UNIVERSITÀ DEGLI STUDI DI TRENTO
CIMeC - Center for Mind/Brain Sciences

Doctoral school in Cognitive and Brain Sciences

XXVII cycle

Ph.D. Dissertation

Influence of reward history on visual working memory representations

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Summary

Reward is a strong determinant of human and non-human behavior, influencing the exploration of the world around us and our interactions with it. Interestingly, the impact of reward and reward-associated objects is not limited to strategic changes in approach behavior or attention deployment, but also extends to situations in which prioritizing processing of such objects is not necessarily advantageous for current goals. In spite of converging evidence for the automatic influence of reward on attentional deployment, less is known about the impact of reward on other cognitive processes.

In this thesis I describe a first attempt to investigate the influence of reward in encoding and maintenance of visual representations in working memory. Throughout this thesis I argue that once objects have been associated with a positive outcome in past encounters, they are preferentially encoded and maintained in visual working memory (VWM) even when reward is no longer provided or when there is no consistent pairing between reward feedback and target identity. In Chapters 2 and 3 I demonstrate that reward associated objects interfere with the visual representations of less valuable items maintained in VWM. This interference was already present starting 10 ms from the offset of the memory display suggesting that valuable objects directly affected the encoding of less valuable items. This robust phenomenon was observed at different delays, both when reward-associated objects were task-relevant and when they were not, and was independent of object salience. However, the interference disappeared when task requirements for target selection increased suggesting that items with a positive reward history can effectively capture attention and interfere with VWM representations only when cognitive resources are not exhausted by the main task (Chapter 3).

In the last study presented in this thesis I explored the possibility that reward could impact VWM beyond target selection and encoding, namely influencing the active maintenance process. To investigate this hypothesis I measured reward priming effects on event-related potential (ERP) indices of selective attention – the N2pc - and visual working memory maintenance – the CDA (contralateral delay activity). Results indicate that reward modulated CDA only, speaking for a discrete effect of reward on VWM maintenance. While the precise nature of such modulation is still unknown, these results suggest that reward history might influence the precision or the duration of visual representations maintained in VWM. Further studies are necessary to directly test this hypothesis, but these initial results suggest an interesting direction for future research in better characterizing the nature and extent of the influence of reward history on visual cognition.

1 Motivational and automatic influence of reward on visual processes

Prior experience is one of the key factors in guiding our daily interactions with the world. It influences our behavior, our choices, our expectations, the way we explore and allocate attention in space, and the way we weight sensory inputs and build perceptual representation of the world around us. Experience is fundamental in at least two ways: it has a predictive value yielding to anticipation and guiding interpretation of upcoming situations, and it also brings qualitative information about the value of familiar objects and the consequences of past choices and behaviors.

During my PhD I have worked on how past experience, and especially learned contingencies, can change visual processing, focusing on two main aspects of learning: a) the influence of cues and statistical regularities on our ability to improve in visual tasks, precisely investigating the interaction between expectations and visual perceptual learning (which is not reported in this thesis) and b) the impact of reward history on visual processing, specifically assessing its influence in visual working memory (VWM).

In our daily life, we encounter situations that are familiar to us and that can lead to positive or negative outcomes based on past encounters. In some cases we know it explicitly, whereas in others we may be unaware of it even if our brain has detected these regularities and has automatically driven us towards the most valuable option. Our brain constantly faces the challenge of combining past experience with available sensory information and current goals. In particular, the history of interaction with objects and their associated value plays an important role in influencing the way we explore and analyze the world around us. Crucially, situations or objects that we have learned to be valuable are not always currently relevant and an important challenge consists in understanding how our brain weights information gathered from experience and integrates it with what is relevant for current goals.

We know that our visual processing capacities are limited and objects compete for access to these limited resources (Desimone & Duncan, 1995). Perception and attentional deployment are driven by stimulus characteristics, such as raw salience (Theeuwes, 1991a, 1992; Yantis & Jonides, 1984), or current goals (Chelazzi, 1999; Egeth & Yantis, 1997). Furthermore, motivation and prior experience are two additional factors that play a very influential role (e.g. Anderson, Laurent, & Yantis, 2011a; Della Libera & Chelazzi, 2006, 2009; Engelmann & Pessoa, 2007; Gilbert & Fiez, 2004; Hickey, Chelazzi, & Theeuwes, 2010a; Mohanty, Gitelman, Small, & Mesulam, 2008; Pochon et al., 2002; Small et al., 2005). In the last twenty years, a lot of effort has been put in trying to describe the interplay between these factors and specifically in trying to isolate the automatic influence of reward in visual cognition in absence of motivational or strategic factors.

While it has been demonstrated that reward associated objects receive prioritized processing and can automatically capture visual attention (Anderson et al., 2011a; Anderson, Laurent, & Yantis, 2011b; Della Libera & Chelazzi, 2006, 2009; Hickey et al., 2010a), it is not clear yet to which extent these influences spread to other cognitive processes. The research presented in this thesis is motivated by the goal of further characterizing the influence of reward on visual cognition, specifically addressing its impact on encoding and maintenance of visual representations in VWM. Attention and VWM are two strongly connected cognitive processes (Gazzaley & Nobre, 2012; Zanto, Rubens, Thangavel, & Gazzaley, 2011) and understanding the extent to which reward can influence VWM can improve our understanding of the influence of reward on visual cognition in general.

After reviewing the main evidence for reward influence in vision (Chapter 1), I describe some studies that investigate the influence of reward on iconic and visual working memory (Chapters 2 and 3). The main focus of these experiments is the description of an interference phenomenon induced by reward associated objects in VWM representations of non-valuable items. The modulation of this *interference effect* can be interpreted as evidence for the impact of reward associations in the encoding of information in visual memory. In the second part of this thesis, I discuss the possibility that reward affects VWM also by directly modulating the process of actively maintaining visual representations in memory after targets disappearance (Chapter 4).

1.1 Motivational role of reward

Motivational incentives in attention and memory

Animal theories of reinforcement learning have described that rewards, usually primary rewards such as food or water, can be effective motivators for behavior. In fact, reward has been influentially defined as the thing that makes you “come back for more” (Thorndike, 1911). The ability to learn reward contingencies in the environment is crucial to anticipate positive outcomes and thus to optimize value-oriented behavior.

In terms of physiological mechanisms, influential research has shown that dopamine plays an essential role in reward motivate behavior, mediating learning of reward predicting cues (Schultz, 2002; Schultz, Dayan, & Montague, 1997), influencing behavior by selectively reinforcing associations between rewards and neutral stimuli in order to render them motivationally salient (for a review, see Wise, 2004). Furthermore, according to the “incentive salience hypothesis”, reward-related mesolimbic dopamine can drive approach towards reward-associated stimuli and directly guide perception by prioritizing the selection and processing of behaviorally relevant information that anticipates the arrival of reward (Berridge, 2007; e.g. Berridge & Robinson, 1998; McClure, Daw, & Read Montague, 2003).

In studies involving both humans and non-human primates, reward has often been used to increase motivational engagement in various tasks (e.g. Engelmann & Pessoa, 2007; Hikosaka & Watanabe, 2000; Kiss, Driver, & Eimer, 2009; Krebs, Boehler, Roberts, Song, & Woldorff, 2012; Platt & Glimcher, 1999; Serences, 2008; Watanabe, 1996). In the majority of such experiments, reward is administered in a performance-contingent fashion, namely as a function of performance accuracy or response speed, adopting two kinds of paradigms: proactive (anticipatory) or reactive. In the first case, participants are informed about the availability and magnitude of reward at stake prior to the actual target presentation. Reward cues are unrelated to the perceptual properties of the target and trigger a general motivational engagement that optimizes preparation for stimulus processing and response execution (e.g. Watanabe, 2007 for evidence in monkeys). In reactive paradigms however, different items are associated with different value and no information about trial value is available before target onset (e.g. Boehler, Hopf, Stoppel, & Krebs, 2012; Kiss et al., 2009; Krebs, Boehler, & Woldorff, 2010; Taylor et al., 2004; reactive paradigms are described more in detail in the next session of the Introduction).

Nowadays, there is large evidence that reward predicting cues can produce benefits on attentional orienting and motor response initiation towards valuable stimuli (Ikeda & Hikosaka, 2003; Peck, Jangraw, Suzuki, Efem, & Gottlieb, 2009; Platt & Glimcher, 1999; Roesch & Olson, 2003, 2007). Single cell recordings in the macaque brain have revealed that several regions in the frontal cortex show higher firing rate when preparing a saccadic response in highly rewarded trials (Roesch & Olson, 2003, 2007). The greater firing rate to high compared to low reward trials increases progressively moving towards posterior areas dedicated to preparation of motor responses, suggesting a motivation-dependent modulation of motor preparation (Roesch & Olson, 2003). On the other hand, anterior regions, such as the orbitofrontal cortex, appear to encode the value of the expected reward (Roesch & Olson, 2004). For example, in macaque frontal cortex distinct effects of reward can be observed in different frontal areas reflecting value processing and influence of motivation on response preparation (Roesch & Olson, 2007).

Aside from approaching and orienting behavior, reward predicting stimuli can also influence visual selection and subsequent processing of reward predictive stimuli. For example, Peck and colleagues (2009) demonstrated that spatially uninformative cues indicating forthcoming rewards can influence visual processing in different ways. They have a motivational impact on performance in trials were reward is expected compared to when it is not expected, as measured in benefits for saccades initiation and precision. Furthermore, learning of cue-reward associations caused the cue to bias spatial attention; retinotopic cells in the lateral intraparietal cortex (LIP), that are believed to represent a high-level saliency map (for a review, see Gottlieb, 2007), show stronger response to reward cues suggesting that learning of reward-cue associations makes cues become visually salient. However, it is not clear whether this result suggests that reward association automatically influence low-level processing of reward predicting stimuli or whether monkeys strategically attended to the reward cue, because they treated the cue predicting reward as a reward itself (Bromberg-Martin & Hikosaka, 2009; Lauwereyns et al., 2002). These results altogether show that the value of motivational incentives changes activity in cortical and subcortical areas designated to the processing of the upcoming valuable information and the preparation of the motor response to it.

Similar conclusions can be drawn from neuroimaging studies in humans adopting motivational cues in a variety of cognitive tasks (e.g. Adcock, Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli, 2006; Engelmann & Pessoa, 2007; Kiss et al., 2009; Krawczyk, Gazzaley, & D'Esposito, 2007; Pochon et al., 2002; Small et al., 2005). Prospects of reward, especially monetary ones, have been used as a form of incentives to increase motivational engagement of participants while performing a task (for a review, see Pessoa, 2009). Behavioral and imaging studies have demonstrated that monetary incentives can improve efficiency in orienting and re-orienting of attention towards the most valuable objects (Engelmann & Pessoa, 2007; Engelmann, Damaraju, Padmala, & Pessoa, 2009; Small et al., 2005) resulting in faster reaction times, RTs (Small et al., 2005) and increased sensitivity for targets presented at the most valuable location both when this validly predicted target appearance and when it did not (Engelmann & Pessoa, 2007; Engelmann et al., 2009). In one of the first human studies addressing the impact of motivation in cognition, Small and colleagues (2005) investigated the interaction between motivation and top-down attention using an attentional orienting task (Posner, 1980). They showed a general benefit of incentive motivation in RTs in both valid and invalid trials, suggesting a benefit in orienting and decrease in cost of re-orienting spatial attention. These results were associated with enhanced responses in areas associated with visuospatial expectancy as well as areas associated with the disengagement of attention (Small et al., 2005). In the work of Small and colleagues, incentives did not contain any spatial information; on the contrary, other studies have used spatial incentives that could be used to strategically bias the distribution of attention towards the most valuable portion of the screen, even when exogenous informative spatial cues were available (Engelmann & Pessoa, 2007; Engelmann et al., 2009; Pessoa & Engelmann, 2010). These studies lead to similar conclusions: they specifically reported an increase in sensitivity for the targets presented in the most valuable side of the screen (Engelmann & Pessoa, 2007; Engelmann et al., 2009; Pessoa & Engelmann, 2010). An interesting recent electroencephalography

(EEG) study started to investigate more in detail the mechanisms underlying motivational benefits in spatial attention, specifically aiming to disentangle the contribution of cognitive and motor preparation (Risa Sawaki, Luck, & Raymond, 2015). Using spatial motivational cues that did not predict the specific motor response required to perform the task, Sawaki and colleagues demonstrated a behavioral benefit of reward that was not relying on motor preparation (Mir et al., 2011), but solely on the opportunity to engage in cognitive preparation.

It is crucial to notice that all the experiments reviewed so far report converging evidence for the strong influence of reward on cognitive processes, but they clearly describe benefits that are dependent on strategic and unspecific preparatory mechanisms that reflect participant's engagement in performing the task. In our everyday experience, the behavioral relevance of an object is often determined by the positive or negative valence of consequences experienced at previous encounters, rather than by an explicit cue anticipating the value of the object. However, this literature constitutes a crucial framework for the work presented in this thesis given that almost all the research describing the role of reward on memory is based on proactive paradigms, similar to those described up to this point (but see Gong & Li, 2014; Taylor et al., 2004). In the following paragraphs, before introducing the influence of learned object-reward associations in cognition, I review the main studies concerning the behavioral benefits and the neural correlates of reward incentives in long-term and working memory.

Memory is the ‘‘neurocognitive capacity to encode, store, and retrieve information’’ (Tulving, 2000). Long-term memory for visual scenes can significantly improve when high-value reward cues are available (Adcock et al., 2006; Wittmann et al., 2005). As shown in functional magnetic resonance imaging (fMRI) studies, this behavioral advantage is associated with a greater blood oxygen level dependent (BOLD) response in the dopaminergic midbrain and the nucleus accumbens, but only for scenes that were remembered and not for those that were forgotten (Adcock et al., 2006; Wittmann et al., 2005). Interestingly, increased connectivity between areas sensitive to reward, such as the ventral tegmental area (VTA), and the hippocampus for remembered trials suggests that prior motivation can promote memory formation by facilitating the encoding and storage of relevant items (Adcock et al., 2006).

Single cell recordings in non-human primates and imaging studies in humans have suggested an interaction of reward incentives also in cognitive control networks recruited during working memory tasks (Beck, Locke, Savine, Jimura, & Braver, 2010; Kawasaki & Yamaguchi, 2013; Krawczyk et al., 2007; Pochon et al., 2002; Taylor et al., 2004; Watanabe, 1996; Watanabe, Hikosaka, Sakagami, & Shirakawa, 2005). Reward incentives of different magnitude in a verbal working memory task can modulate activity in cortical areas already activated by working memory processing and sensitive to memory load, such as the dorsolateral prefrontal cortex (DLPFC) (Gilbert & Fiez, 2004; Pochon et al., 2002). Analogous observations has been reported by Krawczyk and colleagues (2007) that tested the influence of incentives in a VWM task. In this experiment, participants were presented with a stream of face or scene images and their task consisted in focusing on either one or the other category according to the instructions provided at the beginning of the trial. Importantly, the initial instructions also informed participants about the value of the current trial. Neural response in ventral visual areas responsible for processing of scenes or faces was significantly modulated by category relevance. Most importantly, this pattern was significantly amplified in high reward trials. As in previous studies (Gilbert & Fiez, 2004; Pochon et al., 2002; Watanabe, 1996), a significant response enhancement was measured in prefrontal regions for high reward trials. Krawczyk and colleagues suggested that reward motivation drives performance through top-down signaling in frontal regions involved in WM as long as in those visual areas that are selective for processing the visual inputs that had to be remembered.

It is worth noticing, however, none of the aforementioned studies measured any benefit in accuracy or any improvement in visual capacity for highly valuable targets compared to less valuable ones (but see Kawasaki & Yamaguchi, 2013). In some cases, no significant behavioral benefit was observed (Pochon et al., 2002) and, in general, a clear benefit was measured only in RTs for rewarded over non-rewarded or poorly rewarded trials (Beck et al., 2010; Krawczyk et al., 2007) or for most preferred over least preferred rewards (Watanabe, 1996; Watanabe et al., 2005). These results suggest that, at least in a proactive paradigm, the behavioral effects of reward seem to rely mainly on an increase in arousal more than a real benefit in working memory capacity.

Despite the absence of clear improvements in working memory capacity, these studies coherently suggest that reward incentives can significantly affect the neural activity in those cortical areas that were relevant for encoding and maintain relevant representations in working memory (Gilbert & Fiez, 2004; Pochon et al., 2002; Small et al., 2005; Taylor et al., 2004).

As discussed previously, this literature focuses on the strategic benefits of general arousal or increased invested effort aimed at optimizing task performance and maximizing the final income (Bijleveld, Custers, & Aarts, 2009, 2010; Pessoa, 2009). In the next section, I describe other approaches to assess behavioral and neural consequences of reward on cognitive processes in the absence of preparatory cues. Importantly this does not exclude the influence of top-down strategies, but it might rely on different mechanisms triggered at target onset (reactive paradigms).

Learned reward associations in attention and memory

In our daily experience, we interact with objects or situations that are familiar to us and bring an intrinsic associated value that we have learned to recognize through previous encounters. Numerous studies have investigated the response evoked by stimuli according to their explicitly (Kiss et al., 2009; Krebs et al., 2012) or implicitly (Kristjánsson, Sigurjonsdottir, & Driver, 2009) learned value. Behavioral benefits are observed in a variety of cognitive tasks: faster responses are measured in spatial orientation of attention (Krebs et al., 2012), visual working memory (Taylor et al., 2004), and cognitive control tasks (Locke & Braver, 2008), but rewards can also facilitate response inhibition (Boehler et al., 2012) or influence performance in conflict tasks (Krebs et al., 2010; Krebs, Boehler, Egner, & Woldorff, 2011). Imaging studies have demonstrated that valuable items can influence information processing, modulating neural gain already at early stages of sensory processing thus competing more effectively for cortical representation (Serences, 2008). Moreover, objects' value can induce a specific bias towards the features characterizing reward-associated objects also when they are presented outside the focus of attention (Serences & Saproo, 2010). Serences and Saproo have shown that this benefit in representations can be measured in the sharpening of the response profile across the populations of neurons within the regions of sensory cortex that are most important for encoding the relevant properties of objects. These results imply that objects value can influence performance not only by differentially weighting motor responses, but also by biasing the quality of relevant sensory inputs.

Among the studies on reward influence on visual cognition, one of the most investigated aspects concerns the influence of objects' value on mechanisms of attention deployment and specifically on how objects' value interacts with current goals (e.g. Della Libera & Chelazzi, 2006, 2009; Hickey et al., 2010a; Kiss et al., 2009; Kristjánsson et al., 2009) and stimulus properties (Navalpakkam, Koch, Rangel, & Perona, 2010). Top-down and bottom-up mechanisms have been identified as fundamental factors in orienting attention towards the most relevant objects and locations in space (Desimone & Duncan, 1995). Recent evidence suggests that together with individual goals and objects saliency, reward might hold a special role in determining how our limited resources should be distributed in exploring the environment around us.

