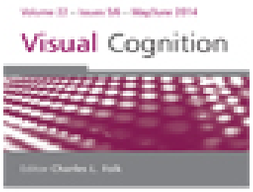

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Reward-priming impacts visual working memory maintenance: Evidence from human electrophysiology

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ABSTRACT
Reward can benefit visual processing of reward-associated objects in a non-strategic way. Recent studies have suggested that such influence extends also to visual working memory (VWM) representations of reward-associated stimuli. However, it is not clear yet which mechanisms underlie the behavioural effects in VWM tasks: reward could directly impact on our ability to maintain representations in VWM or it could influence memory indirectly via priming of attentional selection. To distinguish between these alternatives we measured event-related potential indices of selective attention – the N2pc – and VWM maintenance – the CDA (contralateral delay activity) – while participants completed a VWM task. Results show that reward outcome in one trial caused similarly coloured targets to be strongly represented in VWM in subsequent trials, as expressed in a larger-amplitude CDA This was not preceded by a corresponding effect on attentional selection, in so far as our key manipulation had no impact on the N2pc. In a second experiment, we found that reward priming produced a behavioural benefit that emerged over time, suggesting that the representations of reward-associated items stored in VWM are more resistant to interference and decay. We conclude that when the task stresses VWM maintenance, it is at this representational level that reward will have impact.

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KEYWORDS
VWM; reward priming; N2pc; CDA; maintenance

Learning to identify objects that can lead to a desirable outcome is a fundamental function of our brain, promoting effective behaviour when analogous situations are encountered in the future. Theories of reinforcement learning suggest that reward can directly guide perception (e.g., Pascucci, Mastropasqua, & Turatto, 2015) and prioritize the selection and processing of behaviourally relevant information (e.g., Berridge & Robinson, 1998). In humans, rewards have been used to modulate motivational engagement in task performance. Results have shown that cognitive resources can be flexibly distributed to increase the efficiency in orienting and reorienting attention towards valuable stimuli (Engelmann & Pessoa, 2007; Kristjánsson, Sigurjonsdottir, & Driver, 2010; Pessoa, 2009; Sawaki, Luck, & Raymond, 2015). In particular, attention is preferentially deployed to stimuli characterized by reward-associated features (Anderson, Laurent, & Yantis, 2011, 2012; Anderson, Laurent, Yantis, & Lauwereyns, 2011; Della Libera & Chelazzi, 2006, 2009; Raymond & O'Brien, 2009), locations (Hickey, Chelazzi, Theeuwes, & Geng, 2014; Rutherford, O'Brien, & Raymond, 2010), and latencies (Hickey & Los, 2015; Raymond & O'Brien, 2009), even when reward is no longer available (e.g., Anderson, Laurent, & Yantis, 2011) or when there is no consistent pairing between stimuli characteristics and outcome (e.g., Hickey, Chelazzi, & Theeuwes, 2010).

Although the investigation of reward effects in visual cognition has focused mainly on influences on the deployment of attention, recent studies have started to address the impact of reward associations on other cognitive processes that require sustained cognitive control, such as visual working memory (VWM). The key role of working memory is to temporarily retain relevant information that is no longer available to the senses. Given the limited capacity of this system (Alvarez & Cavanagh, 2004; Bays & Husain, 2008; Zhang & Luck, 2008), it is important to efficiently guide it to encode and maintain the information that is most relevant to upcoming behaviour. In this regard, VWM can be seen as the active maintenance of attention to the visual representations that are important for behaviour, suggesting a strong overlap between

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visual attention and VWM (Awh & Jonides, 2001; Awh, Vogel, & Oh, 2006; Chun, 2011; Gazzaley & Nobre, 2012). Mechanisms of attentional selection have been shown to flexibly modulate the content of VWM (Kuo, Stokes, Murray, & Nobre, 2014; Kuo, Stokes, & Nobre, 2012) and common neural substrates have been identified for VWM and attention (Mayer et al., 2007). Motivated by the commonalities between these two processes, previous studies have demonstrated that incentives can influence top-down attentional signals leading to a motivational improvement in VWM performance (Kawasaki & Yamaguchi, 2013; Krawczyk, Gazzaley, & D'Esposito, 2007; Sanada, Ikeda, Kimura, & Hasegawa, 2013). However, in these experiments, it is not possible to disentangle the motivational influence of reward on memory from non-strategic improvements in performance due to effects on attention or perception. This distinction is important if one wants to determine if reward can automatically bias the way we perceive, attend, and remember the world around us, in a way that is theoretically distinct from the known role of reward in the strategic establishment of the attentional set (Hickey et al., 2010; Maunsell, 2004).

Recent studies have started to explore the influence of reward associations on VWM in the absence of direct incentive motivation. This work has been centred around experimental paradigms that measure the impact of learned feature–reward associations during extinction, when the reward-associated stimulus no longer provides any valid information about outcome (Gong & Li, 2014; Infanti, Hickey, & Turatto, 2015; Thomas, FitzGibbon, & Raymond, 2016; Wallis, Stokes, Arnold, & Nobre, 2015). These studies report non-strategic benefits in VWM performance for stimuli previously associated with higher gains (Gong & Li, 2014; Thomas et al., 2016; Wallis et al., 2015), costs for items associated with losses (Thomas et al., 2016), and costs when task-irrelevant reward-associated items lie alongside task-relevant memory targets (Infanti et al., 2015).

The precise neural and cognitive mechanisms underlying these behavioural effects are unknown. On the one hand, it could be the case that reward association has a direct impact on our ability to maintain visual representations in memory (Thomas et al., 2016). However, current behavioural results leave open the alternative possibility that influences on VWM reflect an indirect influence of reward on attentional selection: if reward-associated stimuli are better attended, this "boost" may cause them to be better remembered even if reward has no discrete impact on VWM (Gong & Li, 2014; Infanti et al., 2015; Wallis et al., 2015).

Here we address this issue by measuring electrophysiological activity in a VWM task in which we varied the magnitude of the reward feedback provided for correct responses. We adopted the reward priming paradigm introduced by Hickey and colleagues (2010), which involves the categorization of experimental trials based on two factors: the magnitude of reward received in the preceding trial and the repetition or swap of the target and distractor colours. We hypothesized that high-magnitude reward would benefit VWM relative to low-magnitude reward for targets whose colour was repeated among trials, but that this benefit would not appear when the colour of targets was swapped among trials. We looked for this interactive pattern in two components of the event-related potential (ERP), one that indexes attentional selection – the N2pc – and the other that tracks VWM maintenance – the CDA (contralateral delay activity).

