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The role of reward and reward uncertainty in episodic memory ☆

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ABSTRACT

Declarative memory has been found to be sensitive to reward-related changes in the environment. The reward signal can be broken down into information regarding the expected value of the reward, reward uncertainty and the prediction error. Research has established that high as opposed to low reward values enhance declarative memory. Research in neuroscience suggests that high uncertainty activates the reward system, which could lead to enhanced learning and memory. Here we present the results of four behavioural experiments that examined the role of reward uncertainty in memory, independently from any other theoretically motivated reward-related effects. Participants completed motivated word learning tasks in which we varied the level of reward uncertainty and magnitude. Rewards were dependent upon memory performance in a delayed recognition test. Overall the results suggest that reward uncertainty does not affect episodic memory. Instead, only reward outcome appears to play a major role in modulating episodic memory.

Introduction

The ability to selectively encode and retrieve events is an adaptive feature of episodic memory (Castel, 2007; Nairne, 2014). During motivated learning people are able to prioritise the learning of specific pieces of information to maximise reward. These effects have been shown using a variety of episodic memory tests including free and serial recall, and recognition memory (Adcock, Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli, 2006; Castel, Benjamin, Craik, & Watkins, 2002; Eysenck & Eysenck, 1982; Harley, 1965; Loftus & Wickens, 1970; Madan, Fujiwara, Gerson, & Caplan, 2012; Spaniol, Schain, & Bowen, 2013; Weiner & Walker, 1966). In addition, educators have a particular interest in how rewards promote episodic memory in order to "gamify" the learning environment (Gee, 2003; Howard-Jones, Demetriou, Bogacz, Yoo, & Leonards, 2011; Howard-Jones, Jay, Mason, & Jones, 2016) and there is some evidence that uncertainty of reward may promote learning in classroom-based environments (Howard-Jones & Jay, 2016; Ozcelik, Cagiltay, & Ozcelik, 2013).

The neuroscience of reward processing has guided research on the relationship between reward and memory (Adcock et al., 2006; Shohamy & Adcock, 2010; Wittmann, Dolan, & Düzel, 2011). Single-cell neurophysiology in non-human primates and imaging work in humans strongly suggests that the dopaminergic reward system responds to different components of reward: expected value; outcome or prediction error; and uncertainty of reward (Cromwell & Schultz, 2003; Fiorillo, Tobler, & Schultz, 2003; Hollerman & Schultz, 1998; Schultz, 1998, 2002; Schultz et al., 2008; Tobler, Fiorillo, & Schultz, 2005). The aim of this paper is to examine which aspects of the reward signal promote memory performance in *motivated* learning. In particular, the key question examined here is whether uncertainty about reward has effects on episodic memory. We also assess more generally the role of these different reward components in episodic memory. Across the four experiments presented in this paper, we isolate and assess the contributions of different aspects of reward to episodic memory encoding. The factors of interest are listed in Table 1. As we review in the sections below, these reward components were selected based on previous demonstrations that they are signalled in reward-related brain areas (Cromwell & Schultz, 2003; Fiorillo et al., 2003; Liu, Hairston, Schrier, & Fan, 2011; Preuschoff, Bossaerts, & Quartz, 2006; Schultz, 2010) and/or have been shown to affect reward-related learning (Adcock et al., 2006; Bunzeck, Dayan, Dolan, & Duzel, 2010; Mather & Schoeke, 2011; Wittmann et al., 2011).

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Table 1
Reward-related predictors of memory performance tested across the series of experiments. The last column shows the experiments for which each predictor was tested.

Predictor	Description	Experiment
Expected Value (EV)	*Probability of obtaining a reward multiplied by the reward magnitude*	1
Reward Outcome (O)	*Magnitude of the reward obtained*	2, 3, 4
Prediction Error (PE)	*Expected value of the reward minus the reward outcome*	2, 3, 4
Reward Uncertainty (U)	*A binary variable indicating the presence or absence of uncertainty*	1, 2, 3
	The entropy $-\sum^{O} P_O \log_2 P_O$	4
Surprisal (S)	*The degree to which information has changed after the outcome of an event* $-\log_2(P_O)$ *where* P_O *is the event outcome (reward or no reward)*	4