By means of an EEG study, Kiss and colleagues have shown that valuable objects can orient attentional selection and subsequent more in-depth processing of visual stimuli (Kiss et al., 2009). They adopted a visual search paradigm in which a color singleton, either a red or a green target among gray distractors, had to be detected and then further analyzed in order to identify the location of a notch (Mazza, Turatto, Umiltà, & Eimer, 2007). Crucially they informed participants of the different value associated with each target color and measured their performance and neural activity during the task. Interestingly, targets were color singletons and therefore could automatically attract attention (Theeuwes, 1991a). Event-related potentials (ERPs) were analyzed focusing on two main components in order to explore the influence of reward at different stages of target processing. The first component considered, the N2pc, is an enhanced negativity arising around 200 – 300 ms from stimulus onset measured at posterior electrodes contralateral to the target which is believed to reflect target selection and distractor suppression processes (S J Luck & Hillyard, 1994a, 1994b). The contralateral delayed activity, or CDA (also known as SPCN, sustained posterior contralateral negativity), is a later component measured at posterior electrodes contralateral to the target which reflects additional processing of stimuli after their selection, including maintenance in visual working memory (Mazza et al., 2007; Mccollough, Machizawa, & Vogel, 2007; Vogel & Machizawa, 2004). The crucial result of this work is that more valuable objects evoked larger and earlier N2pc response than less valuable targets indicating a significant influence of reward on target selection that does not depend on the saliency of the object or the top-down attentional set. Interestingly, also CDA's amplitude was increased for more valuable targets showing that reward influence does not restrict to initial selection of targets only, but it can also extend to the following processing stages. More cognitive resources are dedicated to the selection and further analysis of valuable items resulting in overall better performance. This study interestingly suggests that reward associated with objects can benefit their processing at different stages going beyond attentional capture and potentially contributing to any cognitive process that is relevant for efficiently dealing with the task. However, it is difficult to argue whether the benefit in CDA is the result of a genuine benefit on later object processing or if it reflects a carryover of benefit in selection: items that are better attended are also better processed after selection.

In the previous section, I reviewed some evidence that reward incentives can benefit VWM, however all these studies used motivational cues to strategically increase participants' engagement with the task. Taylor and colleagues (2004) asked participants to perform an object working memory task with abstract visual shapes where load and reward (associated with different target colors) were varied orthogonally. Behaviorally, they found a trend for faster RTs for high reward trials but no benefits in terms of accuracy. Previous studies have shown modulations of activity in prefrontal (Pochon et al., 2002) and extrastriatal visual areas (Krawczyk et al., 2007) in relation to the amount of reward that could be gained with correct response, but without distinguishing at which stage of the working memory process these modulations arise. In this work, Taylor and colleagues, showed that different reward outcomes associated with different objects modulated BOLD response in the premotor superior frontal sulcus and the intraparietal sulcus mainly during the delay phase, when objects' representation were maintained in VWM. These areas, involved in maintenance of information, also increased in response to working memory load.

The hypothesis that the influence of reward extends to different cognitive processes according to current task demands motivates the entire work reported in this thesis (Chapter 2 and Chapter 4). In particular, we focused on the impact of reward on different stages of a VWM task, from encoding (Chapters 2 and 3) to maintenance (Chapter 4). As suggested in the last studies I reviewed (Kiss et al., 2009; Taylor et al., 2004), reward could directly affect the processing of relevant information also after object selection. The study reported in Chapter 4 specifically aims to investigate this issue by testing whether changes in VWM can arise in absence of a measurable effect in attentional capture.

Crucially, all studies reviewed so far do not allow one to disentangle the contribution of reward per se from the influence of top-down strategic effects. Such studies rely on varying targets' value that directly affects participants' motivation resulting in prioritized processing or allocation of resources to the most valuable target. This is an important limitation because it does indicate whether reward can automatically guide perception (and other cognitive processes) beyond current goals. In other words, the influence of reward is indistinguishable from that of top-down selection.

A first indication of the coexistence of automatic mechanisms and top-down effects of reward emerges from two clever experiments focusing on attention mechanisms (Kristjánsson et al., 2009) and cognitive control (Krebs et al., 2010, 2011).

Kristjansson and colleagues (Kristjánsson et al., 2009) adopted a visual search paradigm, similar to the one described in Kiss et al. (2009), to investigate how unknown reward contingencies affected search performance. Interestingly, the effect of reward was analyzed at two different levels: a) in relation to color-value associations; and b) as a function of target repetition effects. Prior trials influence visual processing of items at subsequent encounters and this is generally measured as a benefit in the repetition of the same target singleton in successive trials, known as priming of pop-out (Maljkovic & Nakayama, 1994, 2000; Olivers & Meeter, 2006). In this work it has been shown how this phenomenon, considered resistant to top-down influences (Maljkovic & Nakayama, 1994), can be modulated by the reward value associated with objects. In Experiment 1, targets' colors were paired with either high or low reward with a fixed probability. Interestingly, not only performance was improved for highly valuable items, but automatic phenomena, such as repetition effects, were significantly affected by the actual reward feedback obtained in the preceding trial. This is an intriguing observation that suggests that objects' value is continuously and automatically updated and can have immediate effects in subsequent encounters.

This interesting work shows that reward history, here characterized by reward contingencies and immediately preceding encounters, can drive attention orientation in both bottom-up and top-down ways. Krebs and colleagues found coherent results in a cognitive control task, but they also significantly extended them suggesting that reward associations can impact performance also against current goals (Krebs et al., 2010, 2011) .

Krebs and colleagues designed an elegant experiment using a Stroop color-naming paradigm (Stroop, 1935) in which they demonstrated that reward can have an double impact on cognitive control (Krebs et al., 2010, 2011). Participants are required to name the ink color of a color word while ignoring its semantic meaning. Coherently with previous studies, reward associations sped up RTs by reducing the interference of incongruent irrelevant information when targets were highly rewarded. Crucially, reward associations also revealed to be detrimental for performance when the irrelevant color word was semantically related to the rewarded color. This critical result extends the impact of reward beyond current goals and shows how learned feature-reward associations can come into play even when they are detrimental for performance.

Growing evidence suggests that reward can affect attention and cognitive control in two distinct ways. Top-down, strategic or task related benefits can be induced by preparatory cues or learned reward associations. Moreover, under appropriate circumstances, also involuntary, bottom-up, and sometimes disadvantageous effects can be observed. In the last 10 years a growing body of research focused on this second type of effects of reward on visual cognition, addressing the impact of reward associations beyond current goals, when attending to more valuable objects can be detrimental for performance (e.g. Hickey et al., 2010a; Krebs et al., 2010), when reward is no longer delivered (e.g. Anderson et al., 2011b; Della Libera & Chelazzi, 2006, 2009), or when there is no consistent pairing between items and reward (e.g. Hickey et al., 2010a). In the next session, I describe in detail the paradigms and main results of such studies that constitute the relevant methodological framework for the experimental work reported in this thesis.

1.2 Automatic and non-strategic influence of reward on visual processes

The importance of reward history

As noted earlier, in most of animals and human studies, trials value is typically manipulated by changing either the amount of reward delivered for a correct response or the probability with which a reward is associated with a particular location or stimulus. Both manipulations have the effect of motivating individuals to mobilize resources for a more efficient control of attention in order to maximize success. Under these conditions the effects of reward on attention are hardly separable from those that can be elicited by any other cue or instruction inducing attentional deployment in a strategic fashion (Maunsell, 2004).

Recently, a growing number of studies has started to focus on non-strategic effects of reward, aiming at describing whether and how objects change their ability to recruit cognitive resources as a function of their reward history, without any overt advantage in prioritizing these objects over others in the current task. Different paradigms have been developed to this purpose, namely to investigate how exposure to items-reward associations affects the way these items are treated in future encounters. Two main lines of research can be identified on this respect: a) automatic immediate effects of reward feedback on subsequent encounters with the same stimuli in the absence of consistent object- or feature-reward associations; b) influence of learned object- or feature-reward associations during extinction.

The study of the immediate effects of reward feedback on visual perception derives from the literature on priming which documents the influence of recent selection history in the processing of newly encountered objects (e.g. Hickey, McDonald, & Theeuwes, 2006; Maljkovic & Nakayama, 1994, 2000; Tipper, 2001). According to this first line of research, the strength of priming effects can be modulated by the more or less rewarding consequences of previous acts of attentional selection (Della Libera & Chelazzi, 2006; Hickey & Peelen, 2015; Hickey & van Zoest, 2012; Hickey et al., 2010a; Hickey, Chelazzi, & Theeuwes, 2014; Hickey, Kaiser, & Peelen, 2015). Appropriate attention mechanisms engaged in performing a task, leading to selection or suppression of certain items, are reinforced, while less optimal ones, are suppressed. In other words, these studies suggest that mechanisms of visual selective attention can be adaptively adjusted to optimize the interactions with the environment.

Other approaches investigated the impact of learned reward-stimulus association in the absence of reward delivery, in what is known as extinction period (e.g. Anderson et al., 2011b; Pool, Brosch, Delplanque, & Sander, 2014; Raymond & O'Brien, 2009). Stimuli are imbued with a more or less positive value by means of a value learning procedure based on the reinforcement of appropriate attentional selections. Value learning paradigms can highly differ from experiment to experiment. Reward associations can be established by means of a single session training with a rewarded visual search task (Anderson et al., 2011b), or multiple training sessions distributed in consecutive days (Della Libera & Chelazzi, 2009); classical conditioning paradigms (Pool et al., 2014) or choice games (Raymond & O'Brien, 2009).

Both approaches have been used in the research reported in this thesis in order to address the impact of reward history on VWM, so it is worth describing more in depth the main differences and the individual specificities of the two general methods.

In a seminal work, Della Libera and Chelazzi (2006) adopted a modified version of the negative priming paradigm in which discrimination performance to a prime display was followed by a reward feedback before the appearance of a second probe display. Negative priming is a measure of the costs in selection of targets that have previously served as distractors and it is thought to rely on the lingering of inhibitory attention mechanisms (Tipper, 2001). The hypothesis motivating this study was that the strength of the inhibitory mechanisms triggered by prime processing could be sensitive to the more or less rewarding consequences of the response to the prime. In the first experiment, Della Libera and Chelazzi adopted a Navon-like paradigm (Navon, 1977) in which participants had to report either the local or the global digit displayed on the screen (e.g. the global number 6 could be composed by the distribution of small 5s in the appropriate configuration). Participants could obtain a high or a low reward feedback on their response. They were misled to believe that the amount of reward received was based on their performance, while it was in fact randomly assigned based on a predetermined schedule. Authors’ attention focused on the automatic influence of the amount of reward received on the following probe display, in which a second discrimination task was required. The authors reported a robust negative priming effect following highly rewarded responses to the prime stimuli, though the effect was eliminated when correct responses to the same stimuli were poorly rewarded. Analogous results were found in Experiment 2 with different stimuli (colored meaningless shapes) and task. These observations suggest that the attention mechanisms engaged to select a relevant target and to suppress a concurrent distractor were sensitive to the magnitude of reward obtained after response to the prime and were immediately coherently adjusted.

On a similar note, Hickey and colleagues (2010) have designed a task aimed at determining whether reward has an immediate and automatic low level impact on vision. They developed a paradigm based on the additional singleton paradigm (Theeuwes, 1991b) in which the magnitude of reward feedback was manipulated at the end of each trial. In the additional singleton paradigm participants searched for a shape singleton target presented among an array of uniformly colored distractors. In a subset of trials, an additional singleton, defined on a task irrelevant dimension such as color, was included in the visual search display. The color singleton captured attention and consequently delayed discrimination response to the target. The task-irrelevant color characterizing targets and distractors could repeat or swap from trial to trial producing benefits or costs in performance known as inter-trial priming (Hickey et al., 2006). Precisely, attention was driven towards items sharing the same features that characterized previous trials, resulting in faster responses when features were repeated from one target to the next and slower responses when colors swapped from one target to the following distractor. Hickey and colleagues provided participants with a high or a low reward feedback for correctly performing the task. Reward was randomly assigned and participants were explicitly informed that the amount of reward received was not linked to the target features and was not informative about the feature characterizing the upcoming trial. Results confirmed that the strength of priming was influenced by the magnitude of reward feedback received in the preceding trial. A high reward feedback produced a benefit in visual search for a target repeating the same task-irrelevant feature, but slowed responses when target and distractor features swapped. The opposite pattern of result was observed for low reward trials, suggesting that a poor outcome could cancel the cost of switch. Interestingly these results did not depend on participants strategically perseverating in selecting the previously rewarded item, because the same results were observed when participant were explicitly told that high reward feedback predicted a swap in target color (Experiment 1). When participants were able to strategically use the provided information to optimize performance (Experiment 2), the automatic effects of reward seemed to overcome the strategic attentional set adopted by participants.

Together these studies suggest that attentional mechanisms can flexibly and rapidly adapt to the more or less optimal consequences of a certain attentional set. In absence of reward feedback, priming effects show that cognitive processes can be adjusted online according to an internal evaluation of the consequences of recent selection, by means of an internal reinforcement mechanism that consolidates adaptive choices and devalues inappropriate ones (Roelfsema, van Ooyen, & Watanabe, 2010). The obtainment of an external reward feedback overwrites this internal evaluation and re-defines the most adaptive attentional mechanisms based on the external information. In particular, external reward feedback can yield to the reinforcement of attentional mechanisms that led to positive outcomes and the devaluation of those considered less optimal given the external feedback. Following this hypothesis, in Chapter 4 I report an experiment in which Hickey’s paradigm has been adapted to a visual working memory task to assess the cognitive and neural mechanisms underlying the impact of reward feedback on encoding and maintenance of visual representations in VWM.

While reward priming effects highlight the automaticity and flexibility of the reward influence in visual processing in conditions where reward is randomly assigned, other approaches have examined the effect of learned reward associations in absence of reward delivery: during extinction (Anderson et al., 2011a, e.g. 2011b; Della Libera & Chelazzi, 2009; Raymond & O’Brien, 2009; Rutherford, O’Brien, & Raymond, 2010). These associations are believed to leave behind memory traces that can guide attention for future tasks. The relevance of these studies is twofold: on the one hand, they highlight the ability of our brain to detect relevant contingencies in the environment and quickly learn to take advantage of them to optimize behavior; on the other, they show how these automatic biases continue to drive attention also when it is detrimental for performance, when, for example, such motivationally salient objects become task-irrelevant distractors.

Raymond and O’Brien (2009) have adopted a choice game paradigm with win and losses to imbue face stimuli with different valence and motivational salience in order to investigate how these factors affect the subsequent ability to recognize these objects. In this framework, the value learning procedure was based on the explicit choice of one face between two alternatives with the explicit goal to try to maximize the gains. Individual faces were characterized by different motivational salience, i.e. the degree of their ability to predict a certain outcome (either high or low) and the valence of that outcome (win or loss). This paradigm is quite different from those described previously because it is explicitly based on the ability to learn the expected value of each individual stimulus. In a following testing phase, the ability to recognize such items is assessed in conditions where attentional resources are more or less available. Results showed that motivationally salient objects are better recognized than less salient ones irrespective of their predictive value. However, only rewards prioritize processing of objects when low attentional resources are available, making them resilient to the attentional blink phenomenon (Raymond, Shapiro, & Arnell, 1992; Shapiro, Raymond, & Arnell, 1997).

The strength and generality of value learning procedures has been demonstrated also in studies implying primary rewards, instead of monetary ones, to modulate the affective relevance of otherwise neutral stimuli (Pool et al., 2014). Pool and colleagues adopted a Pavlovian conditioning paradigm to demonstrate that initially neutral stimuli can acquire the capacity to orient attention once they acquire affective relevance by the association with a primary reward such as a chocolate odor. They showed that reward associated figures were more efficient than neutral figures in the initial capture of attention in a spatial cueing paradigm (Posner, 1980), but that they would lose the ability to do so once they lost their affective relevance because of devaluation of the primary reward (satiation).

In these paradigms, a “simple” form of value learning has been employed, such that different objects have been paired with different outcomes, and consequently imbued with a positive, negative or neutral value, but no actual task is performed on these items during training. Other approaches have embraced a slightly more sophisticated hypothesis suggesting that reward or value does not simply benefit salience of the associated object, but affects a more specific prioritization process (Anderson et al., 2011b; Della Libera & Chelazzi, 2009).

Della Libera and Chelazzi demonstrated that attentional processing of objects can be durably adjusted according to the more or less rewarding consequences of prior attentional episodes concerning the same objects, persisting beyond the stop of reward delivery (Della Libera & Chelazzi, 2009). They designed an extensive training procedure distributed in three days in which participants performed a same/different task in which they had to compare the shape of a meaningless wire-frame target superimposed over a distractor with a reference. Different shapes were used during training and each of them was associated with a high reward or a low reward outcome with different probability. Some shapes were associated with higher probability to a high reward outcome when they were presented as targets while others only when they were presented as distractors. On the other hand, other shapes were mainly associated with low reward outcomes, some when they were presented as targets and some when presented as distractors. Participants were unaware of these associations and were made believe that the magnitude of reward feedback was determined by their performance. Participants were then tested several days later either on the same task (Experiment 1) or a simple visual search employing the same stimuli (Experiment 2), but no reward feedback was provided during test. Results showed that items that acted as good-outcome targets during training were easier to select when serving as targets (Experiment 2), but more difficult to reject when serving as distractors (Experiment 1), while poor-outcome targets were easier to reject when presented as distractors (Experiment 1), but more difficult to select when presented as targets (Experiment 2). Interestingly, a different pattern of results was measured for good and poor-outcome distractors. Items followed by favorable outcomes when correctly rejected during training were more difficult to select when presented as targets (Experiment 2) and easier to ignore when presented as distractors (Experiment 1). In contrast, poor-outcome distractors were easier to select when acting as targets (Experiment 2), but harder to select when presented as distractors (Experiment 1). The most interesting result of this experiment is that the impact of reward associations is dependent on the specific attentional process activated during learning. The authors suggest that “every episode of attentional selection leaves behind a memory trace that incorporates information about the specific items involved, the specific attentional processes applied to them, and, crucially, the adaptive value associated with the episode”. To account for the better inhibition of good-outcome distractors, it is necessary to assume that learning does not blindly benefit stimuli processing or representation, but specifically reinforces the attentional process engaged for the obtainment of that reward (e.g. target selection or distractor inhibition, but see Della Libera, Perlato, & Chelazzi, 2011; Hickey, Chelazzi, & Theeuwes, 2011).

Eventually, a further value learning procedure have been developed to describe how contextually irrelevant stimuli can capture attention (Anderson et al., 2011a, 2011b). In their first study, Anderson and colleagues measured the amount of capture elicited by irrelevant and non-salient objects imbued with value after a single session of training (in contrast to the multiple days of training used in Della Libera & Chelazzi, 2009), showing that reward associations can have long lasting effects also when established with brief training sessions (Anderson & Yantis, 2013; Anderson et al., 2011b). The authors designed a value learning procedure in which participants performed a visual search task where they had to identify a red or a green target among other differently colored distractors (Anderson et al., 2011b). Importantly, reward was provided for the correct discrimination of an oriented line presented inside the target, while, unbeknown to participants, the magnitude of reward feedback obtained for correct performance was defined by target color. One color was associated with higher probability to high reward (80% of the trials) than low reward (20% of the trials), while opposite odds were assigned to the other color. A short training session was sufficient to imbue colors with a high or low value such that in a following visual search task, while looking for a unique shape, performance would be significantly slowed by the presence of an irrelevant, non-salient and not-rewarding distractor that had been associated with high reward. Importantly, these results do not simply reflect the persistence in selecting previous targets, because analogous attentional capture effects are not detected when training is performed without reward manipulations. Furthermore, the authors reported that when items imbued with different reward values were presented as salient distractors, the strength of attentional capture during test was also modulated by the magnitude of associated reward (Anderson et al., 2011a).