The N2pc arises around 200 ms after stimulus onset and consists of a more pronounced negative activation at the posterior electrodes contralateral to an attended stimulus (Luck & Hillyard, 1994a, 1994b). It can be used to index the deployment of attention and target selection during visual search (Eimer, 1996; Hickey, Di Lollo, & McDonald, 2009; Mazza, Turatto, & Caramazza, 2009a, 2009b; Woodman, Arita, & Luck, 2009; Woodman & Luck, 1999, 2003) and VWM tasks (Becke, Muller, Vellage, Schoenfeld, & Hopf, 2015) and it has been shown to be sensitive to target and distractor value associations (Hickey et al., 2010; Kiss, Driver, & Eimer, 2009). In contrast to the N2pc, the CDA is a sustained posterior contralateral negativity that typically arises approximately 300 to 400 ms after display onset and reflects the active maintenance of representations in VWM (Drew & Vogel, 2008; Ikkai, McCollough, & Vogel, 2010; Mccollough, Machizawa, & Vogel, 2007; Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005). The amplitude of the CDA is modulated by the number of items in VWM (Ikkai et al., 2010; Vogel & Machizawa, 2004), the precision of these memory traces (Machizawa, Goh, & Driver, 2012), and task motivation (Reinhart, McClenahan, & Woodman, 2016; Schneider, Bonmassar, & Hickey, 2017).

By looking at discrete ERP indices of selective attention and working memory maintenance, we hoped to identify the locus of reward's impact on VWM in a working memory task. We approached the experiment with three hypotheses. First, reward might benefit attentional encoding without affecting VWM maintenance, thus expressing in the N2pc but not CDA. This would suggest that the reward effects on VWM reported in existing studies might be indirect in nature, ultimately caused by the known influence of reward on attentional selection and encoding (Gong & Li, 2014; Infanti et al., 2015; Wallis et al., 2015). Alternatively, reward might benefit VWM maintenance, indexed in the CDA, without preceding impact on attentional selection and the N2pc. This would be the case if reward were to act at the level of representation that is critical to task performance, thus VWM maintenance in a VWM task. Finally, reward might impact on both components, consistent with the idea that benefits to encoding translate to benefits in maintenance.

To foreshadow, results from our ERP experiment show a significant impact on CDA only, suggesting that reward can directly affect the maintenance stage of VWM in a visual memory task. We find no corresponding impact on overt task performance. To probe this dissociation we conducted a second behavioural experiment to determine how reward affects visual representations in working memory over time. Results from Experiment 2 suggest that reward's impact on VWM maintenance emerges in overt performance only when retention intervals are relatively long. We interpret this as evidence that reward acts to shelter representations of valuable information from interference and decay.

Experiment 1

Methods

General paradigm and rationale

Participants performed a VWM task similar to that described in Vogel et al. (2005). In each trial, they were instructed to attend to one side of the screen and memorize the orientation of uniformly coloured target rectangles presented together with irrelevant squares. Each correct response in a trial was followed by feedback indicating a high- (+100 points) or low-magnitude (+1 point) reward outcome. Participants were paid based on the number of points accumulated throughout the experiment, but, at the same time, they were informed that the magnitude of reward received in each trial was completely random.

Two main features characterized the reward conditions in our paradigm (adapted from Hickey et al., 2010): (1) in each trial the colour of the target rectangles could be either red or green and in the following trial the colour could either repeat or change; (2) each trial resulted in a high- or low-magnitude reward outcome (and thus each trial was preceded by a trial that garnered either a high- or low-reward outcome). We were interested in sequential effects in this task reflecting the interaction of these factors: does high-magnitude reward in one trial impact on mnemonic performance when the target-defining colour is repeated in the next trial?

The design leads to four experimental conditions in which (a) participants received a high-magnitude reward on trial $n - 1$ and they had to perform the VWM task on a target of the same colour on trial n (high-reward repetition condition [HR]), (b) participants received a high-magnitude reward on trial $n - 1$, then target colour was swapped (high-reward swap condition [HS]), (c) participants received a low-magnitude reward on trial $n - 1$, then target colour was repeated (low-reward repetition condition [LR]), and, finally, (d) participants received a low-magnitude reward on trial $n - 1$, then target colour was swapped (low-reward swap condition [LS]).

Participants

Twenty-two healthy volunteers from the University of Trento (mean ± SD age = 22.3 ± 3.4; 13 female) participated in the experiment. They had normal colour vision and normal or corrected-to-normal visual acuity and were all naïve as to the purpose of the experiment. Participants were reimbursed for their participation proportionally to their performance (up to €25). Written informed consent was obtained from all participants, and the experiment was carried out in accordance with the Declaration of Helsinki and with the approval of the local ethical committee.

Apparatus

Stimuli were presented on a ViewPixxEEG monitor with 1920 × 1080 pixels resolution at a refresh rate of 100 Hz. Participants were seated in a dimly illuminated room at approximately 1 m from the display. Stimuli

were presented using the Psychophysics Toolbox 3.8 (Brainard, 1997; Pelli, 1997) for Matlab (Mathworks) running on Windows 7.

Stimuli

Displays consisted of the bilateral presentation of rectangles (0.3° × 0.7° visual angle) and squares (0.3° × 0.3°) placed randomly within an area of 5° × 3° centred at 4° to the left or to the right of the central fixation point (see Figure 1). The stimuli could be either red or green, with their colour adjusted to be physically equiluminant (approximately 8 cd/m^2), and were presented on a uniform dark grey background (6 cd/m^2). The rectangles had various orientations (selected from 0°, 45°, 90°, and 135°) and all rectangles on each side of the display had the same colour (e.g., left red and right green). In contrast, half of the squares on each side of the display were red and half were green.

Design and procedure

The schematic of a trial is illustrated in Figure 1A. Trials started with a grey fixation dot (0.2° × 0.2°) presented at the centre of the screen for a random interval of 500–900 ms. A grey arrow appeared for 200 ms pointing either to the left or the right of the screen and was followed by the onset of the memory display after a random inter-stimulus interval of 100–500 ms. Each side of the memory display consisted of two or four target rectangles and four distractor squares and was visible for 100 ms. Distractors were included to increase the need for attentional selection and promote the emergence of the N2pc (Luck & Hillyard, 1994b). After a retention interval of 900 ms, a probe display appeared. The probe display consisted of a single rectangle in one of the target locations on the cued side. The task was to indicate whether the orientation of this probe rectangle was the same as or different from that of the corresponding stimulus presented in the memory display. The test display remained on the screen up to 1500 ms or until response, which was made on a standard keyboard, the "m" key indicating that the probe matched the memory stimulus and "z" indicating that this was not the case. Each response was followed by a 1000-ms feedback interval. Correct responses were followed by either "+001" or "+100". Incorrect responses were indicated by the loss of one point ("−001"). Each point had a value of approximately €0.006.

The experiment took about 90 minutes to complete and was composed of 20 practice trials and 960 experimental trials divided into 16 blocks. Probed visual hemifield (left/right), correct response (match/non-match), target colour repetition (same/different colour as in trial n – 1), and magnitude of reward available in trial n – 1 (high/low) were all fully counterbalanced across the experiment.

