated as being better in a good restaurant than a bad one.

We investigated contextual effects on choice by focusing on decision-making under risk. We designed a paradigm wherein subjects repeatedly chose between a sure amount of money (called the trial monetary amount), that varied trial-by-trial, and a gamble associated with an equal probability of obtaining either double the sure amount or zero (Fig. 1A). The trial outcome was displayed after each choice and one randomly selected outcome was paid out to participants at the end of the experiment. Crucially, trials were arranged in blocks each associated with one of two subtly different gambling contexts involving specific, but partially overlapping, distributions of monetary amounts. A high-value context involved monetary amounts drawn uniformly from £2-£6, and a low-value context involved monetary amounts drawn uniformly from £1-£5. In terms of contextual adaptation, for choices that are objectively equivalent across contexts, the rescaling hypothesis predicts larger subjective values (inferred from choice behaviour) in a low-value context (Ludvig et al., 2013; Stewart et al. 2003, 2006), whereas the Bayesian hypothesis predicts larger subjective values in a high-value context (Seymour and McClure 2008). Note that, since we did not aim to dissociate the effect of average monetary amount and variance of individual gambles on risky choice, we used simplified options in which these covaried perfectly.

A main goal was to investigate the relationship between behavioural and neural contextual adaptation effects. It is well-established that response in dopaminergic ventral tegmental area/substantia nigra (VTA/

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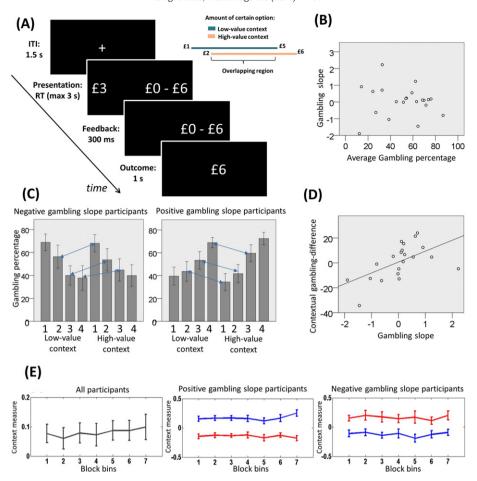


Fig. 1. A: Experimental paradigm. Participants repeatedly made choices between certain gains (on the left in the example) and gambles (on the right in the example) associated with a 50% probability of either double the certain gain or zero. After a choice, the unchosen option disappeared and 300 ms later the trial outcome was shown for 1 s. The intertrial interval (ITI) was 1.5 s. At the end of the experiment, a single randomly chosen outcome was paid out to participants. B: Relationship between average gambling percentage (x-axis) and gambling slope (y-axis). This relationship was not significant (r(21) = -0.06, p = 0.78, non-significant). Note that the gambling slope corresponds to the individual effect (i.e., the slope of a logistic regression parameter) of monetary amount on gambling, thus positive and negative gambling slopes correspond to increased gambling preference with increasing and decreasing amounts, respectively. A distribution of subjects (represented as dots) with positive and negative slopes is evident. C: Gambling percentage for different monetary amounts (grouped in 4 increasing magnitude bins: [1 2 3 4]) for each context (low and high). Participants are split in two groups based on their gambling slope (negative gambling slope: n = 9; positive gambling slope: n = 12). Blue arrows connect equivalent amounts presented in the two contexts. Consistent with a contextual normalization effect, subjects who gambled more with increasing amounts also gambled more when equivalent choices were relatively larger, that is in the low-value context. By contrast, subjects who gambled more with decreasing amounts also gambled more when equivalent choices were relatively smaller, that is in the high-value context. D: Relationship between gambling slope (x-axis) and contextual gambling difference for overlapping amounts (y-axis), corresponding to the gambling percentage in low-value minus high-value context for equal amounts (r(21) = 0.56, p = 0.008). E: Analysis of the evolution of the context effect over time. Blocks are separated into 7 bins. Values labelled as "context measure" represent an index of the context effect (see main text to see how this is obtained). Lines represent average across subjects and error bars represent standard error. The left panel combines all participants and shows that, after bins were aggregated in two sets (without considering the fourth bin), the values of the first three bins were overall not different from the values of the last three bins (t(20) = -1.02; p = 0.319). Also, the value of the first bin was not significantly different from the value of the last bin (t(20) = -0.758; p = 0.457) and was significantly larger than zero (t(20) = 2.46, p = 0.023). These data indicate that a context effect emerged from the very start of a new context presentation and remained stable across the duration of the block. On the middle and right panels, lines represent the risk preference for overlapping choices in the two contexts. Red and blue lines are for high- and low-value context, respectively. Participants are separated into two groups depending on whether they have a positive (middle panel) or negative (right panel) gambling slope.

SN) and ventral striatum (VST) reflect a reward prediction error (RPE) signal (D'Ardenne et al., 2008; Lak et al. 2014; Niv et al. 2012; O'Doherty et al., 2003, 2004; Park et al. 2012; Schultz et al. 1997; Stauffer et al. 2014; Tobler et al. 2005), and evidence indicates that such a RPE signal adapts to contextual reward availability (Louie and Glimcher 2012; Park et al. 2012; Rangel and Clithero 2012; Tobler et al. 2005). However, whether such neural adaptation impacts choice behaviour remains to be tested, and there is controversy surrounding this issue (Louie and Glimcher 2012; Padoa-Schioppa and Rustichini 2014; Rangel and Clithero 2012). We were specifically interested in probing linkages between behavioural and neural response adaptation in VTA/SN and VST. Thus we used functional magnetic resonance imaging (fMRI) to measure neural activity during simultaneous task performance.

We also planned to exploit individual differences in choice preference to investigate the neural mechanisms underlying risky decision-making. Previous observations have shown that the degree of behavioural loss aversion is connected with the individual strength of VST activation for gains compared to losses (Tom et al. 2007), while the degree of behavioural risk preference is connected with a VST response to risky compared to non-risky options associated with equal average amount (Niv et al. 2012). Additionally, it has been reported that the VST response to reward probability follows a non-linear probability weighting function akin to that proposed within Prospect Theory (Hsu et al. 2009). However, whether the VST response to choice options with different levels of reward amount/variance reflects a non-linear subjective value function akin to that predicted by economic theories remains unclear (D'Acremont and Bossaerts 2008; Kahneman and Tversky 1979; Schultz et al. 2008; von Neumann and Morgenstern, 1944). We explored this question by exploiting the variability in participants' risk preference as a function of the monetary amounts presented.

Ventromedial prefrontal cortex (vmPFC; as distinct from the adjacent lateral orbitofrontal cortex which has been the topic of single-cell

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