In Chapters 2 and 3, I describe a value learning procedure modelled on the one introduced by Anderson and colleagues. In Chapter 2, a rewarded visual search task was used to imbue different colors with different reward associated values. In the following test, their influence on iconic and visual working memory performance was measured when they were presented as salient targets in an array of to-be-memorized objects. In Chapter 3, the training procedure, loosely based on Anderson and colleagues (Anderson et al., 2011b), was adapted to a visual working memory task. Participants performed a VWM task and were differently rewarded for their performance according to target color. During the test phase, the influence of feature-reward associations was measured on VWM representations of targets presented simultaneously with distractors of different value. Both studies documented the influence of learned reward associations in a VWM task during extinction. Importantly, in contrast to what found in previous studies (Anderson et al., 2011b), the influence of reward was visible both when reward-associated objects were salient singletons (Chapter 2) and when they were not (Chapter 3).

Cognitive and behavioral consequences of reward history

In the previous paragraph, I have already described the basic findings about the impact of reward history on mechanisms of deployment of attention, but interestingly reward influence extends more broadly to other aspects of visual cognition.

As mentioned before, reward associations have been shown to be able to emphasize salience-based attentional capture (Anderson et al., 2011a; Hickey et al., 2010a). In particular, highly valuable distractors are more efficient in capturing attention than equally salient, but less valuable ones. These observations reveal that learned value can influence attentional priority also in phenomena that are dominated by physical salience. Moreover, valuable objects can capture attention and disrupt performance when presented as distractors even when they are not physically salient (Anderson et al., 2011b), suggesting that reward association can directly increase objects saliency.

These observations suggest that attention is oriented towards the location occupied by the reward associated item which gets prioritized processing. Location specific inter-trial effects indicate a modulation of RTs to targets presented at locations previously occupied by highly valuable objects (Anderson et al., 2011b; Hickey et al., 2014). On the one hand, responses to a target are delayed when it appears in a location occupied by a high-value distractor on the previous trial (Anderson et al., 2011b), suggesting not only that attention is drawn at that location but also that the following suppression of the valuable distractor leaves an inhibitory trace at that location that hinders target discrimination. By contrast, locations occupied by previously rewarded items tend to receive prioritize analysis in future encounters, thus facilitating processing in case of targets and disrupting performance in case of distractors (Hickey et al., 2014).

While there is clear evidence that objects with reward history can capture attention and influence response speed in visual search tasks (Anderson et al., 2011a, 2011b; Della Libera & Chelazzi, 2006, 2009; Hickey et al., 2010a; Hickey, Chelazzi, & Theeuwes, 2010b), less is known about whether and how reward associations significantly changes behavior and exploration of the environment. In recent years, some studies have started to assess the influence of reward associations on eye movements reporting a direct evidence for spatial displacement of attention, expanding the boundaries of reward impact directly on overt behavior (Anderson & Yantis, 2012; Hickey & van Zoest, 2012, 2013; Theeuwes & Belopolsky, 2012). Saccade trajectories to targets are deviated by the onset of reward associated distractors even when their location is known in advance (Hickey & van Zoest, 2012). Moreover salient distractors have an higher probability of producing oculomotor capture when they share a feature with a previously selected and highly rewarded target (Hickey & van Zoest, 2013) or when they have been associated with higher value and they are not currently rewarded (Theeuwes & Belopolsky, 2012). These studies reveal a pattern of effects in oculomotor capture that resembles that produces by physically salient distractors (Godijn & Theeuwes, 2004), supporting the interpretation that valuable objects become more salient and can capture attention. Taken together, these studies support the conclusion that reward-driven selection involves low-level and non-strategic mechanisms that act automatically, biasing exploration of visual scenes towards objects that have led to positive outcomes in previous encounters.

Beyond affecting attentional capture, it has been argued that influence of reward associations also extends to other cognitive processes. Della Libera and Chelazzi reported that valuable distractors were indeed more difficult to select when presented as targets, but also easier to ignore when presented as distractors (Della Libera & Chelazzi, 2006, Experiment 1) proposing that the attentional set recruited to perform a task is adjusted according to the more or less rewarding consequences it leads to. However, a subsequent study did not fully replicate these results and suggested that reward associations can mainly prioritize or hinder target selection, while they cannot make distractors easier to suppress (Hickey, Chelazzi, et al., 2011).

Attention is strongly and deeply interconnected with a variety of other cognitive processes and plays a pivotal role in visual cognition. Therefore, it is not surprising that reward associations, either by enhancing the representation or by recruiting cognitive resources, emphasize conflict in control tasks (Anderson, Laurent, & Yantis, 2012; Krebs et al., 2010) or modulate context effects in cognitive control (Braem, Hickey, Duthoo, & Notebaert, 2014). In particular, attention and visual working memory are two processes that are strongly interconnected (Awh, Vogel, & Oh, 2006; Gazzaley & Nobre, 2012; Zanto et al., 2011) and the consistent effects of reward on attention measured with different paradigms raises the question of whether reward associations would improve memory performance for the reward-associated items as well.

Objects predictive of positive or negative outcomes are recognized more quickly and more easily than non-valuable objects (O’Brien & Raymond, 2012); moreover reward associated objects are identified also when the cognitive resources available are limited, partly overtaking the costs of attentional blink (Raymond & O’Brien, 2009). Interestingly, a recent study showed that learned feature reward associations can influence VWM as well (Gong & Li, 2014).

Only a limited subset of visual information that is perceived can be selected and transferred into the VMW, where it can be actively maintained for several seconds (Cowan, 2001). Gong and Li (2014) reported that VWM capacity can be enhanced when targets had been associated with high reward by means of a value learning procedure. They showed that change detection performance was increased for items associated with high reward (Experiment 1), but not for non-valuable physically salient items (Experiment 2). Interestingly, an increase in VWM capacity was observed not only when one single reward-associated object was present on the display (Experiment 1), but also when all the relevant items were rendered in the same color (Experiment 3). This result suggests that reward can directly benefit the encoding of reward associated objects in a way that goes beyond attentional capture.

Despite reward was no longer provided during the test phase, it is difficult to exclude that these results do not reflect the perpetuation of previously advantageous strategies. Indeed, participants might engage more resources in memorizing objects that they have learned to be more valuable, given that perpetuating with this strategy produces no actual cost. In one of the studies reported in this thesis (Chapter 3), the reward value associated with distractors was manipulated during the test phase, rendering disadvantageous the persistence of strategies adopted during training. Nonetheless, a clear influence of learned feature-reward associations was observed.

In two experiments in Chapter 2, the influence of learned reward associations in visual memory representations is investigated at different intervals from the offset of a memory display, from the early stages of iconic representations towards later phases in visual working memory. In contrast to previous reports (Gong & Li, 2014; Kawasaki & Yamaguchi, 2013), in this study there was no evidence for a direct benefit of reward on VWM capacity, nevertheless a clear index of reward influence on memory was observed. Both at short and at long intervals from memory display offset, the response to the target was significantly affected by the information conveyed by the adjacent salient item when it was associated with high reward (*interference effect*). Results suggested that reward associated object interfere with VWM representations of neutral items presented together in nearby locations. Since no difference was observed in the amplitude of the interference at different time intervals from the offset of memory display, we hypothesized that valuable items can influence the content of VWM by means of driving the process of encoding information in memory.

The extent and limits of reward influence in visual cognition

Reward has been shown to effectively influence processing of specific stimuli, specific individuals of a certain category that are predictive of reward outcome, such as outlined nonsense shapes (Della Libera & Chelazzi, 2006, 2009; Della Libera et al., 2011), faces (Raymond & O’Brien, 2009), geometric figures (Pool et al., 2014). However, it is interesting to notice that reward can also be associated with simple visual features. In fact, most of the studies in the literature of reward influence on visual perception focused on how simple visual features, specifically color, showing that they can be imbued with different reward values and drive exploration. Importantly, this seems to influence the perception of the rewarded color also when it is presented in different contexts (Anderson & Yantis, 2012) and it also generalizes to its abstract meaning (Krebs et al., 2010). In an ecological context, being able to recognize color-reward associations has a clear adaptive value, for example helping to distinguish a sweet and juicy fruit from an unripe one. Color however is a very salient feature and it is important to verify how pervasive reward associations can be. In fact, it has been shown that reward can be effectively associated with other simple visual features such us orientation (Theeuwes & Belopolsky, 2012) and direction of motion (Seitz, Kim, & Watanabe, 2009). Interestingly, it has been recently shown that reward can also promote the processing of a whole category of objects when it is associated with positive outcomes, independently of the specific instantiations of that category (Hickey et al., 2015). This suggests that according to the task performed, the reward association can work at different levels, relying on simple features, individuals or whole categories. Lastly, different reward values can be paired not only with items, but prioritize also the processing of information presented at reward associated locations (Hickey et al., 2014) or moments in time (Hickey & Los, 2015).

Taken together, these observations show that reward can have a very wide influence on the way we process visual information and this strongly depends on the task performed and on the specific cognitive processes that are required to efficiently perform the task.

Beyond being very general, the influence of reward history on visual perception appears to have robust and durable effects. Once established, object-reward associations keep influencing attention deployment in similar context days (Della Libera & Chelazzi, 2009; Della Libera et al., 2011) also several months later without further training (Anderson & Yantis, 2013).

As noted before, these effects do not emerge only when it is advantageous for performance, but also when the prioritization of reward associated objects plays against current goals (Hickey & van Zoest, 2012; Hickey et al., 2010a), suggesting that reward influence on visual processing does not depend on top-down attentional set (Hickey & van Zoest, 2013; Munneke, Hoppenbrouwers, & Theeuwes, 2015).

In Chapter 3 I report a series of experiments aimed at assessing the limits of reward influence of visual processing, specifically testing under which circumstances learned feature-reward associations are effective in influencing visual representations in VWM and when, on the other hand, they fail. In particular, influence of reward in VWM is assessed in conditions of increased attentional demands for target selection showing that the interference of reward-associated distractors is negligible when fewer resources are available for distractors processing.

Neural evidence of reward influence in visual cognition

In line with behavioral evidences, a handful of electrophysiological studies have shown that sensory and perceptual processing of reward associated objects is facilitated compared to less valuable ones as reflected in increase in amplitude of early components of visual processing such as P1 and N2pc (Hickey et al., 2010a; Qi, Zeng, Ding, & Li, 2013). The P1, a lateralized component which reflects early visual processing in extra-striate visual cortex and is not normally sensitive to endogenous attentional set (Hillyard, Vogel, & Luck, 1998), increases in amplitude in trials preceded by the obtainment of a high reward feedback (Hickey et al., 2010a). Specifically, an increase in amplitude of the P1 contralateral to the target was observed when target features were repeated in the following trial, while an increase in amplitude of P1 contralateral to distractor was measured when target features were swapped. No corresponding patterns were observed after low reward. These results show that reward can have a very early impact in visual processing (see also Pool et al., 2014) and support the hypothesis that values have a direct effect on human perception, automatically increasing salience of valuable objects. Similarly to the P1, also the N2pc was modulated in amplitude as a function of the amount of reward obtained in the preceding trials and the repetition or swap or target and distractor irrelevant features.

Analogous changes in N2pc amplitude have been also documented for non-salient distractors that had been associated with high reward but were not currently rewarded (Qi et al., 2013). When a non-salient but valuable distractor was presented on the side of the screen opposite to target location, two N2pc components were elicited: the distracter-elicited N2pc followed by the target-elicited N2pc with opposite polarity. Despite this pattern of results provides compelling evidence for the attentional capture hypothesis, it was not observed on all trials, but only for those leading to slow RTs to the visual search task, and thus when reward associated distractor efficiently captured attention. By contrast, in fast RT trials, the emergence of a Pd component, reflecting active distractor suppression (Hickey, Di Lollo, & McDonald, 2009; R. Sawaki, Geng, & Luck, 2012; Risa Sawaki & Luck, 2010), suggested that in order to efficiently select task-relevant targets, the valuable distractor had to be actively suppressed.

Interestingly, Hickey and colleagues (2010a) suggested that the impact of reward on performance was mediated by an underlying interaction between processing of reward feedback in dopaminergic structures in the midbrain and visual processing in the cortex. Clearly, no direct measure of midbrain activity could be detected with scalp recordings. However, the authors indexed the individual sensitivity to reward feedback with the amplitude of the medial frontal negativity (MFN), considered to reflect the evaluation of the motivational impact of an event such as a reward feedback (Gehring & Willoughby, 2002). The source of this component was located in the anterior cingulate cortex (ACC), an area with strong connections to dopaminergic structures in the midbrain. Interestingly, participants who were more sensitive to the obtainment of reward as indicated by MFN modulation, showed larger impact of reward associations in visual processing and attentional deployment towards reward associated objects. Recently the connection between the observed effects of reward in vision and the dopamine system has been made more explicit by showing that the strength of BOLD response in dopaminergic midbrain predicted the enhancement of encoding of reward-associated targets and the suppression of reward-associated distractors in visual cortex (Hickey & Peelen, 2015).

These observations suggest that reward influences processing of visual stimuli already at early stages (Hickey et al., 2010a). By contrast, the study reported in Chapter 4 addresses the hypothesis that, according to the specific requirements of the task performed, reward could also influence other stages of visual processing, namely active maintenance of visual information in VWM. To test this hypothesis, the influence of reward is assessed on different components of evoked potentials measured while participants perform a VWM task.

Previous studies, investing strategic effects of reward on visual processing, have reported that objects value not only modulates N2pc amplitude, reflecting target selection, but also the following CDA component suggesting further impact on the analysis of the selected target (Kiss et al., 2009). In Chapter 4, I report the results of an electrophysiological study that investigates such post-selection processes in the absence of motivational incentives. While experiments described in Chapters 2 and 3 reported effects of interference in VWM representations that could be easily interpreted as the consequence of benefits in visual encoding of reward associated objects because of their increased salience and therefore capacity to capture attention; other studies have shown benefits in VWM capacity also in absence of competition between reward associated and non-reward associated objects, excluding a benefit resulting from attentional capture (Gong & Li, 2014). However, none of the previous studies directly addressed whether reward influence in a VWM task benefits encoding or maintenance stages of visual processing. The work reported in Chapter 4 starts to investigate this issue by evaluating which components in the evoked scalp activity are affected by reward associations. Specifically, the aim of the study was to assess whether a benefit in VWM could be measured in the absence of detectable changes in the deployment of attention. Interestingly in the specific task we adopted, it was possible to highlight an effect of reward on maintenance stages only, reflected in modulation of CDA amplitude, while no changes were observed for N2pc.

In the next chapters I report evidence for reward influence on visual representations stored in VWM at different stages of visual processing, namely encoding and interestingly also maintenance. A possible interpretation for these results is that more resources are recruited for processing and maintaining objects that have been associated with positive outcomes in the past and consequently more precise representations can be created and maintained. However, the study of reward influence on VWM is just at the beginning and further work is necessary to explicitly test this interpretation.

2 Reward associations impact both iconic and visual working memory

Adapted from: Infanti, E., Hickey, C., & Turatto, M. (2015). Reward associations impact both iconic and visual working memory. Vision research, 107, 22-29.

2.1 Abstract

Reward plays a fundamental role in human behavior. A growing number of studies have shown that stimuli associated with reward become salient and attract attention. The aim of the present study was to extend these results into the investigation of iconic memory and visual working memory. In two experiments we asked participants to perform a visual-search task where different colors of the target stimuli were paired with high or low reward. We then tested whether the pre-established feature-reward association affected performance on a subsequent visual memory task, in which no reward was provided. In this test phase participants viewed arrays of 8 objects, one of which had unique color that could match the color associated with reward during the previous visual-search task. A probe appeared at varying intervals after stimulus offset to identify the to-be-reported item. Our results suggest that reward biases the encoding of visual information such that items characterized by a reward-associated feature interfere with mnemonic representations of other items in the test display. These results extend current knowledge regarding the influence of reward on early cognitive processes, suggesting that feature-reward associations automatically interact with the encoding and storage of visual information, both in iconic memory and visual working memory.

2.2 Introduction

Rewards play a fundamental role in human cognition. The ability to learn reward contingencies in the environment is crucial to anticipate positive or negative outcomes and optimize value-oriented behavior. Rewards can accordingly act as motivational incentives, guiding the deployment of cognitive resources in order to effectively orient attention and prioritize processing of task relevant information (Engelmann et al., 2009; Pessoa & Engelmann, 2010; Pessoa, 2009; Watanabe, 2007).

A growing number of studies have shown that learned stimuli-reward associations can modulate the allocation of attention when rewards are no longer provided (for a review see Chelazzi et al., 2013). Reward associations appear to automatically bias selective attention in favor of the associated object or feature even when individuals are not aware of the established feature-reward associations. Importantly, the processing of reward associated stimuli is prioritized when this confers no strategic advantage, and perhaps even when it creates a performance cost (Anderson, Laurent, & Yantis, 2011a, 2011b; Della Libera & Chelazzi, 2006, 2009; Krebs, Boehler, & Woldorff, 2010). Initially neutral visual features that have been linked to reward through experience seem to subsequently become salient, acquiring the ability to draw attention in space (Anderson, Laurent, & Yantis, 2011a, 2011b; Della Libera & Chelazzi, 2006, 2009; Hickey, Chelazzi, & Theeuwes, 2010a, 2010b, 2011) and time (Hickey & Los, under review; Raymond & O'Brien, 2009), and to drive oculomotor capture (Anderson, Laurent, & Yantis, 2012; Hickey & van Zoest, 2012, 2013; Theeuwes & Belopolsky, 2012). These results have led to the proposal that reward may act on attention through a mechanism that is independent of the traditional dichotomy of bottom-up and top-down processes (Awh, Belopolsky, & Theeuwes, 2012).

While increasing effort has been made in the last years to study the influence of learned value associations on attentional and visual search tasks, fewer studies have been dedicated to the relation between reward and other cognitive processes. With the present study, we aim to expand the existing literature addressing the non-strategic influence of reward-value associations on the encoding and storage of information in visual memory.

Memory is the "neurocognitive capacity to encode, store, and retrieve information" (Tulving, 2000). In the visual domain, the early stages of visual memory have been classically distinguished in iconic memory (IM) and visual working memory (VWM). IM is a high capacity, fast decaying storage system where visual representations are encoded and stored only for a few hundreds of milliseconds after the offset of briefly presented stimuli (Coltheart, 1980; Neisser, 1967). Only a limited subset of the information retained in IM is then selected and transferred into the limited-capacity system of VMW, where it can be actively maintained for several seconds (Cowan, 2001). VWM is a system with limited resources where capacity is limited in terms of number of items that can be remembered and accuracy of the encoded representations (Alvarez & Cavanagh, 2004; Bays & Husain, 2008; Bays, Catalao, & Husain, 2009; Zhang & Luck, 2008). Whether information is selected and transferred from IM to VWM depends on its relevance for subject's goals as well as perceptual properties of the visual input (Belopolsky, Kramer, & Godijn, 2008; Schmidt et al., 2002).