E.E.G. recording and analyses

Electroencephalography (EEG) was recorded from 61 Ag/AgCl electrodes mounted in an elastic cap (right mastoid reference; online filter: 0.01–250 Hz; sampling rate: 1000 Hz) using a Brain Amp system (Brain Products GmbH, Munich). Additional electrodes were placed 1 cm lateral to the external canthi of each eye in order to record horizontal electrooculogram (HEOG), 1 cm below the right orbital ridge to record vertical electrooculogram (VEOG), and at the left mastoid. Impedance was kept below 5 kΩ for all electrodes. Analyses were performed using custom scripts for Matlab (Mathworks, Natick, MA) and the EEGLAB toolbox (Delorme & Makeig, 2004). Data were downsampled offline to 500 Hz, referenced to the average of encephalic channels, digitally low-pass filtered at 30 Hz (non-causal 1000-point linear-phase finite impulse response kernel; 0 db attenuation at 29 Hz; −6 dB at 30 Hz), and epoched around events of interest. Epochs tainted by head motion or other non-stereotyped artefacts were removed after visual inspection (mean: 1.4%; range: 0–2.5%). Epochs affected by horizontal eye movements during the interval between cue onset and memory display offset (HEOG exceeding ± 30 μV; mean: 1%; range: 0.1–6.7%) were removed to guarantee that stimuli appeared at lateralized positions relative to gaze. Independent component analysis (ICA: Bell & Sejnowski, 1995; Delorme & Makeig, 2004) was applied to the data and used to identify and correct artefacts resulting from blinks and muscular activity.

Event-related potentials were calculated using standard signal-averaging procedures (Luck, 2005). All ERPs were baseline corrected to the 200-ms interval preceding the onset of the memory array. Average activity was computed separately for electrodes contralateral and ipsilateral to the to-be-memorized side of the screen. Contralateral waveforms were measured at occipital, posterior parietal, and parietal electrode sites as the difference in mean amplitude between

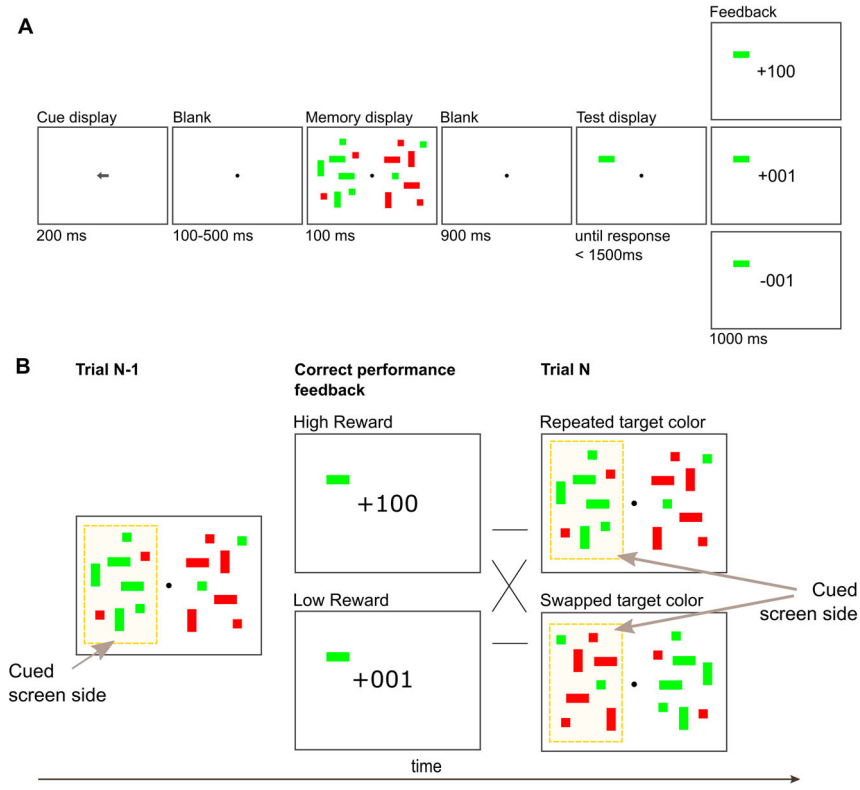

Figure 1. Trial schematic and experimental design. (A) Trial schematic. A memory display of either two or four targets appeared on each side of the screen. Targets could be either red or green (dark grey and light grey in the printed version of the article). Participant response was followed by a feedback display that indicated the number of points that were earned on each trial. The magnitude of reward feedback was randomly assigned and, critically, was not dependent on target colour. (B) General paradigm. Trials were divided into four conditions according to the magnitude of reward received in trial $n - 1$ (high vs. low) and the repetition or swap of the target colour (irrespective of cued side). The rectangle that indicates the to-be-memorized side in the figure was not shown in the experiment.

the contralateral and ipsilateral waveforms. We defined N2pc and CDA in accordance with previous studies (Hickey et al., 2010, 2009; Mccollough et al., 2007; Vogel et al., 2005; Vogel & Machizawa, 2004). We defined a relatively large interval for N2pc that was measured between 200 and 300 ms after the onset of the memory display (Luck, 2014; Mccollough et al., 2007). We computed CDA from 350 ms after display onset until the end of the retention period (1000 ms). This is a conservative measure of CDA in comparison with the standard 300-ms onset employed in the literature (e.g., Mccollough et al., 2007; Vogel et al., 2005; Vogel & Machizawa, 2004), which we employed to avoid the risk of measuring residual N2pc variance. However, this choice had no bearing on our results, and all findings described below were reproduced when a 300–1000-ms interval was employed. Only correct trials were included in ERP analysis.

Analysis and results

Our motivating hypothesis was that reward would increase the quality of visual representations held in VWM We expected that high-magnitude reward would positively impact on the encoding or maintenance of stimuli representations when the colour characterizing target stimuli was repeated between trials. To test this hypothesis, we looked at the modulation of performance (accuracy and response times [RTs]) and electrophysiological responses on each trial as a function of the magnitude of reward received in the preceding trial and the repetition or swap of the target colour (Figure 1B). Considering that the magnitude of reward obtained at trial $n - 1$ was a key factor in our design, only trials preceded by a correct response (i.e., trials in which reward feedback was received) were analysed. This garnered 178 trials per condition on average for behavioural analysis of

accuracy, where 127 of these trials garnered correct response and were used to calculate ERPs.