Dopamine signalling of reward cues, outcomes and uncertainty

Evidence from neuroscience (both single cell recordings in non-human primates and neuroimaging in humans) suggests that the reward system—comprising areas such as the ventral tegmental area (VTA), the ventral striatum, the frontal cortex and amygdala—show several changes in activity in response to rewards and reward-predicting cues (Cromwell & Schultz, 2003; Fiorillo et al., 2003; Paton, Belova, Morrison, & Salzman, 2006; Schultz, 1998, 2002). Dopaminergic neurons in the midbrain exhibit two patterns of firing. The first, known as the phasic bursts, are transient responses to reward cues and outcomes. One view is that this phasic response encodes the reward prediction error: if the reward is smaller than expected the neurons respond below their baseline firing rate, and if it is larger than expected the neurons fire above their baseline rate (Fiorillo et al., 2003; Glimcher, 2011; Hollerman & Schultz, 1998; Schultz, 1998, 2010; Tobler et al., 2005). The second type of signal, tonic firing, refers to sustained activity in response to anticipation and expectancy. This tonic firing has been linked to reward uncertainty (Hsu, Krajbich, Zhao, & Camerer, 2009; Liu et al., 2011; Preuschoff et al., 2006; Preuschoff, Quartz, & Bossaerts, 2008; Tobler et al., 2005; Tobler, O'Doherty, Dolan, & Schultz, 2007). Uncertainty refers to the predictability of the outcome of an event. Whereas expected value refers to a combination of reward magnitude and probability, uncertainty refers to the spread of the reward probability distribution irrespective of the magnitude (Tobler et al., 2007). In the case where there are two possible outcomes (e.g. reward vs. no reward), uncertainty follows uncertainty follows an inverted U-shaped function of probability of reward, so that it maximal at $p = 0.5$. A common measure of uncertainty is entropy. Entropy is calculated as minus the weighted sum of the logarithm of the probabilities of each possible outcome. Unlike variance it is not dependent on the reward magnitude (Preuschoff et al., 2006). An additional information theoretic term we will examine is surprisal. Surprisal refers to the information gained from an event when it occurs, (i.e., the reduction in uncertainty) and is bigger for less probable events: less probable events are more surprising when they do occur. Surprisal differs from signed prediction error as a surprisingly good and surprisingly bad outcome will generate the same surprisal value, but will be associated with different prediction errors (positive vs negative).

While much of the work on reward uncertainty coding has been conducted with non-human animals, separate responses to value and uncertainty have also been observed in humans using fMRI (D'Ardenne, Mcclure, Nystrom, & Cohen, 2008; Glimcher, 2011; Hsu et al., 2009; Liu et al., 2011; Ludvig, Sutton, & Kehoe, 2008; Preuschoff et al., 2006, 2008; Schultz et al., 2008; Tobler et al., 2005, 2007). Using a monetary gambling task Preuschoff et al. (2006) found evidence of neural encoding of expected value and uncertainty in regions including the midbrain and ventral striatum. In this study, and as similarly observed in other studies, the authors find both a linear and quadratic components to the reward signal (Cooper & Knutson, 2008; Dreher, Kohn, & Berman, 2006; Rolls, McCabe, & Redoute, 2008). In summary, there is compelling evidence indicating that expected value and uncertainty are represented by temporally distinct signals in the brain.

As we review next, there is both neurobiological and behavioural evidence that these reward signals linked to reward cues and outcomes are associated with enhanced memory consolidation (Lisman & Grace, 2005; Lisman, Grace, & Duzel, 2011; Shohamy & Adcock, 2010). However, there are no studies to date that directly examine the role of reward uncertainty in memory.

Reward-related memory enhancements

Reward-related enhancements in memory have also been found for items where memory is incidental. Under incidental learning conditions, the rewards are not contingent upon memory but instead rewards or reward cues are presented in close temporal proximity to memory targets (Murayama & Kitagami, 2014; Murayama & Kuhbandner, 2011; Wittmann et al., 2005). These reward-related enhancements are only seen for items tested after a delay (24 h) (Murayama & Kuhbandner, 2011; Wittmann et al., 2011). This type of learning is thought to be supported by the functional links between the reward circuitry in the brain and the hippocampus (Lisman & Grace, 2005) and emerging evidence suggests that dopaminergic activity modulates hippocampal encoding (Shohamy & Adcock, 2010). Although studies have focused on the potential role of dopamine, it is likely that other neurotransmitters such as acetylcholine and noradrenaline are coreleased with dopamine and play a critical role in reward processing and memory consolidation (Clewett & Mather, 2014; Mather, Clewett, Sakaki, & Harley, 2015; Murty, Labar, & Adcock, 2012; paper284, Preuschoff, 't Hart, & Einhauser,2011; Preuschoff et al., 2011; Shaikh & Coulthard, 2013; Takeuchi et al., 2016).

The incidental learning literature has investigated—to a greater degree than motivated learning—which aspects of the reward signal may be critical to the reward-related memory enhancement. A key question has been whether the fidelity of the reward memory enhancement is sufficient to reflect small changes in magnitude? Wittmann et al. (2011) found that recognition memory for items showed a non-linear effect of reward on memory performance with only significant differences in memory performance between cases where reward was delivered and where it was not, regardless of the reward value. The focus has now shifted to the relationship between reward cue and reward outcome (Bunzeck et al., 2010; Mason, Ludwig, & Farrell, 2016; Mather & Schoeke, 2011). Mather and Schoeke (2011) propose that the critical factor is the reward outcome relative to expectation as opposed to absolute amount of reward received on each trial. In their study participants were presented with a reward cue indicating one of three trial types (monetary loss and no outcome trial). Participants had to respond as quickly as possible to a picture target after which the reward outcome was revealed. The reward outcome could either be congruent or incongruent with the reward cue meaning that trials could be classified as either rewarded or loss avoided (regardless of actual reward outcome). Recognition memory performance for the target pictures was significantly better for trials resulting in a "hit" outcome, which includes trials where the reward value may have been 0. Similarly in our recent direct replication (Mason et al., 2016) of findings by Bunzeck et al. (2010) we found evidence that memory performance was primarily influ-