Recent studies have demonstrated that incentives can improve performance in a visual memory task, increasing VWM capacity (Kawasaki & Yamaguchi, 2013) and speeding response times for the most valuable stimuli (Krawczyk, Gazzaley, & D'Esposito, 2007). Interestingly, learned feature-reward associations have been shown to influence VWM also in the absence of direct incentive motivation, when rewards are no longer provided. Learned item-reward associations lead to enhanced VWM capacity for stimuli associated with high compared to low reward (Gong & Li, 2014).

The current study was designed to further characterize the influence of reward on the early stages of visual memory. On the one hand, we aimed to describe the influence of learned feature-reward associations on visual memory over time, from the earliest sensory storage of IM gradually moving to VWM. On the other, we wanted to investigate how the presence of a previously reward-associated item in the memory array influences the capacity to encode and store the identity of other neutral items in the display.

To address these issues, we combined a value-learning procedure with a visual memory task. During value-learning participants performed a visual search task loosely based on that employed by Anderson, Laurent, and Yantis (2011). Two magnitudes of reward outcome were associated with two colors that characterized the target object. Participants conducted a visual memory task immediately after this training. In this test phase they were presented with a number of items arranged in a circle, where a probe identified a single item in the array and participants reported the orientation of a line element within this item. Importantly, one of these items could have the color associated with reward during training, rendering it a *color singleton*. This item was no more likely to act as memory target than any of the other elements in the array.

Our test task was modeled on the partial report technique introduced by Sperling (1960). By presenting the probe at short or long delays after stimulus offset, Sperling used this task to investigate the content of IM independent of the limitations of working memory. As compared to full report paradigms, where observers are able to report around 3 to 5 items from the memory array, partial report studies suggest the presence and availability of much more information at short probe delays (i.e. partial report superiority).

We approached our results with interest not only in raw accuracy, but also in the interference created when a singleton stimulus was present in the display and participants were probed to report a non-singleton item. We quantified this interference effect as the accuracy difference between conditions where the response associated with the line inside the singleton was congruent to that of the line inside the probed target (same response, *congruent trials*) versus when it was incongruent (different response, *incongruent trials*; see Theeuwes & Burger, 1998). This measure was examined for modulation as a function of the color-reward association established during the training phase.

Our hypothesis was that learned reward associations could act on visual memory at different levels, influencing IM, VWM, or both. To foreshadow, we did not find direct evidence for enhancement of visual memory performance for a reward associated item, but we did observe a stronger interference effect on performance when an irrelevant singleton had its color associated with high-magnitude reward. This interference effect was insensitive to the timing of the probe, suggesting that the entrained reward association impacted both IM and VWM.

2.3 Experiment 1

Methods

Participants. Thirty students of the University of Trento (26 female) participated in the experiment. Mean age was 22 (ranging from 19 to 37). All had normal or corrected-to-normal vision, normal color vision, and were naïve to the purpose of the experiment. Participants were reimbursed for their participation, with compensation varying between 7.50€ and 9€ based on performance. Written informed consent was obtained from all participants and the experiment was carried out in accordance with the Declaration of Helsinki and was approved by the local Ethics Committee.

Apparatus. Stimuli were presented on a gamma-calibrated ViewSonic Graphic Series G90fB 19’’ CRT monitor (1024 x 768) at a refresh rate of 100Hz. Participants were seated in a dimly illuminated room approximately 60 cm from the display with their head supported by a chinrest. Stimuli were created using a custom Matlab script (Mathworks Inc., Massachusetts, USA) and the Psychophysics Toolbox 3.8 (Brainard, 1997; Pelli, 1997).

Stimuli. All stimuli appeared on a uniform gray background (2.58 cd/m^2) and were regularly displaced along an imaginary circle at a radius of 5° of visual angle from the fixation point (0.12° in diameter). Stimuli were light gray lines (36.1 cd/m^2; 1.5°x0.12°) oriented vertically or horizontally, presented inside a circle of 2° diameter (width 0.12°). We selected 7 colors to assign to the circles and these colors were adjusted to be physically equiluminant (~24 cd/ m^2).

Procedure. The experiment lasted for about an hour and was structured in two parts. ***Visual Search Training***. In the training phase participants completed a visual search task where the target was defined by one of two colors, one associated with high reward and one associated with low reward (Figure 2.1A). The training began with 40 practice trials which were followed by 480 experimental trials divided in 8 blocks. Each trial began with a fixation display; after a variable delay of 400, 500, or 600 ms a visual search display was presented for 100 ms. The search display consisted of 6 gray lines each surrounded by a uniquely colored circle. Targets were defined as circles of one of two possible colors and only one of them could be presented in each trial. Participants were instructed to report as fast and as accurately as possible the orientation of the line inside the target circle, pressing “m” for vertical or “z” for horizontal on a standard computer keyboard. Feedback was provided for 1500 ms beginning immediately after response. The feedback display was identical to the memory display except that light gray text indicating the number of earned points was overlaid at the center of the screen subtending about 1° of visual angle. Participants received either “+01” points or “+10” points for correct responses (10 points corresponded to €0.032). No points, indicated with three dashes “---“, were assigned for incorrect responses or trials where participants failed to response within 1400 ms. At the end of each block participants received feedback about the overall number of points accumulated.

Participants were informed prior to beginning the training procedure that one of the two target colors was associated with high and the other to low reward. The reward schedule was probabilistic such that correct responses with high reward targets were followed by high reward on 80% of trials and by low reward in 20% of the trials (and vice versa for low reward targets). The two target colors were selected among three alternatives (red, green or blue). The non-target color was assigned to one of the distractors presented in the search array. Target color and value were counterbalanced across participants. Target identity and location were fully balanced for each participant and presented in random order.

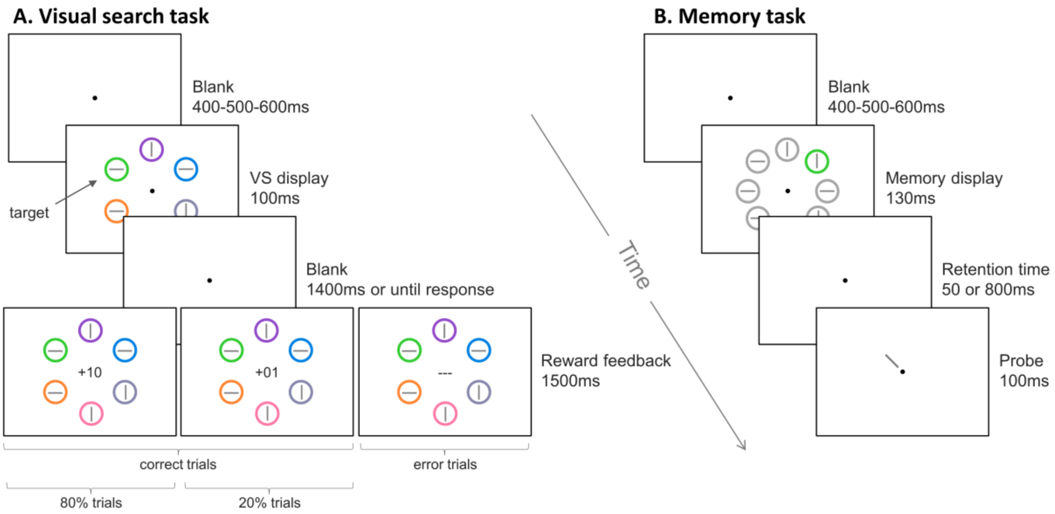

Figure 2.1 Experimental design

(A) Visual search task. A visual search display of 6 elements was presented for 100 ms after a variable fixation delay. Either a green or a red target was presented in each trial and participants reported the orientation of the line inside it. Participants' response was followed by a feedback display that indicated the number of points that were earned on each trial. The feedback did not depend on participants speed, but was determined by means of the probabilistic schedule: for each participant either red or green target were associated with high reward in 80% of the trials and to low reward in the remaining 20% of the trials (green in the illustrated example); the opposite association was made for the other color. **(B)** Memory task. A memory array of 8 elements was presented for a 130 ms. All but one item were gray. The uniquely colored circle could be defined by a color previously associated with a high or low reward target or a distractor. After a variable delay (50 or 800 ms) a line appeared and indicated one of the 8 locations. Participants' task was to report the orientation of the line presented at the probed location. All locations were selected with the same probability. Neither reward nor feedback was provided during this task.

Iconic and Visual Working Memory Test. In the test phase participants completed a visual memory task where the to-be-remembered target was identified by a probe (Figure 2.1B). Importantly, at this stage of the experiment participants were not rewarded for performance. After 20 practice trials, the experimental session began with 480 experimental trials divided in 6 blocks. Memory trials started with a fixation cross that sustained for a random interval of 400, 500, or 600 ms before being replaced by the memory array for 130 ms. The memory array consisted of 8 circles evenly spaced around fixation, all of but one with gray color. The uniquely colored circle could be defined by a color that had characterized high-reward targets, low-reward targets, or distractors during training. After a 50 or 800 ms delay a line cue (3°x0.05°) indicated the memory target for 100 ms.

Each item in the memory array was probed with equal probability. Participants were required to report the orientation of the line seen at the probed location using the keyboard (“m” for vertical; “z” for horizontal”). Responses were unspeeded and accuracy was emphasized, but no feedback was provided. Target identity and position was fully counterbalanced and trials were randomly presented during the experiment.

Analyses and Results

Visual Search training performance. Statistical analysis of response times (RTs) over the course of training in the visual search task took the form of a repeated measures analysis of variance (ANOVA) with time (trials were divided in 4 bins of 120 trials each) and target-color-association (high-reward color vs. low-reward color) as factors. RT was significantly faster for high reward targets (main effect of reward F(1, 29) = 4.80; p = .037; η_p^2 = .14) and became faster over the course of the training (main effect of time F(1.8, 51.9) = 19.03; p < .001; η_p^2 = .40) but these factors did not interact (F(3,87) = .67; p = .571; η_p^2 = .02). A similar ANOVA based on arc-sine transformed accuracy revealed an improvement over the course of training (F(2.3, 65.3) = 28.1; p < .001; η_p^2 = .49) but no effect involving target-color-association (F(1, 29) = 3.08; p = .090; η_p^2 = .10; interaction: F < 1). Note that statistical results here and below reflect Greenhouse-Geisser corrected degrees of freedom where appropriate.

These results suggest that participants successfully learned the reward contingencies and became faster in recognizing the targets when they were associated with high reward value.

Iconic and Visual Working Memory task performance. Statistical analysis of the visual memory task began with a repeated-measures ANOVA of arc-sign transformed accuracy values with factors for target color (unique color vs. gray), singleton color-reward association (high-reward vs. low-reward vs. distractor color) and probe-delay (50 ms vs. 800 ms). Accuracy was significantly higher for singletons than non-singleton items (F(1,29) = 58.33; p < .001; η_p^2 = .67) and for short compared to long delay (F(1,29) = 6.26; p = .018; η_p^2 = .18). We accordingly examined performance for singleton and non-singleton targets separately. Accuracy for singletons was significantly higher at the short delay (F(1, 29) = 4.26; p = .048; η_p^2 = .13), but no effect of reward-color association was observed (F(2, 58) = .11; p = .898; η_p^2 = .00) and these factors did not interact (F(2,58) = 1.16; p = .321; η_p^2 = .04). Analysis of accuracy for gray items also revealed a main effect of delay (Figure 2.2; F(1, 29) = 4.59; p = .041; η_p^2 = .14), but no effects of singleton-reward-association (reward: F(2, 58) = 1.15; p = .325; η_p^2 = .04; reward X delay: F(2, 58) = .16; p = .850; η_p^2 = .01). Additional analyses of RTs for correct responses, in the form of a repeated-measures ANOVA with target color (unique vs. gray), probe-delay (50 ms vs. 800 ms) and reward (high-reward vs. low-reward vs. distractor color) as factors, revealed a trend for shorter RTs for singletons than gray items (color: F(1, 29) = 4.16; p = .051; η_p^2 = .13), but no other significant results (delay: F(1, 29) = 3.34; p = .078; η_p^2 = .10; color X delay: F(1, 29) = 3.45; p = .073; η_p^2 = .11; all other Fs <1).

Analysis of interference took the form of a 3x2 repeated measures ANOVA with factors for singleton-color-association (high-reward color vs. low-reward color vs. distractor color) and probe-delay (50 ms vs. 800 ms). This revealed a main effect of reward (Figure 2.2; F(2, 58) = 3.17; p = .049; η_p^2 = .10), but no effect of probe-delay (F(1, 29) = 2.33; p = .138; η_p^2 = .07) and no interaction (F(2, 58) = 0.69, p = .933, η_p^2 = .00). Given that delay had no reliable impact on the memory performance we collapsed the data across this factor in subsequent analyses. Pairwise comparisons (t test) revealed significant differences in the interference effect when the singleton was characterized by the high-reward versus neutral color (t(29) = 2.26; p = .030; Cohen’s d = .50) and a trend towards a difference when the singleton was characterized by high-reward versus low-reward color (t(29) = 1.99; p = .056; Cohen’s d = .52). There was no difference when the singleton was characterized by the low-reward versus neutral color (t(29) = -.02; p = .981; Cohen’s d = -.01).

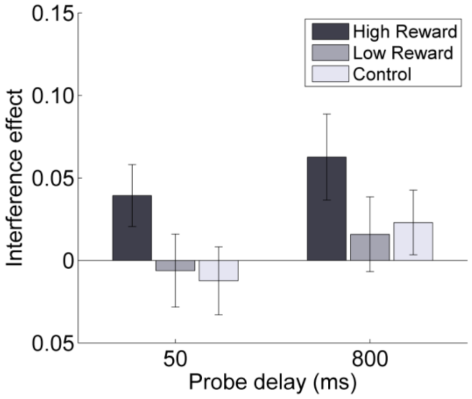

Figure 2.2 Experiment 1: interference effect in memory task.

The interference effect is an index of interference in memory performance for the target as a function of the congruency of the response to the singleton (it was computed as the difference in accuracy between congruent and incongruent trials). The interference effect was dependent on reward history and was strongest for high reward associated colors compared to low reward associated color or control. Errorbars here and below represent SEM.

We conducted an additional analysis to examine the impact of target-singleton distance on the interference effect (Figure 2.3). To this end we conducted an ANOVA similar to that described above but with an added factor for the distance of the probed item from the singleton (distance zero: no items between target and singleton, distance one: one item between; distance two: two items between). This revealed a) that the interference effect was strongest for items closer to the singleton (main effect of distance F(2,58) = 9.08; p < .001; η_p^2 = .24), and b) that the interference effect was dependent on reward (F(2,58) = 3.31; p = =.044; η_p^2 = .24). No significant interaction between reward and distance was observed (F(4,116) = 1.74; p = .145; η_p^2 = .06) and no other main effects or interactions were detected (all Fs <1). An analogous measure of interference was computed for RTs (difference in RTs for congruent and incongruent trials), but analysis revealed no significant effects (delay: F(1,29) = 1.54; p = .224; η_p^2 = .05; reward: F(2,58) = 1.59; p = .213; η_p^2 = .05; delay X reward: F(2,58) = .16; p = .849; η_p^2 < .01).

Follow-up analyses revealed that when the probed item was adjacent to the singleton a strong main effect of reward could be detected (10% difference in accuracy; F(2,58) = 5.29; p = .008; η_p^2=.15). Planned contrasts confirmed that the interference effect was larger when the singleton had high-reward versus low reward color (t(29) = 2.28; p =

.030; Cohen's d = .51) and when the singleton had high-reward versus neutral color (t(29) = 3.2 ; p < .001; Cohen's d = .72), but that there was no difference when the singleton had low-reward versus neutral color (t(29) =. 8; p = .429; Cohen's d = .18). The interference effect was negligible and was not significantly modulated by reward at other target-singleton distances (1-away: mean = -2%, se = 2%, 2-away: mean = 0%, se = 2%).

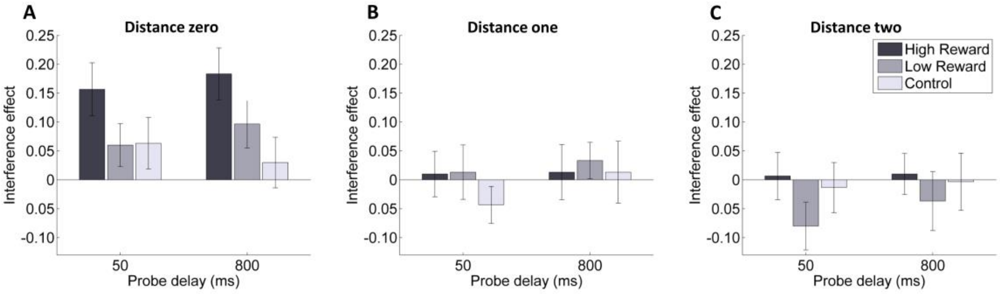

Figure 2.3 Experiment 1: interference effect as a function of target-singleton distance.

The strength of the interference effect is modulated as a function of distance of target and color singleton. **(A)** Interference effect at distance zero (no items between target and singleton). **(B)** Interference effect at distance one (one item between target and singleton). **(C)** Interference effect at distance two (two items between target and singletons).

A core goal of Experiment 1 was to test the idea that an object characterized by a reward-associated color would be better represented in visual memory. Results in fact show that such an object will interfere with the mnemonic representation of other items in the array, supporting this notion. Experiment 1 had an additional purpose, namely to test whether the reward effect might be specific for a particular type of memory, and thus differentially impact IM or VWM representations. To test this we included two probe-delays in Experiment 1, 50 ms and 800 ms, under the assumption that the short probe would index representation in IM and the long probe VWM. However, results showed no difference as a function of this manipulation. This null result may simply reflect insufficient power to detect a difference, and with this in mind we ran a second experiment. This importantly included a larger number of probe-delays with the intent of identifying a systematic variation in the reward effect over levels of this manipulation.

2.4 Experiment 2

Methods

Participants. A new group of 20 students of the University of Trento (13 females) took part in Experiment 2. The mean age of participants was 22 (ranging from 19 to 36). All had normal or corrected-to-normal visual acuity and color vision and were all naïve to the purpose of the experiments. Participants were reimbursed for their participation; the overall compensation could vary between 8€ and 10€ based on their performance. All participants gave their written consent to the participation to the experiment. The experiment was carried out in accordance with the Declaration of Helsinki and was approved by the local Ethics Committee.

Stimuli and procedure. Display settings and stimuli were as in Experiment 1 and the training procedure was unchanged. The aim of Experiment 2 was to better characterize the temporal dynamics of the effect of reward on memory. To this end we had the memory probe appear at four temporal delays (10 ms, 50 ms, 100 ms and 500 ms).

While we maintained the structure of the memory display as in Experiment 1, only a subset of the 8 possible locations was probed. The rationale behind this change was to increase power to detect modulation of the interference effect, which was strongest at the location adjacent to the singleton in Experiment 1. Only 5 of the 8 locations of the memory display were probed: the position occupied by the color singleton (16% of trials), the two adjacent locations at distance zero (20% of the trials at each location) and the two locations at distance two (22% of the trials at each location). We adopted this distribution in order to avoid participant adoption of a strategic bias toward the items centered around the color singleton. Note that while probe location was not fully random in this design, the target location was not rendered predictable and the location of the singleton was fully counterbalanced and randomly presented during the experiment.