Behavioural performance

We analysed behavioural performance by means of a repeated-measures analysis of variance (ANOVA) with reward × repetition × display size (2 × 2 × 2) as factors. Working memory performance was better for two-item arrays than for four-item arrays in terms of both accuracy (2 items: 81.35 ± 7.27%; 4 items: 66.17 ± 7.54%; $F(1,21) = 291.95$; $p < 0.001$; $\eta_p^2 = 0.93$) and RTs (2 items: 714 ± 91 ms; 4 items: 787 ± 93 ms; $F(1,21) = 174.18$, $p < 0.001$; $\eta_p^2 = 0.89$). Contrary to our expectations, the magnitude of reward received in the previous trial did not influence accuracy as a function of the repetition or swap of the target colour (reward × colour repetition: $F(1,21) = 0.51$; $p = 0.482$; $\eta_p^2 = 0.02$; display size × reward × colour repetition: $F(1,21) = 2.63$; $p = 0.120$; $\eta_p^2 = 0.11$), nor were other effects of reward or colour repetition observed (colour repetition × display size: $F(1,21) = 1.48$; $p = 0.237$; $\eta_p^2 = 0.07$; other Fs < 1). A facilitation of colour repetition was observed on RTs ($F(1,21) = 6.46$; $p = 0.019$; $\eta_p^2 = 0.24$; display size × repetition: $F(1,21) = 1.88$; $p = 0.185$; $\eta_p^2 = 0.08$), but no main effects or interactions with reward emerged in this analysis (all Fs < 1).

Electrophysiological results

Following previous studies (Ikkai et al., 2010; Mccollough et al., 2007), we measured N2pc and CDA amplitude at a set of posterior and occipital electrodes (O1/2, PO3/PO4, PO7/PO8, P3/P4, P5/P6, P7/P8; Figure 2A) and compared the contralateral-minus-ipsilateral difference waves across reward and repetition conditions. We averaged N2pc and CDA amplitudes across the pre-specified time intervals and we analysed these results with repeated-measures ANOVA with factors for display size (2 vs. 4 targets arrays), prior reward (high- vs. low-magnitude reward in trial $n - 1$) and target colour repetition (repeat vs. swap; Figure 3). Consistent with an existing study, N2pc amplitude was significantly larger for target colour repetition (main effect of colour repetition: $F(1,21) = 5.08$; $p = 0.035$; $\eta_p^2 = 0.20$), suggesting facilitated selection of stimuli characterized by the target-associated colour (Hickey, Olivers, Meeter, & Theeuwes, 2011). However, prior reward had no reliable effect on N2pc (main effect of reward: $F(1,21) = 0.59$; $p = 0.452$; $\eta_p^2 = 0.03$; reward × colour repetition: $F(1,21) = 0.04$; $p = 0.848$; $\eta_p^2 < 0.01$). Display size did not have a significant impact on N2pc amplitude (main effect of display size: $F(1,21) = 1.34$; $p = 0.259$; $\eta_p^2 = 0.06$) and it did not interact with other factors (display size × colour repetition: $F(1,21) = 1.08$; $p = 0.310$; $\eta_p^2 = 0.05$). Analyses conducted for N2pc centred around the peak of the component (N2pc peak latency measured across conditions: 262 ms) and limited by the intervals of interest defined a priori (200–300 ms) revealed analogous results (N2pc peak interval for all conditions: 224–300 ms; time window: 76 ms; main effect of colour repetition: $F(1,21) = 5.46$; $p = 0.029$; $\eta_p^2 = 0.21$; all other Fs < 1).

To gain further perspective on the null effect of reward magnitude, we analysed the interaction between reward and repetition for the mean N2pc amplitude calculated across 40-ms bins beginning at 180 ms post-stimulus and ending at 300 ms. No effect involving prior reward emerged at any latency interval. We also analysed separately the pairs of

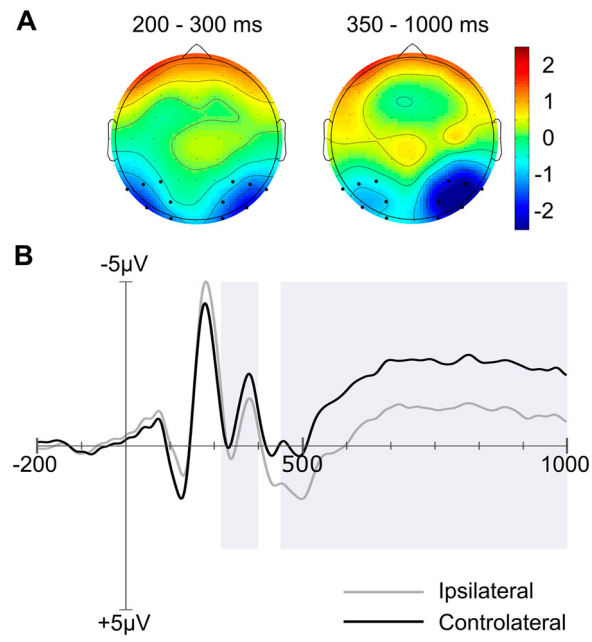

Figure 2. N2pc and CDA topographic maps and ERPs averaged across reward, repetition. and display size conditions. (A) Topographic maps for N2pc (200–300 ms) and CDA (350–900 ms). Electrodes located on the right side of the scalp depict ERPs contralateral to stimulus presentation while electrodes on the left depict ipsilateral potentials (collapsed for "memorize left" and "memorize right" trials). Highlighted are electrodes O1/2, PO3/PO4, PO7/PO8, P3/P4, P5/P6, P7/P8, selected for analysis of N2pc and CDA amplitudes. (B) Mean ipsilateral and contralateral waves at the posterior and occipital electrodes shown in (A). Shaded grey areas indicate the time intervals selected for N2pc and CDA analysis.