Experiment 2 was substantially longer than Experiment 1, with 320 additional working memory trials. With this in mind we divided the experiment into two identical sessions, each consisting of a training and test procedure. Each of the two training sessions comprised 240 trials of the visual search task, with each test session constituting 400 trials of the memory task. Participants took a short break between sessions. Our purpose here was to reduce the potential for extinction of the reward-color association over the course of the memory task (eg. Anderson, Laurent, & Yantis, 2011b).

Analyses and Results

Visual Search training performance. Participants were faster (F(1, 19) = 15.81; p =.001; η_p^2 =.45) and more accurate (F(1, 19) = 6.28; p = .021; η_p^2 = .25) in responding to high reward targets. Moreover, a significant improvement in performance over time was measured in accuracy (F(3, 57) = 32.84; p < .001; η_p^2 = .63), but not response latency (F(3,57) = 1.71 ; p = .174; η_p^2 = .08). No significant interactions were observed (all Fs < 1).

Iconic and Visual Working Memory task performance. As was the case in Experiment 1, we first analyzed the raw accuracy in the visual memory task by means of repeated measures ANOVA with factors for color (unique color vs. gray) and probe-delay (10ms vs. 50 ms vs. 100 ms vs. 500 ms). Accuracy was significantly greater for singletons as compared to non-singleton items (F(1,19) = 57.89; p < .001; η_p^2 = .75). A main effect of delay was also observed (F(3,57) = 3.64; p = .018; η_p^2 = .16) as was a color X probe-delay interaction (F(3,57) = 2.95; p = .040; η_p^2 = .13). This motivated follow-up analyses for singletons and non-singleton targets separately.. Memory performance for non-singleton targets was better for short delays (main effect of probe delay: F(3, 57) = 10.03; p < .001; η_p^2 = .35), and for targets adjacent to the color singleton (main effect of distance: F(1, 19) = 11.31; p = .003; η_p^2 = .37), but reward had no effect on this measure (F(1, 19) = .42; p = .523; η_p^2 = .02). No significant interactions were observed between reward and distance (F(1,19) = 2.79; p = .111; η_p^2 = .13) or reward, distance and delay (F(3,57) = 1.12; p = .350; η_p^2 = .06; all other Fs < 1). The analysis of accuracy for singletons revealed no significant effects (delay: (F(3,57) = 1.31; p = .279; η_p^2 = .07; reward X delay: F(3,57) = 2.03; p = .120; η_p^2 = .10; all other Fs < 1). Additional analyses of RTs, with color, probe-delay and reward as factors, revealed a main effect of color reflecting shorter RTs for singletons than gray targets (F(1, 19) = 20.5; p < .001; η_p^2 = .52) and a trend for color-delay interaction (F(3,57) = 2.77; p =.05; η_p^2 = .13), no other effects were significant (reward X delay: F(3, 57) = 2.25; p = .09; η_p^2 = .11; all other Fs <1).

Statistical analysis of the interference effect took the form of a 2x4x2 repeated measures ANOVA with factors for singleton color-reward association (high-reward color vs. low-reward color), probe-delay (10ms vs. 50 ms vs. 100 ms vs. 500 ms) and distance (adjacent-to-singleton vs. far-from-singleton).

This confirmed that the feature-reward association established in the training phase induced a stronger interference effect when singletons' color was associated with high than low reward (F(1, 19) = 5.90; p = .025; η_p^2 = .24), and this effect was strongest for stimuli adjacent to the singleton (F(1, 19) = 12.34; p = .002; η_p^2 = .39; Figure 2.4). The interference effect did not vary reliably over probe delay conditions (F(3, 57) = 1.11; p = .352; η_p^2 = .06) and no interaction was observed (F(3,57) = 1.21; p = .316; η_p^2 = .03; all other Fs < 1). An analogous measure of interference for RT showed no significant effects of probe-delay or reward manipulations (delay: F(2.44,46.46) = 2.03; p = =.133; η_p^2 = .10; reward: F(1,19) = 1.77; p = =.200; η_p^2 = .09; delay X reward: F(3,57) = 1,92; p = =.136; η_p^2 = .09).

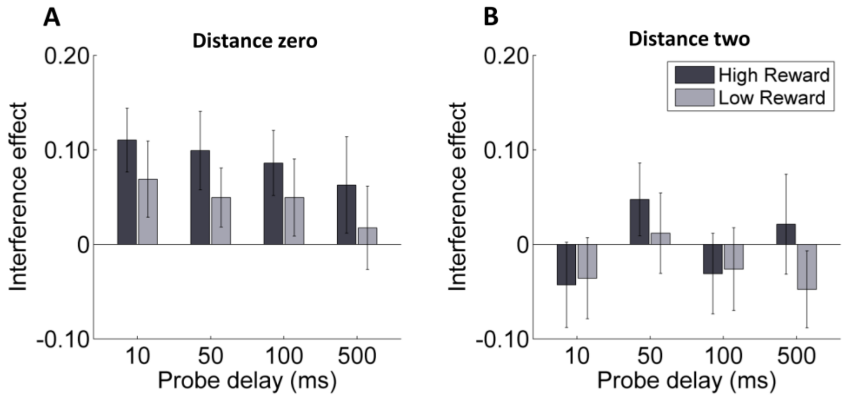

Figure 2.4 Experiment 2: interference effect as a function of target-singleton distance.

The interference effect decreased as a function of target-singleton distance for all delays. A. Interference effect at distance zero (no items between target and singletons). B. Interference effect at distance two (two items between target and singletons).

2.5 Discussion

Features and objects associated with delivery of reward become salient and draw attention in space and time, even when they are no longer rewarded (Anderson, Laurent, & Yantis, 2011a, 2011b; 2012; Della Libera & Chelazzi, 2006, 2009; Hickey, Chelazzi, & Theeuwes,, 2010a, 2010b, 2011; 2014; Krebs, Boehler, & Woldorff, 2010; Raymond & O'Brien, 2009). Recent studies have also shown that reward-associated items are better maintained in visual working memory (Gong & Li, 2014).

The present study expands the existing knowledge about the influence of reward on visual memory, addressing content of visual memory at different delays from display offset and investigating both IM and VWM. This manipulation opens the opportunity to speculate at which stage reward associations can influence the memory process. A further element of novelty in our design is that we investigated VWM and IM not only for items directly associated with reward, but also for simultaneously presented items presented alongside such a reward-associated non-target. To index changes in the mnemonic representation of such items we employed an index reflecting the difference in accuracy between congruent and incongruent trials, which we term the *interference effect*. Importantly, our results show that memory performance for neutral items was influenced by the information contained in the color singleton, in a way that was dependent on the learned color-reward association, but not on the probe-delay.

Our results suggest that the interference effect was dependent on the distance between target and singleton. Memory of the target was not affected by the orientation of the line inside the singleton when they were separated by one or more objects. This observation is in line with a recent study by Anderson and colleagues (2012) in which participants learned a feature-reward association by means of a visual search value learning procedure before performing a flanker task. The flanker target could be surrounded by two letters with the congruent or incongruent identity, and these letters could have high-reward or low-reward associated color. Results showed an increased cost in RTs when the flanking distractors had the high-reward color. Thus, as in our results, proximal stimuli characterized by the reward-associated color interfered more strongly with the target representation. This pattern is evocative of results in the visual search literature showing that salient stimuli such as color singletons will disrupt the representation of targets in close proximity (Caputo & Guerra, 1998; Hopf et al., 2006; Mounts, 2000). This is thought a product of the misdeployment of attention to the salient object, whose selection would cause the suppression of surrounding stimuli including the target. However, in the current results we do not see an impact of proximity as a raw decrease in accuracy, but rather an increase in interference. It is not immediately clear how this effect is related to the suppression described in prior works, and there is a clear opportunity here for further dedicated research.

We tested visual memory at different time intervals from the display offset in order to address the content of both IM and VWM. Our goal was to investigate whether feature-reward associations could have a variable impact on performance at different stages of the memory process. Interestingly, our results show that reward-associated singleton influenced the representation of the target element at very short delays, starting already 10 ms after the offset of the memory array. Moreover, at least for the temporal intervals we have tested, the interference effect was not modulated by the temporal delay of the probe. There are a number of possible accounts for this pattern of results. One is that such early observed interference may arise at the level of encoding of visual information. Several studies have suggested that the VWM capacity depends on an item/resolution trade-off, with mnemonic precision decreasing as the number of to-be-remembered items increases (Alvarez & Cavanagh, 2004; Bays & Husain, 2008; Bays, Catalao, & Husain, 2009; Zhang & Luck, 2008). In the relatively difficult memory task adopted here, the mnemonic representation of stimuli may be low in precision and thus particularly susceptible to interference from other sources of information. Alternatively, it could be the case that stimuli features were represented with adequate precision, but stored information about location was degraded (e.g. Bays, Catalao, & Husain, 2009). In a memory task like the one we adopted, the target was probed with a line that indicated one of the previous items locations. To accurately perform the task, participants needed to correctly remember both the orientation of the items in the array, and the exact location indicated by the probe. Misremembering the location indicated by the probe and responding with the remembered orientation of another item could contribute as a further source of errors. The presence of a reward-associated singleton could bias the remembered location towards that of the singleton itself, interfering with performance.

In either case, it appears that the relatively low-precision of the visual memory representation created an opportunity for the reward-associated object to interfere with memory for other items.

Another possible explanation of the interference effect is that items associated with reward are more persistent over time and less prone to decay. The decay of information from iconic to visual working memory is not abrupt but it follows a smooth decaying function (Graziano & Sigman, 2008). If reward reinforces the persistence of the memory trace, one would expect a slower decay of information for reward-associated items. This suggests that a larger impact of reward associations should be observed at longer probe delays, when the memory trace for neutral items has already faded away while reward-associated items are still accurately represented in memory. However, we failed to detect such a pattern in our results, with no hint of a statistical trend. The apparent stability of the effect over time speaks for an early influence of reward on the encoding of information in visual memory, which remains constant within the first 800 ms. However, it should be noted that we tested only the early period of transfer of information from IM to VWM. Further work with longer probe delays is necessary to directly address the hypothesis of the influence of reward on the maintenance stage of information into working memory.

Finally, there is the possibility that the interference effect arises at the level of response selection, such that the response triggered by the singleton biased participants' performance. The orientation indicated by the singleton could have automatically triggered a motor response that interfered with the selection of the appropriate motor act required for the target. One feature of our design argues against this interpretation: participants performed the memory task with no time pressure and were encouraged to be as accurate as possible, presumably minimizing response-selection errors. Moreover, the interference effect was strongest for items adjacent to the singleton, consistent with the idea that interference occurred during perceptual or selective processing. However, strong evidence for or against this interpretation would also require further dedicated work.

Our results importantly suggest that both IM and VWM for a visual object are significantly modulated by reward history. In particular, memory was affected by the value that each color assumed through a previous procedure of learning: features associated with high value led to a stronger interference effect than features associated with low value or features that were never presented as targets in the previous learning procedure.

Whereas Gong and Li (2014) observed a direct influence of feature reward associations on memory accuracy, we found an influence only on the interference effect, with raw accuracy unaffected. This may stem from our use of color singleton stimuli. Such stimuli automatically attract attention (e.g. Hickey, McDonald, & Theeuwes, 2006) and are better represented in memory (Schmidt et al., 2002), The possibly subtle impact of reward may have been overwhelmed by this raw visual salience. Moreover, our experiment was not designed to have the power to directly detect such change since we had only few trials in which we tested memory performance for singleton targets. On the other hand, in our experiments we tested relatively short delays, ranging from 10 to 800 ms, compared to 1000-2500 ms employed in Gong and Li. It is possible that reward directly affects maintenance of information in memory, but this is detectable only after longer intervals than were employed here.

While a clear interference effect emerged in our work, the paradigm we adopted was not specifically designed to disentangle whether reward associated items affect IM and VWM by means of an attentional capture phenomenon (Anderson, Laurent, & Yantis, 2011; Della Libera & Chelazzi, 2006, 2009; Hickey, Chelazzi, & Theeuwes, 2010, 2011), or if reward produces a proper reinforcement of the information that is encoded and stored in visual memory (Gong and Li, 2014). On the one hand, a shift of attention towards the location occupied by the high reward singleton should be accompanied by a modulation of accuracy at the neighboring locations. While in Experiment 2 we observe an improvement in performance in the locations near the singleton, suggesting that indeed it does attract attention, we fail to observe any modulation of this effect as a function of the reward value associated with the singleton. On the other hand, the stronger interference exerted by the information contained in the high-reward associated singletons seems to suggest facilitated representation of the visual information. However, further studies are necessary to directly investigate these two possibilities and understand the nature of the mechanisms involved in the influence of reward on the earliest stages of visual memory.

To conclude, we have shown that learned feature-reward associations can have an important impact on the encoding of information in memory. Previous experience and learned reward associations not only prioritize processing of associated visual stimuli, but also changes how these objects are stored in visual memory.

3 Limits of reward influence on visual working memory

Adapted from: Infanti, E. & Turatto, M.. Limits of reward influence on visual working memory. **In preparation**

3.1 Abstract

Recognizing objects and situations that are predictive of positive or negative outcomes is fundamental in promoting adaptive behavior. A growing number of studies have shown that once positive associations are learned, reward-associated objects become salient and acquire the capacity to attract attention even beyond current goals and attentional sets. In this work we aim to test the limits of such influence, specifically addressing the impact of feature-reward associations in a visual working memory (VWM) task with increasing attentional demand for target selection. We adopted a value learning procedure to imbue specific colors with different associated values and subsequently tested the impact of such learned color-reward associations on performance in a VWM task. We observed that when items associated with high

rewards were presented as distractors, they significantly interfered with mnemonic representations of simultaneously-presented low-reward targets. However, when the target-defining shape was varied on a trial-by-trial basis, the interference of distractors was no longer modulated by their value. We suggest that exhausting attention in target selection reduces processing of irrelevant information related to interfering items, such as their associated value. While recent studies have shown that reward history impacts attentional selection independently of top-down sets and stimulus-driven shifts of attention, here we advance the idea that such effects are limited by the cognitive demands of the task performed. Increasing attentional requirements for target selection exhausts attentional resources resulting in more efficient filtering of task-irrelevant information, and prevents the emergence of residual effects from learned feature-reward associations.

3.2 Introduction

Reward plays an important role in guiding human behavior (Skinner, 1953). Learning to recognize objects and situations that are predictive of positive or negative outcomes is fundamental for promoting optimal behavior in future encounters. Because of its powerful motivational value, it is well established that reward can efficiently guide the deployment of attention and cognitive resources towards reward-predicting stimuli (Engelmann & Pessoa, 2007; Kristjánsson et al., 2009; Pessoa, 2009; Risa Sawaki et al., 2015).

Frequently, however, the familiar environments we interact with are full of motivationally salient stimuli that are irrelevant for current goals. Interestingly, a growing body of literature over the last 10 years has demonstrated that learned reward associations can automatically influence our ability to select and process visual stimuli even when rewards are no longer provided (see Anderson, 2013; Chelazzi, Perlato, Santandrea, & Della Libera, 2013 for a review). In particular, it has been shown that features that are associated with positive outcomes acquire the power to attract and orient attention even beyond an individual's current goals and interests (Anderson et al., 2011a, 2011b, 2012; Della Libera & Chelazzi, 2006, 2009; Hickey et al., 2010a; Raymond & O'Brien, 2009).

For example, to study the influence of reward history in visual cognition, Anderson and colleagues (2011b) developed a value-learning procedure based on a visual search task that established an association between features, such as colors, and different reward levels. During the subsequent test phase, the residual impact of learned-reward associations on deployment of attention was assessed in a second visual search task in the absence of reward delivery. This paradigm allowed the researchers to demonstrate that stimuli imbued with value can capture attention even when they are presented as irrelevant distractors. The same value-learning procedure has been used to prove that the advantage of high reward-associated features over neutral or less valuable ones can be generalized to new stimuli and tasks (Anderson et al., 2012; Gong & Li, 2014; Infanti, Hickey, & Turatto, 2015).

Given the strong interconnection between visual working memory (VWM) and selective attention (Awh et al., 2006; Gazzaley & Nobre, 2012; Zanto et al., 2011), a few recent studies have suggested that the influence of reward history could also extend to VWM tasks (Gong & Li, 2014; Infanti et al., 2015). VWM is a system with limited capacity in terms of the number of items that can be stored and the precision of the encoded representations (Alvarez & Cavanagh, 2004; Bays, Catalao, & Husain, 2009; Steven J Luck & Vogel, 2013; Zhang & Luck, 2008). Hence, the selection, encoding and maintenance of information in VWM is determined by its relevance for current goals (Gazzaley, 2011; Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005), its likelihood of being selected as a target (Umemoto, Scolari, Vogel, & Awh, 2010), and object salience (Belopolsky, Kramer, & Godijn, 2008). Interestingly, the contents of VWM can also be affected by the value associated with targets (Gong & Li, 2014; Infanti et al., 2015). Learned feature-reward associations can induce an enhancement of VWM capacity for stimuli associated with high compared to low reward (Gong & Li, 2014). Moreover, Infanti and colleagues (2015) documented that salient and reward-associated items interfere more strongly with the memory trace of adjacent neutral stimuli, revealing that reward history can significantly affect both early (Iconic Memory) and late stages (VWM) of visual memory.

In the present work we aim to define the boundaries of such influence by further exploring how variations in the attentional requirements of a task affect the impact of learned feature-reward associations in VWM.

In this work we first aim to extend our previous findings (Infanti et al., 2015) and explore whether reward-associated items interfere with VWM representations of neutral stimuli even when they are irrelevant for the current task. We also investigate whether increasing attentional demands for target selection can limit the influence of value-associated distractors on VWM. It has been suggested that the extent to which a task exhausts available resources determines whether task-irrelevant items will be processed (Lavie, 1995, 2005; Lavie & Cox, 1997; Lavie & Tsal, 1994). With a low attentional load, task-irrelevant stimuli will automatically gain access to attentional resources. However, when a task results in high attentional load, there are no residual resources to process irrelevant stimuli. In this work we ask whether task-irrelevant information such as distractor value is efficiently suppressed when the attentional requirements of the task increase.

To this aim, we employed a value-learning procedure (modeled on Anderson et al., 2011b) adapted to a VWM task, where we associated target colors with either high or low reward outcomes. A second memory task was performed immediately after this training, during extinction. In this test phase, items rendered in either high or low reward-associated colors were presented simultaneously. On each trial, one color was assigned to targets and the other color to distractors. We analyzed the influence of reward on VWM performance by quantifying the *interference effect* of distractors in addition to raw accuracy and response times (RTs). The interference effect calculates the extent of interference exerted by distractor stimuli as a function of their associated reward value. The interference effect thus indexes the impact the distractors on the response to targets. It is quantified as the difference in accuracy between trials in which the probed item requires a response congruent to that evoked by the adjacent distractor (same response, *congruent trials*) and trials in which the responses evoked by the target and the distractor are incongruent (different response, *incongruent trials*) (for an analogous use of this measure see Infanti et al., 2015). An increase in the amplitude of this effect reflects greater intrusion by the distractor.