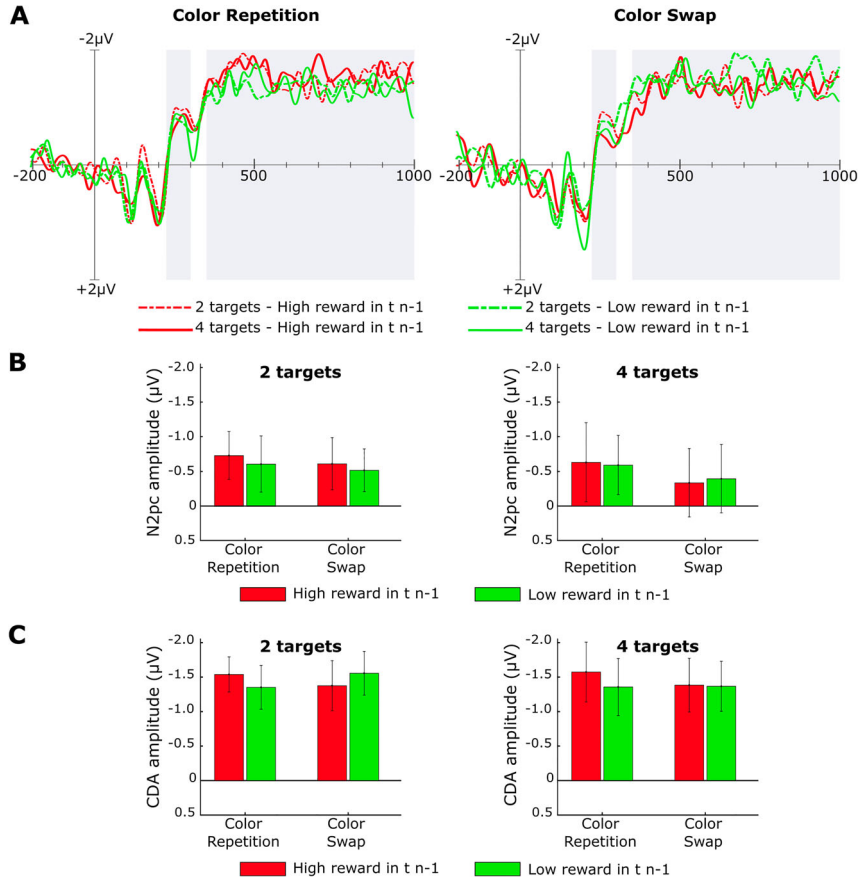

Figure 3. N2pc and CDA amplitude modulation as a function of reward magnitude and target colour repetition. (A) Difference waves from posterior electrodes illustrated in Figure 2A. ERPs as a function of reward received in trial $n-1$ and repetition or swap of target colour in trial n. Shaded grey areas indicate N2pc and CDA time intervals. (B) Mean N2pc and (C) CDA amplitudes over the interval indicated in (A) for two and four targets trials. Error bars here and below represent within-participant confidence intervals (Cousineau, 2005). N2pc amplitude is significantly increased for target colour repetitions, but it is not modulated by reward. In contrast, the CDA is sensitive to the magnitude of reward obtained in trial $n-1$.

electrodes that typically detect the N2pc with the largest amplitude – PO7/PO8 (e.g., Hickey, McDonald, & Theeuwes, 2006; Mazza, Turatto, & Caramazza, 2009b; Sawaki et al., 2015) and PO3/PO4 (Schubö, Wykowska, & Müller, 2007) – and we found no significant modulation of reward priming. (PO7/PO8: main effect of display size: $F(1,21) = 1.39$; $p = 0.252$; $\eta_p^2 = 0.06$; main effect of colour repetition: $F(1,21) = 1.32$; $p = 0.263$; $\eta_p^2 = 0.06$; display size × colour repetition: $F(1,21) = 1.48$; $p = 0.238$; $\eta_p^2 = 0.07$; all other $Fs < 1$. PO3/PO4: main effect of display size: $F(1,21) = 1.13$; $p = 0.300$; $\eta_p^2 = 0.05$; main effect of colour repetition: $F(1,21) = 3.12$; $p = 0.092$; $\eta_p^2 = 0.13$; all other $Fs < 1$.)

Consistent with prior work (Drew & Vogel, 2008; Ikkai et al., 2010; Mccollough et al., 2007; Vogel et al., 2005; Vogel & Machizawa, 2004), the CDA reached its maximum around 400 ms post-stimulus and persisted throughout the entire retention period. Critically, analysis revealed an interaction between target colour repetition and magnitude of reward in trial $n-1$ ($F(1,21) = 7.30$; $p = 0.013$; $\eta_p^2 = 0.26$; main effects of reward and colour repetition $Fs < 1$). Display size did not modulate CDA amplitude and did not interact with other factors ($Fs < 1$). We repeated our analyses across display size and confirmed a significant interaction between target colour repetition and magnitude of reward in trial $n-1$ ($F(1,21) = 8.48$; $p = 0.008$; $\eta_p^2 = 0.29$; main effects of reward and colour repetition $Fs < 1$). Follow-up analyses tested the influence of reward magnitude separately for trials when the target stimuli were characterized by a colour repetition and trials were characterized by a colour swap. Contralateral delay activity amplitude (tested across display size) for targets rendered in a repeated colour was larger when the preceding trial had garnered high-magnitude reward than when it had garnered low-magnitude reward ($t(21) = -2.20$; $p = 0.039$; Cohen's $d = -0.473$; the same comparison for

swap trials did not reveal significant results: $t(21) = 1.22$; $p = 0.236$; Cohen's $d = 0.26$).

In order to contrast the effects of prior reward and colour repetition on the N2pc and CDA we conducted an additional repeated-measures ANOVA with factors for component (N2pc vs. CDA), prior reward (high vs. low), and colour repetition (repetition vs. swap). This revealed a critical three-way interaction ($F(1,21) = 5.55$; $p = 0.028$; $\eta_p^2 = 0.21$; N2pc peak vs. CDA: $F(1,21) = 3.90$; $p = 0.061$; $\eta_p^2 = 0.16$), indicating that the interaction of prior reward and colour repetition had a reliably larger impact on the CDA than the unreliable impact of these factors on N2pc. Uninterestingly, this analysis revealed additional component effects ($F(1,21) = 58.68$; $p < 0.001$; $\eta_p^2 = 0.74$; N2pc peak vs. CDA: $F(1,21) = 31.69$; $p < 0.001$; $\eta_p^2 = 0.60$), indicating that the CDA was larger than N2pc, and a trend of a component × colour repetition interaction ($F(1,21) = 3.92$; $p = 0.061$; $\eta_p^2 = 0.16$; N2pc peak vs. CDA: $F(1,21) = 4.51$; $p = 0.046$; $\eta_p^2 = 0.\ 18$), reflecting a larger effect of colour repetition on N2pc (other comparisons were not significant; main effect of repetition: $F(1,21) = 2.31$; $p = 0.143$; $\eta_p^2 = 0.10$; N2pc peak vs. CDA: $F(1,21) = 2.54$; $p = 0.126$; $\eta_p^2 = 0.60$; reward × repetition interaction: $F(1,21) = 2.01$; $p = 0.171$; $\eta_p^2 = 0.09$; N2pc peak vs. CDA: $F(1,21) = 2.69$; $p = 0.116$; $\eta_p^2 = 0.11$; all other Fs < 1).

Interim discussion

Our results highlight a modulation of CDA amplitude as a function of reward priming. But, puzzlingly, no corresponding effect emerged in behaviour. Two alternative but not exclusive hypotheses could explain the discrepancy between the behavioural and the electrophysiological results in this experiment. On one hand, prior literature has shown that the quality and detail of VWM representations reflected in CDA can be flexibly adapted to changes in circumstance and task constraint (Gao, Li, Liang, Chen, & Shen, 2009; Machizawa et al., 2012). This suggests that the increase in CDA amplitude we observed may reflect an increase in the precision of maintained representations motivated by the reward value associated with targets' colour. On the other hand, the increase in CDA may reflect a modulation of the strength with which targets are represented in working memory and thus sheltered from interference (from distractors in the array or other targets) and decay. This might express behaviourally as a performance benefit at longer time intervals.

The task employed in Experiment 1 required only a coarse discrimination (target and test stimuli could differ only by 45° or 90°), so it was not tailored to detect a behavioural benefit of reward on the precision of VWM representations. Moreover, VWM performance was tested only after a rather brief retention delay. We therefore conducted a second behavioural experiment designed to index effects of reward on the precision and longevity of VWM representations.

Experiment 2

Methods

General paradigm and rationale

Participants performed a VWM task in which they had to memorize the orientation of coloured bars briefly presented on the screen. The goal of the experiment was to explore whether reward priming could affect behavioural performance after longer delays from display offset. In particular, we aimed to find behavioural evidence of reward-priming influence on the maintenance of information in VWM. To this end, we simplified the memory array by removing the features used in Experiment 1 to emphasize the target selection and encoding stage (i.e., distractors), and we focused on the maintenance of information in VWM The targets were accordingly presented around fixation in one colour without distractors. We made two further crucial changes to the design to measure the effects of reward on the precision and longevity of VWM representations: (a) we adopted a VWM task that required finer discrimination, carefully choosing non-canonical orientations and reducing the possible difference between test and target to 30°; (b) we tested performance over a set of longer retention intervals, ranging from 900 ms to 2700 ms.

As in the previous experiment, participants were rewarded for correct responses with either high- or low-reward feedback. Participants were paid based on the total of points accumulated during the task, but they were informed that the value of each trial was randomly assigned. We were again interested in measuring reward-priming effects by taking into account two main factors: target colour repetition and magnitude of reward feedback in the preceding

trial. Moreover, we measured the strength of the reward priming effect as a function of retention interval.

Participants

Fifty-five volunteers from the University of Trento (mean ± SD age = 23.1 ± 2.5; 33 female) participated in the experiment. They had normal colour vision and normal or corrected-to-normal visual acuity. All participants were naïve as to the purpose of the experiment and none of them took part in Experiment 1. Participants were reimbursed for their participation and could earn up to €17, proportionate to the amount of points accumulated.

Apparatus

The experiment was performed in a dimly lit room where participants were seated approximately 60 cm away from the display with their head supported by a chinrest. Stimuli were presented on a gamma-calibrated ViewSonic Graphic Series G90 fB 19″ C.RT (cathode ray tube) monitor (1024 × 768) at a refresh rate of 100 Hz.

Stimuli

Four rectangles (0.4° × 0.9° visual angle) were displayed at 5° from the central fixation point (see Figure 4). The stimuli could be either red or green, with their colour adjusted to be physically equiluminant (approximately 8 cd/m^2), and were presented on a uniform dark grey background (6 cd/m^2). The stimuli had different orientations that were randomly selected from a predefined set (5°, 30°, 55°, 80°, 105°, 130°, and 155°).

Design and procedure

Trials started with a jittered fixation interval (500–900 ms) followed by the presentation of the display containing the oriented rectangles that had to be memorized (100 ms; Figure 4A). After a variable retention interval (900, 1500, 2100, or 2700 ms), the test display appeared and remained on the screen up to 2500 ms or until participant's response. In the test display, all items were grey except for the target, which maintained its original colour. The target could have the same orientation of the rectangle in the memory display or could be rotated 30° clockwise or anticlockwise from the original orientation. The task of the participants was to detect whether there was a change in target orientation (pressing "m" for same and "z" for different on the keyboard). Each response was followed by a 1000-ms feedback interval. As in the previous experiment, correct responses were followed by either "+001" or "+100". Incorrect responses were indicated by the loss of one point ("−001").

The experiment was performed in two one-hour sessions run on two consecutive days. A practice block of 24 trials was performed on the first day, followed by the experimental session consisting of 448 experimental trials divided into eight blocks (56 repetitions per condition).[1]

Analysis and results

We analysed the modulation of responses as a function of the magnitude of reward received in the preceding trial and the repetition and the swap of the target colour (Figure 4B). We particularly focused on the modulation of the interaction between these two factors (reward magnitude and colour repetition) as a function of the duration of the retention interval. Based on the idea that reward might make memory representations less vulnerable to interference and decay, our primary hypothesis was that such positive effects of reward would be particularly evident with longer delays.

As in Experiment 1, only trials preceded by a correct response were analysed. Moreover, trials in which participants' response occurred more than three standard deviations from the individual mean RT across conditions were discarded (1.76%). This resulted in a mean of 37 trials per condition for behavioural analysis of accuracy. One participant was excluded because their accuracy across experimental conditions was highly variable (conditional variance in accuracy was >2.5 standard deviations from the sample mean).

We directly compared the first and the last temporal delays in order to assess whether the impact of reward priming was significantly larger in the longer delay. We performed a three-way repeated-measures ANOVA with reward, repetition, and delay (2 × 2 × 2) as factors. Accuracy was significantly higher for the shorter retention interval (900 ms: 72.06 ± 6.97%; 2700 ms: 67.15 ± 7.01%; $F(1,53) = 39.25$; $p < 0.001$; $\eta_p^2 = 0.43$). More importantly, we found a significant three-way interaction ($F(1,53) = 5.32$; $p = 0.025$; $\eta_p^2 = 0.09$; Figure 4C), demonstrating that the impact of reward emerged more strongly with the longest