We hypothesized that reward-associated distractors would interfere with VWM performance only under specific circumstances. Specifically we hypothesized that the interference effect would be limited by increasing demands on the target selection process. We manipulated the task demands for target selection by either continuously varying or blocking the shape characterizing the target. To anticipate the results, we observed a significant interference with visual memory representations of targets in the presence of high value distractors, but the influence of reward on interference was abolished by increasing attentional load for target selection.

3.3 General paradigm and rationale for the experiments

Each experiment lasted for about an hour and was organized in two parts: a VWM task was performed during the initial training session, followed by a similar task during the test session. During the first phase, reward was provided for correct performance, and different reward magnitudes were paired with different target colors, enabling the establishment of feature-reward associations. During the second phase, no reward was provided for correct performance so that we could measure the residual effects of learned feature-reward pairings during extinction. The training session was identical across all experiments, while the criteria defining targets during the subsequent test session were varied to explore under which circumstances reward associations were able to affect VWM performance.

3.4 Experiment 1

Methods

Participants. Eighteen young adults (14 females; mean age ± standard deviation: 22.7 ± 2.1 years; 3 left handed) participated in this experiment. All participants had normal or corrected-to-normal visual acuity and color vision. One participant was excluded from the analysis because of poor performance during the test phase (accuracy not different from chance at both display sizes). The experiment was conducted in accordance with the Declaration of Helsinki and with the approval of the local ethical committee. All participants gave their written informed consent and received a reimbursement for their participation.

Apparatus. The experiment was performed in a dimly illuminated room. Participants were seated approximately 60 cm away from the display with their head supported by a chinrest. Stimuli were created using a custom Matlab script (Mathworks Inc., Massachusetts, USA) and the Psychophysics Toolbox 3.8 (Brainard, 1997; Pelli, 1997) and presented on a gamma-calibrated ViewSonic Graphic Series G90fB 19’’ CRT monitor (1024 x 768) at a refresh rate of 100Hz.

Stimuli. All stimuli appeared on a uniform gray background (3.7 cd/m^2) inside a subset of the 16 square placeholders (1.65°x1.65°) displaced along an imaginary circle with a radius of 5° of visual angle centered around the central fixation point (0.2° in diameter). Targets were circles (diameter 1.2°; width 0.1°) or diamonds (diagonal 1.3°; width 0.1°) with a central light gray line (28.5 cd/m^2; 0.7°x0.15°) oriented vertically or horizontally. Three approximately equiluminant colors (~22.6 cd/ m^2), red, green, and blue, were assigned to the stimuli.

Design and Procedure. *Visual Working Memory training*. An example of a trial is depicted in Figure 3.1A. Targets were circles rendered in one of two possible colors (e.g. red and green) and participants were instructed to memorize the orientation of the gray bars presented inside them while ignoring circles rendered in a third color (e.g. blue) that were always present as distractors. Unbeknownst to participants, one of the target colors was associated with a high reward in 80% of trials while the other target color was mainly associated with low reward (high reward in 20% of trials). Color assignments were counterbalanced across participants. The training phase started with 20 practice trials and was followed by 256 experimental trials organized in 8 blocks. Each trial started with the onset of a fixation cross at the center of the screen and the array of placeholders for a variable interval ranging from 300 to 500 ms. Then, a memory display of 4 or 8 elements, half rendered in one of the target colors and half in the distractor color, was presented for 200 ms. Each target on the display was flanked, either on the left or on the right, by a distractor. The participant’s task was to memorize the orientation of the lines presented inside the target circles and ignore the information associated with the distractors. The orientation of the line inside the target was congruent, in half of the trials, and incongruent, in the other half, with that of the adjacent distractor. The orientation of the target line had to be encoded and stored in VWM for 2 seconds until a probe appeared. The probe (“?”), indicating the target location, was visible until the participant responded. Participants reported the target orientation by pressing the corresponding key on the keyboard. Keys were labeled with a vertical or horizontal line. Accuracy, but not response speed, was emphasized. Correct responses led to a high ("+100 points") or low ("+1 point") reward feedback; incorrect responses were signaled by the loss of one point ("-1 point"). Points were accumulated during the experiment and determined the final reimbursement obtained for participation which could range from €6 to €8. The running total of points accumulated and the corresponding gains in euros were shown at the end of each block.

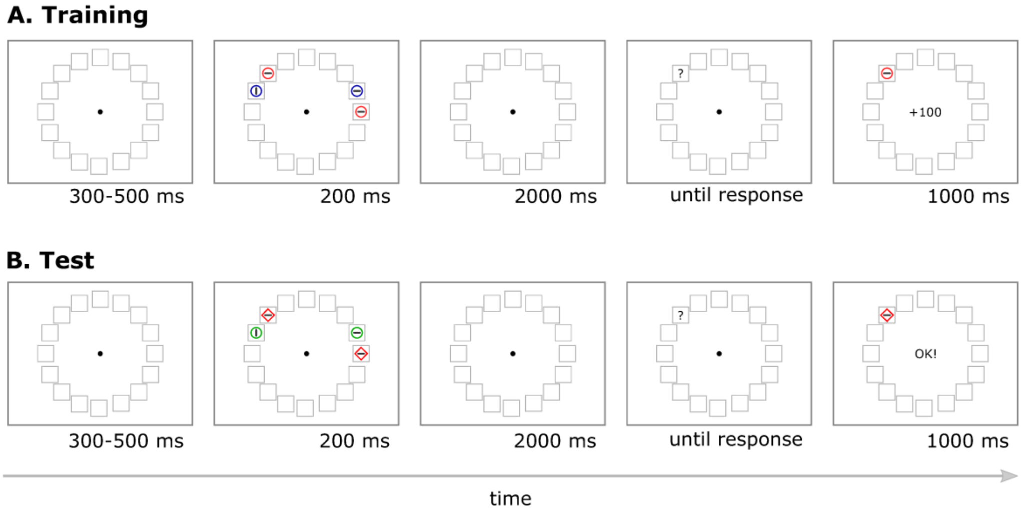

Figure 3.1 Experimental design.

(A) Trials schematic of the training phase. Memory display included the same number of targets and adjacent distractors rendered in different colors. Targets could be rendered in one of two colors associated with high or low reward outcome with a different probability. Correct responses for colors paired with high reward led to the obtainment of 100 points in 80% of the trials and 1 point in the remaining 20% of the trials, while the opposite was true for low reward associated color. Incorrect responses were penalized with the loss of 1 point irrespectively of the target color. **(B)** Trials schematic of the test phase. The structure of the task was analogous to the one used during training with the exception that targets were now defined based on their shape and irrespective of their color. Only the colors of previous targets are used in this phase. No reward was provided.

Visual Working Memory test. The test phase consisted in a VWM task analogous to the one performed during training, the only difference was the features that defined targets. The session started with 20 practice trials, followed by 256 experimental trials divided into 8 blocks. An example of a trial is depicted in Figure 3.1B. During this phase, the oriented lines were presented inside objects of different shapes that could be either circles or diamonds. Only diamonds were relevant for the memory task while circles were always distractors. Stimuli were rendered in the colors used for targets in the training phase (e.g. red and green), but no consistent shape-color pairing was present during this phase. In other words, for half of the trials the targets (diamonds) were rendered in red and for the other half of the trials they were rendered in green. The opposite color was assigned to the distractors. Participants indicated the orientation of the line presented at the probed location by pressing the corresponding key on the keyboard. They received feedback on their performance (“OK” or “error”), although no reward was obtained.

Analyses and Results

Training VWM task. All statistical analyses of VWM performance for all the experiments (unless otherwise specified) took the form of a 2x2 repeated measures analysis of variance (ANOVA) with reward magnitude (high vs. low) and display size (two vs. four targets) as factors. Accuracy and RTs were analyzed only for responses occurring within 3 standard deviations from the mean RT, resulting in the exclusion of 1.47% of trials. Accuracy was significantly higher for small than for large display size (F(1,16) = 135.94; p < 0.001; η_p^2= 0.90), but no significant effects of reward were observed (all Fs < 1). Equivalent results were found for RTs, indicating faster responses for small than for large display size (Display size: F(1,16) = 28.85; p < 0.001; η_p^2 = 0.65; all other Fs < 1).

Test VWM task. Accuracy and RTs for responses occurring within 3 standard deviations from the mean RT (1.54% of trials discarded) were analyzed as a function of the reward magnitude associated with distractors (and targets) and display size. Not surprisingly, raw accuracy and RTs revealed better performance for displays with 2 rather than 4 targets (Accuracy. F(1,16) = 36.78; p < 0.001; η_p^2= 0.70; RTs. F(1,16) = 36.15; p < 0.001; η_p^2 = 0.69), but showed no relevant effects of reward (Accuracy. Reward: F(1,16) = 1.45; p = 0.245; η_p^2= 0.08; Reward X Display size: F < 1. RTs. Reward: F(1,16) = 3.63; p = 0.075; η_p^2= 0.19; Reward X Display size: F < 1) (Figure 3.2A). We further investigated the influence of reward on representations in VWM by computing the interference effect induced by distractors of different value on target representations. The interference effect was operationalized as the difference in accuracy between congruent and incongruent trials. A positive interference effect was measured across conditions showing that distractors significantly influenced the response provided to the targets (t(16) = 2.65; p = 0.017; mean interference = 3.9%). The analysis for different reward magnitude and display size revealed larger interference for targets rendered in the low reward associated color flanked by high reward distractors, irrespective of the display size (Reward: F(1,16) = 12.12; p = 0.003; η_p^2 = 0.43; Display size: F(1,16) = 1.52; p = 0.235; η_p^2 = 0.09, Reward X Display size: F(1,16) = 1.04; p = 0.323; η_p^2 = 0.06) (Figure 3.2B). A similar analysis of interference performed for RTs did not reveal any significant effect (all Fs < 1);

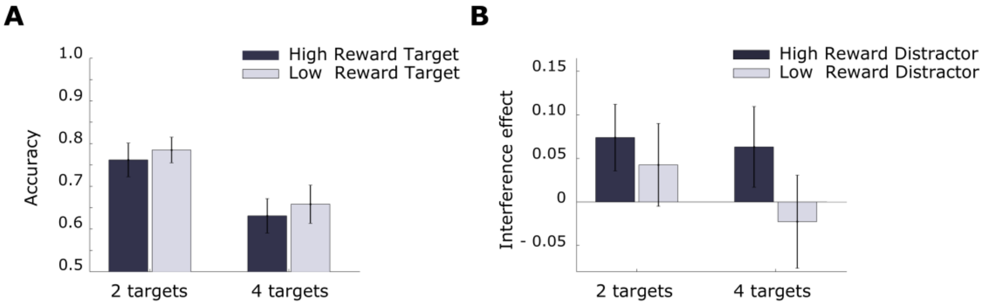

Figure 3.2 Accuracy and Interference Effect in Experiment 1

(A) Mean accuracy for VWM task during test for high (black) and low (gray) reward-associated colors at different display size (2 vs. 4 targets). Accuracy is significantly higher for smaller display size, but no significant modulations of are measured as a function of reward. **(B)** Interference effect for VWM task during test. The interference effect is a measure of the interference of distractors in VWM representations of nearby targets. It is computed as the difference between congruent and incongruent trials. Higher interference is executed by high reward (black) than low reward (gray) distractors. Error bars here and below represent within-participant 95% confidence intervals (Cousineau, 2005).

Discussion

The first experiment provides clear evidence for the influence of learned reward associations on object representations stored in VWM. Learned feature-reward contingencies persist beyond the cessation of reward delivery and interfere with VWM performance. Analogous costs in performance have been previously documented in attentional selection (Anderson et al., 2011a, 2011b, 2012) and VWM paradigms

(Infanti et al., 2015) by using a value learning procedure based on a visual search task (Anderson et al., 2011b).

In this work, we generalized the training procedure showing the efficiency of a different task: a VWM task where valuable targets and neutral distractors are simultaneously presented. During the training phase, no significant effects of reward were measured. Although these results may seem surprising, they are consistent with those obtained with different value-learning procedures (Anderson et al., 2011b, 2012; Anderson & Yantis, 2012, 2013; Gong & Li, 2014; Sali, Anderson, & Yantis, 2014; but see Infanti et al., 2015).

During the test phase, two colors were presented on the same display, each of which was associated with a different value during training. One color was assigned to the targets and one to the distractors in an orthogonal fashion. While no direct modulation of raw accuracy or RTs was observed as a function of reward magnitude, a highly significant variation in the amplitude of the interference effect was observed with variations in the relative values associated with targets and distractors. A positive interference effect indicates that response accuracy to a probed target is higher when the adjacent distractor has the same orientation, thus evoking a congruent response, while accuracy is lower when the adjacent distractor is oriented differently. The stronger interference effect generated by high reward distractors (Figure 3.2B) supports the hypothesis that the presence of highly valuable items cannot be completely suppressed and the information they convey might be integrated with the representation of targets. These results reinforce and expand our previous observations (Infanti et al., 2015) showing that effects of interference also hold even when reward-associated items are neither singletons, nor salient and are completely irrelevant to the task.

3.5 Experiment 2

In the following experiments, we varied the shape of the target objects on a trial-by-trial basis aiming to establish whether increased cognitive demands on target selection limit the residual influence of reward on VWM.

Method

Participants. A different group of 24 participants (18 females; mean age ± standard deviation: 23.2 ± 4.6 years; 2 left handed) took part in this experiment. All participants had normal or corrected-to-normal visual acuity and color vision. Two participants were excluded from the analysis because of poor performance during the test phase (accuracy not different from chance at both display size). The experiment was conducted in accordance with the Declaration of Helsinki and with the approval of the local ethical committee. All participants give their written informed consent and received a reimbursement for their participation.

Stimuli and procedure. After the initial training session, participants performed a VWM task during extinction. The test phase for Experiment 2 was analogous to that in Experiment 1 with the only difference being that the shape of the target stimulus was variable and was defined on a trial by trial basis. At the beginning of each trial a cue, presented around the fixation dot and rendered in the same color, was presented for 300-500 ms. The cue shape could be either a diamond (diameter 1.3°; width 0.1°) or a circle (diameter 1.2°; width 0.1°) indicating the corresponding target shape for the current trial. The memory display was then presented including both diamonds and circles in the same way as in Experiment 1. After a retention interval of 2 seconds, a probe indicated the location occupied by one of the target shapes and participants reported the orientation of the line inside it.

Analyses and Results

Results of the training phase mimicked those obtained for Experiment 1 in terms of both accuracy and RTs revealing only the impact of difficulty due to display size (discarded trials: 1.78%; Accuracy: F(1,21) = 193.10; p < 0.001; η_p^2 = 0.90; and RT: F(1,21) = 54.74; p < 0.001; η_p^2 = 0.72), but no effects of reward (Accuracy. Reward: F(1,21) = 1.09; p = 0.308; η_p^2 = 0.05; RTs. Reward X Display size: F(1,21) = 1.83; p = 0.191; η_p^2 = 0.08; all other Fs < 1). Similarly, in the VWM task during the test phase, performance was better for small display size (discarded trials: 1.58%; Accuracy: F(1,21) = 133.68; p < 0.001; η_p^2 = 0.86; RTs: F(1,21) = 50.96; p < 0.001; η_p^2 = 0.71), but no other significant modulations were measured (Accuracy. Reward: F(1,21) = 1.83; p = 0.190; η_p^2 = 0.08; Reward X Display size: F(1,21) = 3.91; p = 0.061; η_p^2 = 0.16; RTs. all Fs < 1). In contrast to Experiment 1, despite a significant interference effect across conditions (t(21) = 3.34; p = 0.003; mean interference = 4.8%), no difference in the magnitude of interference was observed as a function of target and distractor reward associated value (Display size: F(1,21) = 1.99; p = 0.173; η_p^2 = 0.09; Reward: F(1,21) = 0.54; p = 0.470; η_p^2 = 0.03; Reward X Display size: F(1,21) = 2.20; p = 0.153; η_p^2 = 0.10) (Figure 3A).

Discussion

In Experiment 2 we tested whether the interference of reward-associated objects was affected by an increase in cognitive control and task demands. As in the first experiment, target selection was defined on a neutral feature, shape, while the reward-associated feature, color, was task irrelevant and was free to switch between target and distractors on a trial by trial basis. Differently from Experiment 1, in the current task, the shape of the target was not fixed across the entire experiment, but was randomly varied on each trial according to the instructions provided by the central cue. The variability of target shape increased the cognitive demands of the task by requiring continuous shifts between different templates in order to identify the correct subset of items to memorize.

Our results suggest that increased attentional demands for target selection can limit the interference from reward-associated but task-irrelevant information on the display. We suggest that the more resources are required to control target selection, the stronger the filtering of irrelevant attributes of distractors, such as the reward value previously associated with them. On the other hand, when the target template remains constant across trials, the residual resources available can be captured by irrelevant information such as the color of stimuli and their previously associated value (Lavie, 1995; Lavie & Cox, 1997).

In this second experiment, continuous changes in target shape increased task demands, but could also interfere with task performance by leading to inaccurate target selection due to insufficient cue processing or produce costs for target switching (Maljkovic &

Nakayama, 1994; Pinto, Olivers, & Theeuwes, 2005). Inaccurate target selection can drive the interference effect independently of a distractor’s associated value. Indeed, the results of this study indicate the presence of an overall significant interference effect, despite the fact that the level of interference was not affected by the associated value of distractors.

3.6 Experiment 3

In the next study, we replicated Experiment 2, but organized the trials in separated blocks according to the shape defining the target. In this way we maintained the same number of targets for each shape type as in Experiment 2, but reduced the cognitive load associated with the task by keeping the shape of the target (and the distractor) fixed within each block. The aim of this experiment was to test whether, by releasing attentional load on target selection, the interference effect of high reward distractors would be restored.

Method

Participants. Twenty-four new participants took part to this experiment (19 females; mean age ± standard deviation: 24.0 ± 3.4 years; 4 left handed). All participants had normal or corrected-to-normal visual acuity and color vision. Two participants were excluded from the analysis because of poor performance during the test phase (accuracy not different from chance at both display sizes). The experiment was conducted in accordance with the Declaration of Helsinki and with the approval of the local ethical committee. All participants give their written informed consent and received reimbursement for their participation.

Design and procedure. After the initial training session, a VWM task analogous to the one described for Experiment 2 was performed during the test phase. At the beginning of each block, a warning appeared instructing participants about the shape of the target for the following 32 trials. In each block participants attended either to diamonds or to circles and ignored the other shape (either circles or diamonds). As in the former experiments, the orientation of the bar presented inside the probed target was reported by pressing a key on the keyboard and feedback was provided.

Analyses and Results

Results of the training phase replicated those obtained for previous experiments with no evidence of reward influence on performance (discarded trials: 1.60%; Accuracy. Reward F(1,21) <1; Reward X Display size: F(1,21) = 3.19; p = 0.089; η_p^2 = 0.13; RTs. Reward: F(1,21) = 1.16; p = 0.295; η_p^2 = 0.05; Reward X Display size: F(1,21) = 1.338; p = 0.260; η_p^2 = 0.06), but a clear advantage for small over large displays (Accuracy: F(1,21) = 106.24; p < 0.001; η_p^2 = 0.84; RTs: F(1,21) = 22.17; p < 0.001; η_p^2 = 0.51).