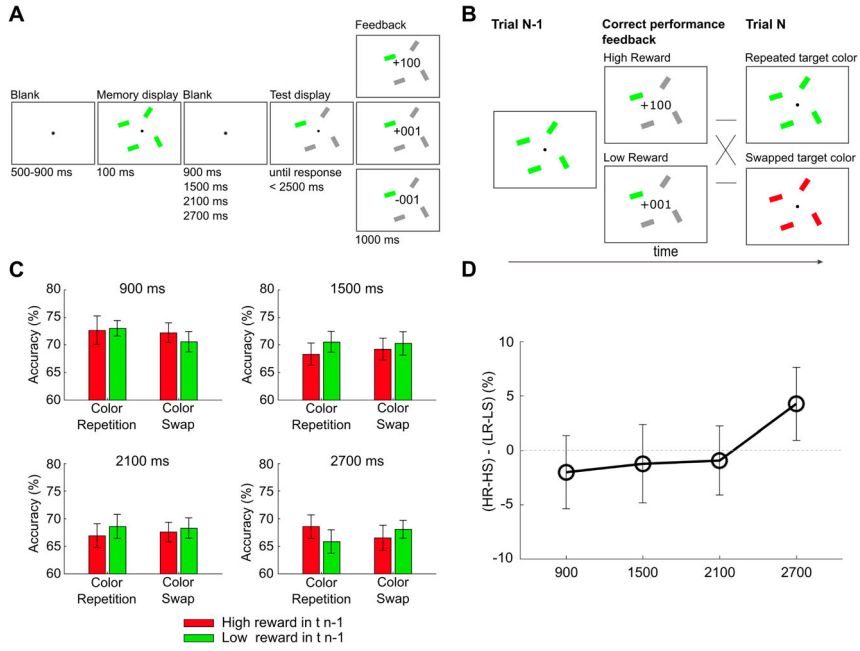

Figure 4. Behavioural results of Experiment 2. (A) Trial schematic. Targets could be either green or red and participants memorized and maintained their orientation in VWM for a variable delay (900, 1500, 2100, or 2700 ms). Participant response was followed by a feedback display that indicated the number of points that were earned on each trial. As in Experiment 1, the magnitude of reward feedback was randomly assigned and was not dependent on target colour. (B) General paradigm. As in Experiment 1, trials were divided into four conditions according to the magnitude of reward received in trial $n-1$ (high vs. low) and the repetition or swap of the target. (C) Each quadrant represents accuracy (%) for different temporal intervals as a function of reward in trial $n-1$ and repetition or swap of target colour in trial n. (D) The point estimate of the interaction between reward and repetition is computed ((HR – HS) – (LR – LS)) and displayed for different temporal intervals showing that the reward-priming effect on VWM significantly increases over time and becomes significant at 2700 ms.

delay. No other significant effects were found (repetition × delay interaction: $F(1,53) = 1.16$; $p = 0.287$; $\eta_p^2 = 0.02$; other Fs < 1).

We further explored the impact of reward priming in the first and the last retention intervals separately. In each of these intervals we conducted a 2 × 2 repeated measures ANOVA with reward and repetition as factors. As in Experiment 1, no significant reward benefits were observed for the 900-ms interval (main effect of reward: $F < 1$; main effect of repetition: $F(1,53) = 1.63$; $p = 0.207$; $\eta_p^2 = 0.03$; reward × repetition: $F(1,53) = 1.16$; $p = 0.286$; $\eta_p^2 = 0.02$). In contrast, a significant reward × repetition interaction emerged at the 2700-ms interval ($F(1,53) = 4.67$; $p = 0.035$; $\eta_p^2 = 0.08$; other Fs < 1).

To explore the time course of the reward influence on memory, we performed a full factorial ANOVA with reward, repetition, and all delays (2 × 2 × 4). The results confirm a clear effect of delay ($F(3,159) = 18.44$; $p < 0.001$; $\eta_p^2 = 0.26$), but only a trend for three-way interaction between reward, repetition, and delay ($F(3,159) = 5.32$; $p = 0.092$; $\eta_p^2 = 0.04$). No other significant effects were found (reward × delay interaction: $F(3,159) = 1.36$; $p = 0.258$; $\eta_p^2 = 0.03$; other Fs < 1). To characterize the time course of the reward influence on memory in greater detail, we computed the point-estimate of the two-way interaction between reward and colour repetition ((HR – HS) – (LR – LS)) for the four different retention intervals. We performed a linear analysis of the point-estimate by computing a linear regression for each participant. We observed that the slope of the resulting linear function was significantly different from zero ($t(53) = 2.21$; $p = 0.032$), supporting the idea that the effect of reward increased over time (Figure 4D).

Analysis of RT revealed no significant effects.

Discussion

We investigated the non-strategic influence of reward on working memory for visual stimuli. Participants completed a task designed to determine whether an implicit association of high-magnitude reward with a colour would change the quality of VWM maintenance

for subsequent stimuli characterized by this colour, even when colour was task irrelevant. Results showed that when memory targets were characterized by the same colour in two consecutive trials, and the previous trial had garnered a high-magnitude reward outcome, an ERP measure of VWM maintenance – the CDA – was larger in amplitude. This maintenance effect appeared discrete and independent of any preceding attentional benefit to VWM encoding, in so far as our manipulation had no detectable influence on attentional selection indexed in N2pc. In a subsequent behavioural experiment, we found a behavioural effect of reward on memory-task performance that discretely emerged at long retention intervals, consistent with the idea that an automatic reward association can benefit the maintenance of visual representations in VWM

To date, studies of reward's impact on VWM have not been able to disentangle influences on attention, encoding, and VWM maintenance. This has led to some ambiguity in the literature. Gong and Li (2014) have suggested that reward could benefit the representation of items stored in VWM, but do not address at which particular stage this benefit might occur, whereas Wallis et al. (2015) have argued for a specific effect on memory encoding. In our own earlier behavioural work, we found that reward impacted on memory both at very early stages of the iconic store (from 10 ms post-stimulus) and at later stages of VWM maintenance (up to 1000 ms; Infanti et al., 2015). This suggested to us that the locus of reward's influence preceded memory maintenance, likely through a modulation of attentional selection and encoding, such that memory performance was impacted upon from very early in time.

In contrast to these accounts, Thomas and colleagues (2016) have suggested that reward might directly facilitate the maintenance of information in VWM They designed a task aimed to minimize the impact of a possible advantage in encoding by allowing a relatively long study interval of the stimuli (2000 ms) and by biasing selection towards the critical, value-associated, objects (performance was analysed for items that were colour singletons and were tested more often that other items). Results showed a benefit in VWM for face identities when these were shaded with a reward-associated colour. However, it is unclear if this effect on VWM was mediated by a benefit in long-term memory (LTM) representation resulting from extensive training. LTM representations of colour–face combinations encountered during training could be stronger for gain-associated colours than for neutral or loss-associated colours, producing an advantage when they have to be retained in VWM (see Reinhart et al., 2016).

It has thus been unclear whether the effects of reward on VWM reflect a direct influence on maintenance or indirect influences on attention and encoding or long-term memory. The dissociation of N2pc and CDA results we observe here addresses this ambiguity, demonstrating that reward can have a discrete influence on an electrophysiological correlate of VWM maintenance without any reliable earlier influence on an electrophysiological correlate of attentional selection. Moreover, the behavioural results in Experiment 2 support the claim of a direct benefit in maintenance by showing benefits in performance only at long memory intervals, when the VWM representation becomes more volatile.

We interpret the apparent absence of a reward effect on attentional selection in our electrophysiological experiment as suggesting that reward effects appear to be a product of the requirements of the experimental task. For example, as noted above, we found that reward modulated the attentional selection and encoding of items in memory in our prior behavioural work, rather than their maintenance (Infanti et al., 2015). However, in the task employed in that study, colour–reward associations were learned by means of a visual search task (Anderson, Laurent, & Yantis, 2011) that had no VWM component. Moreover, at test, participants were required to spatially memorize a set of targets presented alongside a salient colour singleton potentially characterized by a reward-associated colour. Thus our training task was designed to impact on selection, not memory, and our test task was designed to induce biases in the deployment of spatial attention. In contrast, the current experiment did not rely on an attentional training session, but rather looked to sequential effects where characteristics of one trial could influence neural processing in the next. Moreover, the task itself did not require spatial search: participants were pre-cued to orient their attention to targets on one side of the screen in Experiment 1, and all items were task relevant in Experiment 2. Finally, in both experiments, the target stimuli were uniformly coloured and the distractors in Experiment 1 were rendered in both colours. This

created a situation where facilitated attentional selection or encoding of the reward-associated colour would be unlikely to provide substantive benefit to task performance.

It is crucial to note that in the paradigm we used a main benefit of reward magnitude was possible, but would not speak to our central experimental hypothesis. For example, a main effect of reward could indicate a motivational benefit of reward feedback, while we hypothesized that high reward feedback would specifically benefit the processing of targets when their characterizing feature was repeated in consecutive trials. As a result, we approached the study with no strong predictions regarding the broad impact of high-reward feedback on performance when colour is not repeated. In particular, although the reward priming result could be driven by a combination of a benefit of high reward when colour is repeated and a cost when colour is not repeated (e.g., in Experiment 1 switch trials were characterized by previously attended items presented in the contralateral side of the screen), the separate analyses of repeat and switch trials suggests that our results are mainly driven by the former.

Typically, the CDA amplitude increases with increasing display size up to four items, after which it seems to reach an asymptotic limit (Ikkai et al., 2010; Mccollough et al., 2007; Vogel et al., 2005; Vogel & Machizawa, 2004). In contrast, while CDA amplitude was significantly influenced by reward priming in our data, we did not observe a clear modulation as a function of the number of items in the memory array. To understand our result, it is important to notice that the two or four targets forming the memory array were presented alongside four distractors, so that each side of the screen held an array with either six or eight objects. Vogel and colleagues (2005) demonstrated that, in individuals with low VWM capacity, the CDA amplitude measured in a VWM task does not differ for arrays containing two or four targets when targets and distractors are both presented in the attended portion of the screen (Experiment 1 in Vogel et al., 2005). We have no independent measure of working memory capacity in the absence of distractors and reward to address individual differences in our data, but it seems possible that incomplete filtering of distractors may explain the insensitivity of CDA to set size in our results. In particular, two of the distractors shared the same colour of the targets, potentially making it difficult to exclusively select relevant information. The camouflage of targets was further enhanced by the continuous variability of target colour in different trials. Our impression is that, under these circumstances, participants could not optimally filter the distractors, resulting in an increase in CDA amplitude that masked the effect of set size.

In contrast to the clear modulation observed on CDA amplitude as a function of reward priming, in Experiment 1 we did not observe any corresponding behavioural benefit. We approached Experiment 2 with the idea that reward may have a subtle effect on VWM, perhaps affecting the precision of representations (Gao et al., 2009; Machizawa et al., 2012) or the sensitivity of these representations to interference over time. Effects such as these would not emerge in behaviour in Experiment 1 because our task required only a coarse discrimination of orientation and involved only a rather short retention interval. Experiment 2 was designed to test these hypotheses by measuring VWM performance for finer orientation changes at increasing intervals from the offset of the study display. We observed a reward benefit that emerged robustly at the longest interval tested (2700 ms). While it may seem that the reward-priming effect emerged abruptly at the longest delay tested, it should be noted that our data showed a considerable individual variability in the overall accuracy, in the decay of performance over time, and in the emergence of the reward-priming effect over time. It is possible that the reward-priming effect emerged clearly at the group level only when performance was significantly impaired for most of the participants. However, further studies are necessary to directly address whether reward priming on VWM maintenance increases when longer delays are considered and whether it is influenced by individual differences in VWM capacity and decay function.

The absence of any early effect in our data suggests that when task constraints limit the advantages conferred by enhanced target selection and encoding, there is no immediate evidence of a reward benefit in the precision of VWM representations. However, it should be noted that the change detection task adopted here does not allow us to completely rule out the possibility of such benefits. We suggest that future studies will be necessary to shed light on this issue, perhaps employing an analogue recall task

(Bays, Catalao, & Husain, 2009; Bays & Husain, 2008; Wilken & Ma, 2004; Zhang & Luck, 2008) as a more compelling approach to directly quantify the precision of VWM representations.

Recently, the biased competition model of attention (Desimone & Duncan, 1995) has been proposed as a possible account of the limits in VWM capacity, showing that performance in VWM tasks can be improved by reducing biased competition among targets (Cohen, Rhee, & Alvarez, 2016; Druzgal & D'Esposito, 2001; Feldmann-Wüstefeld & Schubö, 2014; Shapiro & Miller, 2011). Moreover, limits in VWM performance can be predicted by receptive field properties of the visual cortex. Evidence for long-range interference has been found for memory arrays constituted by natural objects, while only short-range interference is observed for arrays of colours, reflecting the increase in receptive field size as more complex features are represented (Cohen et al., 2016). Reward may benefit maintenance of VWM representations by reducing competition among valuable stimuli, adaptively focusing the receptive field around targets positions, resulting in a greater amplitude signal (larger CDA) and longer and more stable representations. In this framework, CDA modulations might reflect the enhancement of cortical representations of attended object in memory. Alternatively, reward priming could promote the creation of more robust memory traces that are less susceptible to the passive forgetting of temporal decay. Future studies are necessary to directly test these two accounts and characterize the mechanisms by which reward priming benefits the maintenance of VWM representation.

As a final remark, the analyses of accuracy reported for this study leave open the possibility that our results are driven by a reward-induced bias on responses. A bias-free measure like Cowan's *k* would in principle help in distinguishing between changes in VWM capacity and bias; however, our design is not suitable for such analyses, as we do not have enough power to obtain a stable estimate of such measure. While the impact of bias cannot be completely ruled out and further studies should aim to directly address this, we argue that such an effect would be unlikely, as the number of change and no-change trials is counterbalanced by design in each condition. Moreover, it is unclear how the reward-induced bias should interact with the retention delay.

In conclusion, our work shows how reward priming can automatically affect the neural mechanisms instantiating VWM Recent studies have demonstrated that reward benefits can be measured in VWM tasks, showing that high-reward-associated items are better remembered (Gong & Li, 2014; Thomas et al., 2016; Wallis et al., 2015) and can produce stronger interference in representation of other neutral items (Infanti et al., 2015). With this work, we begin to shed light on the specific VWM mechanisms impacted upon by automatic reward associations, highlighting direct benefits in the maintenance of representations in VWM.

Note

1. Fourteen participants performed 384 trials in either one or both of the two sessions (minimum of 48 repetitions per condition), due to a problem in the experimental programme that caused the presentation of 6 rather than 7 orientations.

Disclosure statement

No potential conflict of interest was reported by the authors.

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