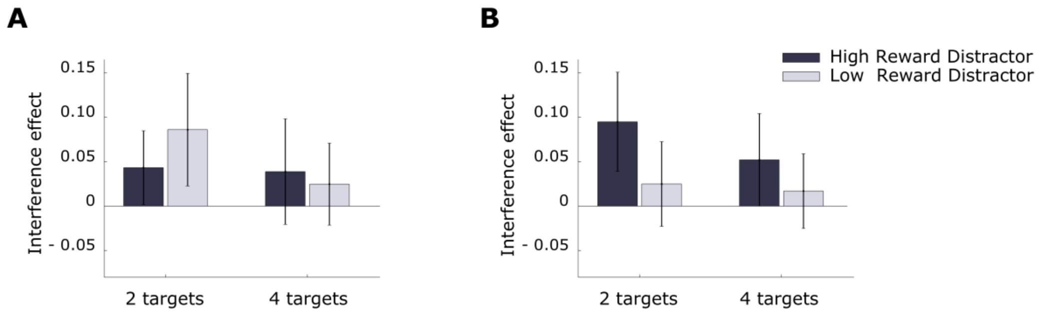

Figure 3.3 Interference Effects in Experiments 2 and 3

(A) Interference effect for VWM task during test in experiment 2. The amplitude of the interference effect is not affected by reward magnitude associated distractors when targets shape changes on a trial-by-trial basis. **(B)** Interference effect for VWM task during test in experiment 3. Interference effect is significantly higher for distractors associated with high reward (black) when target shape changes are blocked.

Performance on the VWM task during the test phase replicated the results observed in Experiment 1 for both accuracy and interference effects. No significant effects were observed for either raw accuracy (discarded trials: 1.51%; Reward: F(1,21) = 1.12; p = 0.302; η_p^2 = 0.05; Display size X Reward: F < 1) or RTs (Reward: F(1,21) = 3.52; p = 0.075; η_p^2 = 0.14; Display size X Reward: F(1,21) = 0.30; p = 0.597; η_p^2 = 0.01), except for better performance for small display size (Accuracy: F(1,21) = 42.94; p < 0.001; η_p^2 = 0.84; RTs: F(1,21) = 32.80; p < 0.001; η_p^2 = 0.61). As expected, a significant interference effect was measured across conditions (t(21) = 3.85; p < 0.001; mean interference = 4.7%), and, most importantly, the interference was significantly modulated by reward magnitude irrespective of display size (F(1,21) = 4.42; p = 0.048; η_p^2 = 0.17; all other Fs < 1) (Figure 3B).

We directly contrasted the interference effect measured in the testing phase of Experiments 2 and 3 which differed only in the segregation of trials with the same target shape. We compared the interference effect in the two experiments by means of a mixed 2 X 2 ANOVA with distractor-associated value (high vs. low) as a within subjects factor and experiment as a between subjects factor. Display size was not included in this analysis given the absence of any significant interaction with reward in both experiments. Our analysis confirmed that there was a significant interaction between a distractor's associated value and the experiment (Reward X Experiment: F(1,42) = 4.44; p = 0.041; η_p^2 = 0.10; Reward: F(1.42) = 1.45; p = 0.236; η_p^2 = 0.03; Experiment: F < 1). This last analysis further supports our conclusion that value associated with distractors had a significant impact on the magnitude of the interference effect only in Experiment 3.

Discussion

Experiment 3 was successful in showing that when target selection was less attentionally demanding because target identity was blocked, learned reward associations modulated interference in VWM performance. The direct comparison between Experiment 2 and 3 confirms that spared attentional resources are necessary for processing the distractors and their previously associated value.

3.7 General Discussion

Reward-associated objects acquire high attentional priority and can capture attention, even when presented as salient or non-salient distractors, in a way that appears in part independent of other attentional mechanisms (Anderson et al., 2011a, 2011b; Awh, Belopolsky, & Theeuwes, 2012; Della Libera & Chelazzi, 2009; Hickey et al., 2010a). The goal of the present study was to delimit the boundaries of the influence of reward on performance in a VWM task, specifically testing whether the attentional requirements of target selection could limit the interference produced by valuable distractors.

In a recent study, we showed that visually salient items interfere with memory for neighboring non-salient objects and that the amplitude of this interference is significantly modulated by the reward magnitude associated with them (Infanti et al., 2015). This interference is evident already at short delays from the offset of the memory display (10 ms) suggesting that valuable objects interfere with encoding of representations in VWM of neutral targets. The results presented in this work corroborate and expand our previous observations, specifically showing that valuable items produce significant interference in VWM representations of relevant objects even when presented as distractors. Both studies tested the influence of learned feature-reward associations during extinction, thus providing no strategic advantage for prioritizing processing and encoding of items identified by a previously rewarded feature. However, in our previous work both valuable and non-valuable objects were equally relevant for the task and it is possible that participants preferentially attended the previously rewarded objects. By contrast, in the current study only a subset of items presented in the initial display was relevant for the VWM task and participants were instructed to ignore distractors irrespective of their color. Furthermore, while in our previous work reward-associated objects were salient singletons presented among uniform non-salient gray objects, in this case the same number of equally salient targets and distractors were presented within the same display demonstrating that saliency is not necessary for the interference effect to emerge.

The overall pattern of results in our work demonstrates that although features with a previous history of reward association have been claimed to automatically drive attention and receive prioritized visual processing even beyond current goals and endogenous attentional set (Anderson, 2013; Chelazzi et al., 2013; Hickey et al., 2010a; Munneke et al., 2015), there are some limits to their capacity to influence visual cognition. More specifically, we suggest that the involuntary processing and interference of high value distractors is limited by increasing attentional demands for target selection.

It is known that the capacity to filter distractors is enhanced by an increase in the perceptual load of the task, typically achieved by changing the number or the discriminability of the targets (Lavie, 1995, 2005, 2010; Lavie & Cox, 1997; Lavie & Tsal, 1994; Lavie, Hirst, de Fockert, & Viding, 2004). In this work, we observed that an increase in attentional demands for target selection results in better filtering of learned-reward associations leading to decreased interference by high value distractors. Similar to the increase in perceptual load, we suggest that a continuous swap of target shape greatly reduces the resources available for processing irrelevant information such as an item’s color and its reward history. Only when target selection can be automatized, are residual resources available to process irrelevant information leading to the emergence of reward effects.

The literature describing the impact of reward-associated distractors on performance has typically employed simple visual search tasks in which the target is a singleton whose defining feature is kept constant across the experiment (e.g., Anderson et al., 2011a). The novel results reported in this work suggest that by increasing task demands for target selection, the influence of learned feature-reward associations can be strongly reduced. However, further studies are necessary to precisely quantify the interaction of these two factors by observing how parametrical modulations of task load interact with the value associated with distractors.

Prioritized processing of objects that have been associated with positive outcomes is important for adaptive behavior. However, the present results demonstrate that, under appropriate circumstances, such as increased task requirements, valuable distractors can be efficiently suppressed.

4 Reward-priming impacts visual working memory maintenance

Adapted from: Infanti, E., Hickey, C., & Turatto, M.. Reward-priming impacts visual working memory maintenance: evidence from human electrophysiology. **Submitted**

4.1 Abstract

Experience plays a central role in guiding human and non-human behavior and reward is one of the key factors in this process. Reward is known to facilitate visual processing, automatically guide attention toward reward-associated objects even under circumstances where this is counter-strategic. A handful of recent studies have begun to investigate similar effects of reward on visual working memory (VWM), suggesting a residual influence of reward on mnemonic representations of previously reward-associated stimuli. However, it is not clear yet which mechanisms underlie these

behavioral effects: reward could have a direct 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 (ERP) indices of selective attention – the N2pc - and visual working memory maintenance – the CDA (contralateral delay activity) - while participants completed a VWM task. Results show that reward outcome in one trial caused similar target stimuli to be strongly represented in VWM in subsequent trials, as expressed in larger amplitude CDA. This was not preceded by a corresponding effect on the N2pc that, nonetheless, was significantly enhanced by target color repetition. The specific reward related modulation of CDA only suggests a discrete effect of reward on VWM maintenance. We suggest that reward's impact on visual cognition is guided by task confines: when the task stresses VWM maintenance, it is at this representational level that reward will have impact.

4.2 Introduction

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

To date, the investigation of reward effects in visual cognition has focused on influences on the deployment of attention. A challenging and largely unresolved issue thus concerns the impact of reward associations on other cognitive processes that require sustained cognitive control, such as visual working memory (VWM). Selective attention and working memory are highly connected cognitive processes (for a review see Gazzaley & Nobre, 2012), and a direct investigation of the influence of reward associations on VWM could be of great interest in understanding the extent to which reward impacts visual cognition. Previous studies have shown that incentives can influence top-down attentional signals leading to a motivational improvement in VWM performance (Kawasaki & Yamaguchi, 2013; Krawczyk et al., 2007). 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 automatic changes in visual mechanisms such as those demonstrated in the attention literature. This distinction is important if one wants to claim that reward can automatically bias the way we perceive, attend and memorize the world around us, in a way that is theoretically distinct from the known role of reward in the strategic establishment of attentional set (Maunsell, 2004).

There is very little existing work exploring the influence of reward associations on VWM in the absence of direct incentive motivation (Gong & Li, 2014; Infanti et al., 2015). However, this nascent literature does suggest a residual influence of reward association on mnemonic representations of reward-associated stimuli. For example, Gong and Li (2014) reported non-strategic benefits in VWM performance for stimuli previously associated with high reward compared to low reward, while Infanti and colleagues (2015) documented the interference of reward-associated items on the memory trace of adjacent neutral stimuli. However, the precise neural and cognitive mechanisms underlying these behavioral effects are unknown. One the one hand it could be the case that reward association has a direct impact on our ability to maintain the corresponding mnemonic visual representations. However, current results largely 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.

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 a reward priming paradigm (Hickey et al., 2010a) in which we categorized each trial based on the magnitude of reward received in the preceding trial and the repetition or swap of the target characterizing feature (color). We hypothesized that high-magnitude reward would benefit VWM only for targets whose color was repeated among trials, while the opposite pattern of results was expected for repetition of low-rewarded items. We looked for this pattern of interaction focusing on two components in the event related potential (ERP) that independently index attentional selection - the N2pc - and 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 during visual search (Eimer, 1996; Hickey et al., 2009; Mazza, Turatto, & Caramazza, 2009a, 2009b; Woodman & Luck, 1999, 2003) and has been shown sensitive to target and distractor value associations (Hickey et al., 2010a; Kiss et al., 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 et al., 2007; Vogel & Machizawa, 2004; Vogel et al., 2005). The amplitude of the CDA is modulated by the number of items in VWM (Ikkai et al., 2010; Vogel & Machizawa, 2004) and the precision of these memory traces (Machizawa, Goh, & Driver, 2012).

By looking to 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, indexed in N2pc, without effecting VWM maintenance reflected in the CDA. This would suggest that reward effects in VWM tasks identified in existing behavioral studies are indirect in nature, ultimately caused by the known influence of reward on attentional selection and encoding. Alternatively, high reward might benefit VWM maintenance, indexed in the CDA, without effecting attentional encoding reflected in 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 both components, suggesting that benefits to encoding translate to benefits in maintenance. To foreshadow, our data show a significant impact on CDA only, suggesting that reward can directly affect the maintenance stage of VWM in a visual memory task.

4.3 Experiment

Methods

General paradigm and rationale. Participants performed a VWM task similar to that described in Vogel, McColloug, and Machizawa (2005). On each trial they were instructed to attend to one side of the screen and memorize the orientation of uniformly colored target rectangles presented together with irrelevant squares. Correct response in a trial was followed by feedback indicating 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 the paradigm we used (adapted from Hickey et al., 2010a): 1) on each trial the color of the target rectangles could be either red or green and in the following trial the color could either repeat or change; 2) each trial resulted in high- or low-magnitude reward outcome (and thus each trial was preceded by a trial that garnered either 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 mnemonic performance when the target-defining color is repeated in the next trial?

The design lead to 4 experimental scenarios 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 color on trial n (High reward Repetition condition), b) participants received a high magnitude reward on trial n-1, then target color was swapped (High reward Swap condition), c) participants received a low magnitude reward on trial n-1, then target color was repeated (Low reward Repetition condition), and d) participants received a low magnitude reward on trial n-1, then target color was swapped (Low reward Swap condition).

Participants. 22 healthy volunteers from the University of Trento (mean ± SD age = 22.3 ± 3.4; 13 female) participated to the experiment. They had normal color 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 1920x1080 pixels resolution at a refresh rate of 100Hz. Participants were seated in a dimly illuminated room at approximately 1m 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°x0.7° visual angle) and squares (0.3°x0.3°) placed randomly within an area of 5°x3° centered at 4° to the left or to the right of the central fixation point (see Figure 4.1). The stimuli could be either red or green, with their color adjusted to be physically equiluminant (approximately 8 cd/m^2), and were presented on a uniform dark gray background (6 cd/m^2). The rectangles had various orientations (selected from 0°, 45°, 90°, or 135°) and all rectangles on each side of the display had the same color (e.g. left red and right green). In contrast, half of the squares on each side of the display had red and half had green color.

Design and Procedure. The schematic of a trial is illustrated in Fig. 1A. Trials started with a grey fixation dot (0.2°x0.2°) presented at the center 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 (ISI) of 100-500 ms. Each side of the memory display consisted of 2 or 4 target rectangles and 4 distractor squares and was visible for 100 ms. 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 of the participants was to indicate whether the orientation of this probe rectangle was the same 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 participant response. Responses were made on a standard keyboard, with 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 1 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 in 16 blocks.

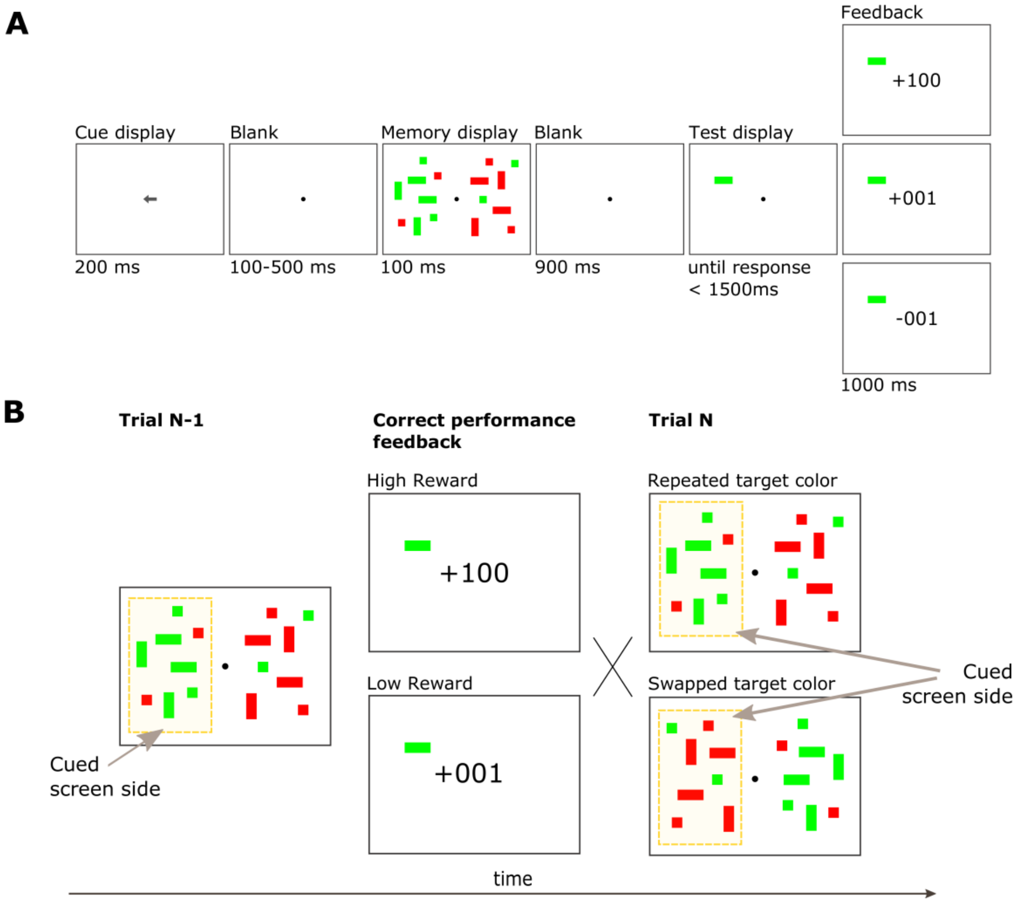

Figure 4.1 Experimental design

A. Trial Schematic. After a cue of 200 ms, a memory display of either 2 or 4 targets on each side of the screen is presented for 100 ms. Targets could be either green or red and participants memorized their orientation for 900 ms, until a test display appeared for a maximum of 1500 ms. Participants indicated if the rectangle presented on the test display was the same or different from the corresponding one in the memory display. 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, specifically, was not dependent on target color. **B.** General Paradigm. Trials where divided in 4 conditions according to the magnitude of reward received in trial n-1 (high vs. low) and the repetition or swap of the target color (irrespective of cued side). The rectangle that indicates the to-be-memorize side in the figure was not shown in the experiment.

EEG recording and analyses. 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). 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, data were down-sampled offline to 500Hz, referenced to the average of encephalic channels, and digitally low-pass filtered at 30Hz (non-causal 1000-point linear-phase FIR kernel; 0db attenuation at 29 Hz; -6dB at 30 Hz). Epochs tainted by head motion or other non-stereotyped artifacts 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 lateralized presentation of targets. Independent component analysis (ICA; Bell & Sejnowski, 1995; Delorme & Makeig, 2004) was applied to the data and used to identify and correct artifacts resulting from blinks, later eye movements, and muscular activity.

Event-related potentials (ERPs) were calculated using standard signal averaging procedures (Luck, 2005). All ERPs were baseline corrected to the 200 ms interval preceding 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 the contralateral and ipsilateral waveforms. We defined N2pc and CDA in accordance with previous studies (Hickey et al., 2009, 2010a; Mccollough et al., 2007; Vogel & Machizawa, 2004; Vogel et al., 2005). We defined a relatively large interval for N2pc that was measured between 200–300 ms after the onset of the memory display (Mccollough et al., 2007).The CDA was computed from 400–900 ms. The CDA is commonly defined starting from 300 ms (Mccollough et al., 2007; Vogel & Machizawa, 2004; Vogel et al., 2005) or 400 ms (Machizawa et al., 2012; Pagano, Lombardi, & Mazza, 2014). We decided to use a more conservative approach selecting a later lower bound for our interval in order to avoid the risk of measuring residuals of modulation in the N2pc, however results equivalent to those reported in the next session were obtained for the 300-900 ms interval. Only correct trials were included in ERP analysis.

Analyses and Results

Our motivating hypothesis was that reward would increase the quality of visual representations held in VWM. As such, we expected that high magnitude reward would positively impact the encoding or maintenance of stimuli representations when the color 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 color. 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 analyzed (leading to a mean of 178 trials per condition for behavioral analysis of accuracy, where 127 of these trials garnered correct response and were used to calculate ERPs).

Behavioral performance. 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%; t(21) = 17.08; $p < 0.001$) and RTs (2 items: 714±91ms; 4 items: 787±93ms; t(21) = -13.31, $p < 0.001$). We analyzed the influence of the magnitude of reward received in the previous trial as a function of the repetition or swap of the target color by means of a repeated measures ANOVA with Reward X Repetition (2 X 2) as factors. Contrary to our expectations, no effects were observed on accuracy (all Fs<1). A facilitation for color repetition was observed on RTs (F(1,21) = 6.68; p = 0.017; η_p^2 = 0.24), but no main effects or interactions with reward (all Fs<1).

Electrophysiological results. Consistent with 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 4.2A) and compared the average difference waves (contralateral minus ipsilateral) across different reward and repetition conditions. Average N2pc and CDA amplitudes were entered into a repeated measures ANOVAs with factors for prior reward (high- vs. low-magnitude reward in trial n-1) and target color repetition (repeat vs. swap). N2pc amplitude was significantly larger for target color repetition (F(1,21) = 6.03; p = 0.023; $\eta_p^2 = 0.22$), suggesting facilitated selection of stimuli characterized by the target-associated color (see Hickey, Olivers, Meeter, & Theeuwes, 2011). However, prior reward had no reliable effect on the N2pc (all Fs<1). To gain further perspective on this null result we calculated mean N2pc amplitude 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 (all Fs<1).

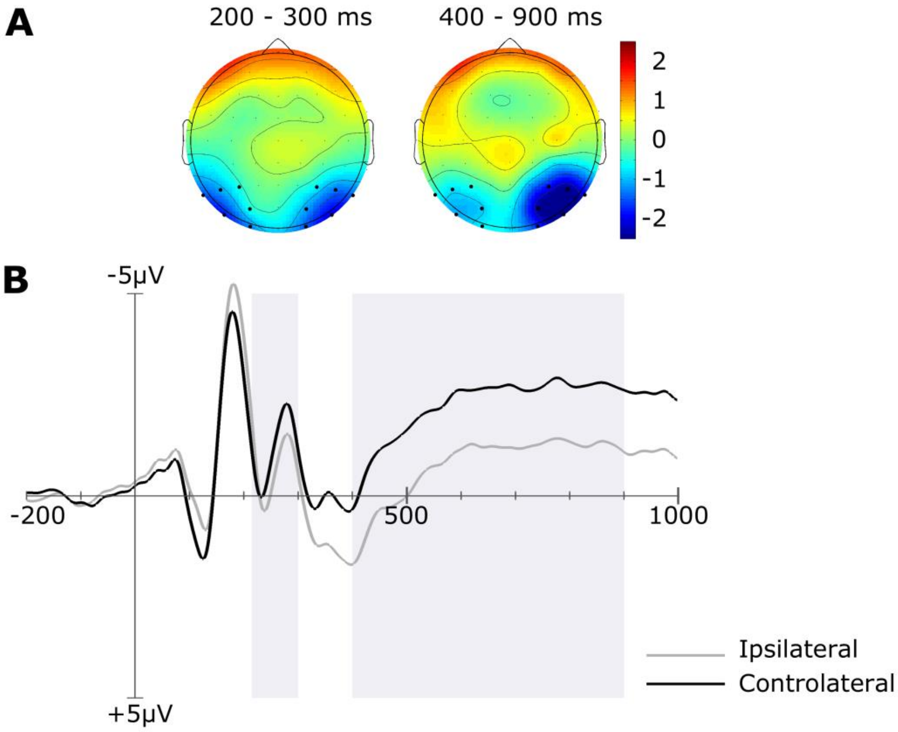

Figure 4.2 N2pc and CDA topographic maps and ERPs

(A) Topographic maps for N2pc (200-300 ms) and CDA (400-900 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 gray areas indicate the time intervals selected for N2pc and CDA analysis

Consistent with prior work (Drew & Vogel, 2008; Ikkai et al., 2010; Mccollough et al., 2007; Vogel & Machizawa, 2004; Vogel et al., 2005), the CDA reached its maximum around 400 ms post-stimulus and persisted throughout the entire retention period. Critically, analysis revealed an interaction between target color repetition and magnitude of reward in trial n-1 ($F(1,21) = 6.85$; $p = 0.016$; $\eta_p^2 = 0.25$; main effects: Fs<1). Specifically, CDA amplitude was larger when the to-be-remembered stimuli were characterized by the same color as in the preceding trial and that trial had garnered high-magnitude reward ($t(21)= 4.54$; $p = 0.044$; Cohen's d = 0.48; for low magnitude trials results are $t(21)= 1.72$; $p = 0.209$; Cohen's d = 0.28).

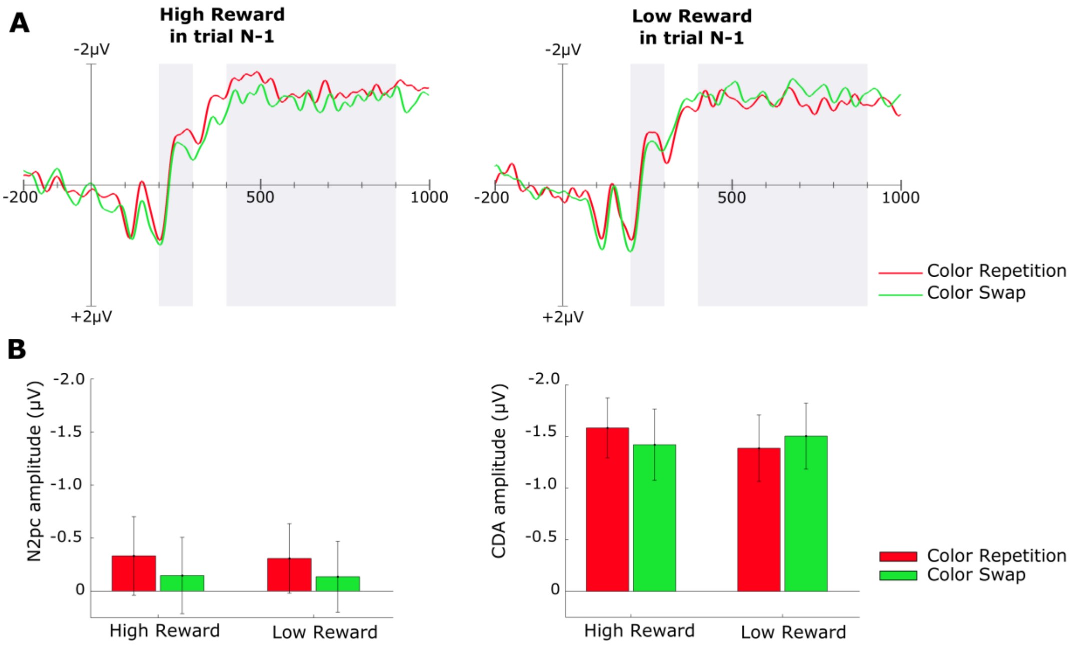

Figure 4.3 Reward-priming on N2pc and CDA

Difference waves from posterior electrodes identified in figure 4.2a. **(A)** ERPs as a function of reward received in trial n-1 and repetition or swap of target color in trial n. Shaded gray areas indicate N2pc and CDA time intervals. **(B)** Mean N2pc and CDA amplitudes over the interval indicated in A. Error bars represent within-participant confidence intervals (Cousineau, 2005). N2pc amplitude is significantly increased for target color repetitions, but it is not modulated by reward. In contrast, the CDA is sensitive to the magnitude of reward obtained in trial n-1.

In order to contrast the effects of prior reward and color 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 color repetition (repetition vs. swap). This revealed a critical 3 way interaction (F(1,21) = 8.52; p = 0.008; η_p^2 = 0.29), indicating that the interaction of prior reward and color repetition had a reliably large impact on the CDA than the unreliable impact of these factors on the N2pc. Uninterestingly, this analysis revealed additional effects of component (F(1,21) = 58.58; p < 0.001; η_p^2 =0.74), indicating that the CDA was larger than the N2pc, and a component X color repetition interaction (F(1,21) = 5.60; p = 0.028; η_p^2 = 0.21), reflecting a larger effect of color repetition on the N2pc (other comparisons were not significant; main effect of repetition: F(1,21) = 2.66; p = 0.118; η_p^2 = 0.11; reward X repetition interaction: F(1,21) = 1.66; p = 0.241; η_p^2 = 0.07; all other Fs<1).

4.4 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 to a color would change the quality of VWM maintenance for subsequent stimuli characterized by this color, even when color was task irrelevant. Results showed that when memory targets were characterized by the same color in two trials, and the previous trial had garnered 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 benefit to VWM encoding, in so far as our manipulation had no detectable influence on attentional selection indexed in the N2pc.

To date, behavioral studies of reward's impact on VWM, including our own, have left open the possibility that effects of reward might be indirect, reflecting changes in how reward-associated stimuli are attended and thus encoded for memory. Gong and Li (2014) suggested that reward could benefit the representation of items stored in VWM, but did not address at which particular stage this benefit might occur. The dissociation of N2pc and CDA results we observe here addresses this ambiguity, demonstrating that reward can have a discrete influence on VWM maintenance without any apparent preceding influence on attentional selection and memory encoding.

We interpret the apparent absence of a reward effect on attentional selection in our data as evidence that reward effects appear as a product of the demands of the experimental task. In our prior behavioral work, for example, we found that reward impacted memory both at very early stages of 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 from very early in time. However, in the task employed in that study color-reward associations were learned by means of a visual search task (Anderson et al., 2011b) that had no VWM component. Moreover, at test participants were required to spatially memorize a set of targets presented alongside a salient color singleton potentially characterized by a reward-associated color. Thus our training task was designed to impact selection, not memory, and our test task was designed to induce biases in the deployment of spatial attention. It is perhaps no wonder that our results showed influence at selective processing stages.

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 brain activity 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. Finally, target stimuli were uniformly colored and presented alongside distractors of both same and different color. This created a situation where facilitated processing of the reward-associated color, if it existed, would impact both representations of target and distractor, providing no net benefit to attentional selection or memory encoding.

We found a modulation of CDA amplitude as a function of the interaction of prior reward and target color repetition. 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 could benefit processing of targets when their characterizing feature was repeated in consecutive trials. By contrast, we had no strong predictions as to whether high reward feedback would produce a cost or have no impact at all on performance when color was not repeated.

In the current study, our results describe a modulation of CDA amplitude as a function of reward priming, but we see no corresponding effect on behavior. This is inconsistent with the idea that an increase in CDA reflects an increase in VWM capacity, as such an increase should have a behavioral correlate. One possibility is that the increase in CDA amplitude we observe rather reflects an increase in the precision of maintained representations. This would be consistent with prior literature suggesting that the quality and detail of VWM representations reflected in CDA can be flexibly adapted to changes in circumstance and task confine (Gao, Li, Liang, Chen, & Shen, 2009; Machizawa et al., 2012). Our task required only a coarse discrimination of orientation, with target and test stimuli differing by 0°, 45°, or 90°. Participants were presumably well able to correctly discriminate whether or not stimuli stored in VWM matched the test object, raising the possibility that a slight improvement in the quality of this representation would have no impact on overt performance.

In conclusion, our work shows how feature-reward associations can automatically affect the neural mechanisms instantiating VWM. Previous studies, mainly focusing on visual search paradigms, have revealed that reward can facilitate visual perception and drive attentional selection (Anderson et al., 2011a, 2011b; Hickey et al., 2010a, 2010b). More recently, the influence of reward have been expanded to other cognitive processes, such as VWM, showing that high reward-associated items are better maintained in VWM (Gong & Li, 2014) 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 by reward association, showing that reward can have a discrete effect on the maintenance of information in VWM.

5 General discussion and conclusions

A long-standing literature documents that reward is a fundamental determinant of animal behavior. In recent years, understanding the role of reward in human cognition has gained renewed interest (for reviews see Anderson, 2013; Awh et al., 2012; Chelazzi et al., 2013; Pessoa, 2009). Importantly, most of these studies aimed at disentangling the automatic effects of reward from strategic deployment of attention (Maunsell, 2004), in order to understand under what circumstances and to what extent reward affects visual cognition beyond current goals (for reviews see Anderson, 2013; Chelazzi et al., 2013). This recent and multifaceted literature demonstrates that reward history does indeed have a residual impact on the way attention is deployed to objects, locations or moments in time, even when it is not strategically advantageous for current tasks (Anderson et al., 2011a, 2011b; Della Libera & Chelazzi, 2006, 2009; Hickey & Los, 2015; Hickey et al., 2010a, 2014, 2015; Raymond & O'Brien, 2009).

During my PhD, I have begun to delineate the extents of reward influence on other aspects of visual cognition. Specifically, in the three studies I report, I address whether reward could have a direct impact on visual representations stored in VWM. In these studies, I argue that reward can influence VWM at different stages. The experiments described in Chapters 2 and 3 suggest that reward impacts information encoding in VWM; whereas in Chapter 4 I suggest that reward can influence memory also at later stages, without necessarily relying on a benefit in target selection.

The study described in Chapter 2 illustrates the influence of learned reward associations in a VWM task at different latencies from display offset when reward-associated objects are both task relevant and visually salient. The results show that items characterized by a reward-associated feature are not necessarily easier to remember, but they do interfere with representations of neutral items presented at the same time at nearby locations. I call this an *interference effect*. While all salient items tended to interfere with responses to non-salient targets, the magnitude of the interference was dependent on their associated value. Interestingly, the strength of the interference effect did not vary when tested at different delays between display and probe (ranging from 10 to 800 ms) suggesting that the interference effect originated at the moment of encoding information in VWM. The suggested explanation for this result is that reward-associated objects receive prioritized processing compared to neutral items leading to stronger representations that can interfere with those of other non-valuable items.

In Chapter 3, I describe a series of experiments which investigate the limits of the influence of reward on VWM, by varying the relevance of reward-associated objects for current goals and the resources required to perform the task. Prior work has shown that task relevant items are better remembered (Gong & Li, 2014) or produce larger interference in a VWM task (Chapter 2) when associated with high value. This study supports and expands those observations demonstrating that reward-associated objects can also exert interference in VWM representations of less valuable items when they are presented as distractors. Moreover, this work extends the results described in Chapter 2 showing that saliency is not a requirement for the emergence of reward influence on VWM representations.

Interestingly, the second experiment described in Chapter 3 indicates potential limits to the influence of reward-associations on visual cognition. Recent work has claimed that reward associations can influence performance (usually in a visual search task) beyond current goals and beyond item salience (Bourgeois, Neveu, Bayle, & Vuilleumier, 2015;

Munneke et al., 2015). Despite the suggested strength of reward influence, results reported in Chapter 3 suggest that such effects depend on the availability of spared cognitive resources for processing task-irrelevant information. When task demands increase, no resources are available for processing task-irrelevant information such as distractors' associated value. While several studies have shown that attention is captured by irrelevant items if these are learned to be valuable (Anderson et al., 2011a, e.g. 2011b), this automatic influence can occur only when the task performed does not completely exhaust attentional resources. This result suggests the existence of a sensible and evolutionary advantageous mechanism that prioritizes processing of valuable, but currently irrelevant, information only when performing a current task does not require our full resources.

The first two studies reported in this thesis were conducted adopting a value learning procedure (adapted from Anderson et al., 2011b) that established an association between different colors and values. Participants learned to select more or less valuable items among distractors in the context of a visual search (Chapter 2) or VWM (Chapter 3) task. The influence of learned associations was then tested in the context of an inhomogeneous display in which items of different value were presented. Results highlighted very early signatures of interference (already detectable at 10 ms from stimulus offset) suggesting that learned feature reward associations can affect the way information is selected and encoded. The type of task performed during training aimed to promote target selection among distractors. If the influence of learned associations is specific to the task performed during test (Della Libera & Chelazzi, 2009), it is perhaps not surprising that the effects observed during test emerged at the encoding stage. Moreover, the uneven displays used to quantify VWM performance during test leveraged competition between objects of different value possibly biasing the initial selection process.

The study presented in Chapter 4 investigates whether, under appropriate circumstances, past reward associations could significantly impact maintenance of visual representations in VWM even when no direct benefit during targets selection and encoding is observed. In this experiment I adopted a reward priming procedure, in which a high or low magnitude reward feedback was randomly assigned for each correct response. Results showed that when memory targets were characterized by the same color in two trials, and the previous trial had a garnered 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 benefit to VWM encoding, in so far as reward had no detectable influence on attentional selection indexed in the N2pc. These results represent initial evidence that reward history can influence different stages of visual processing according to display characteristics and task requirements. Unfortunately, despite clear changes in electrophysiological measures, no corresponding variations were observed in performance. One simple account for this might be that the influence of reward on maintenance is simply too small to be detected at the behavioral level. On the other hand, reward can influence VWM representations in ways not directly addressed by the task used. For example, reward history might influence VWM by increasing the precision of the information stored. This account is supported by previous studies showing that finer representations or representations of more complex objects produce larger amplitude CDAs than simple objects or coarse representations (Gao et al., 2009; Machizawa et al., 2012). This interesting account is not explicitly addressed in the study reported in Chapter 3 and a direct test is necessary to support this hypothesis. Another interesting possibility is that reward history influences the strength of representations in time, resulting in more durable VWM traces. While the work described in Chapter 2 may not appear to support this view, there the analysis of the content and capacity of visual memory was limited to a short interval from display offset, and mainly reflected iconic memory and the early stages of VWM, without testing the duration of the stored representations.

Overall, the work described in this thesis adds to previous studies showing that reward does not simply speed up processing of reward associated objects, prioritizing them and making them more difficult to ignore, but it can also significantly affect the nature of visual representations stored in VWM. However, this effect is not directly observable as a modulation of VWM capacity. This observation is consistent with most of the literature investigating the motivational impact of incentives on working memory. While reward usually benefits response speed, there is no clear improvement in VWM capacity (Gilbert & Fiez, 2004; Krawczyk, Gazzaley, & D’Esposito, 2007; Pochon et al., 2002; but see Gong & Li, 2014; Kawasaki & Yamaguchi, 2013). A fundamental challenge for future research is to better characterize the impact of reward history on VWM maintenance in order to characterize the nature of reward influence on visual representations and the mechanisms that support these effect.

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Acknowledgements

I want to thank all the people, inside and outside academia, whether they were my close friend or not, who motivated me by being a model with their passion, capacity or success and made me want to improve every day.

In particular, I want to thank my advisor, Massimo, for the support and freedom that he guaranteed me during these years. I also want to thank my unofficial co-advisor, Clayton, for insightful discussions, for always being positive and optimistic (even with me and I know that was the hardest part), but also for his support, time, empathy, enthusiasm, and patience.

I want thank David for the infinite discussions and for being a continuous motivation to get better.

I want to thank Magda and James. I am so glad I could have you two on my side on this long journey. You are an infinite source of inspiration with your curiosity, enthusiasm, passionate dedication to work, stubbornness, honesty and sense of justice.

I want to thank my very special office mates, Novella and Ludwig. I am so happy I could have both of you with me, really. It has been so fun and refreshing to have such smart and luminous friends in the office (and out of it).

I want to thank all my friends in Rovereto (Michele, Marta, Elena, Gian, Annalisa, Antimo) for saving me from my work, and all my friend at home that were always there for me even if I do not show up often enough.

I want to thank my family for being incredibly supportive and proud of me even if they have no idea of what I am doing.

Last, I have no words to thank Raf for everything. His love, patience, time, knowledge, curiosity, all.