Rewards teach visual selective attention

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ABSTRACT

Visual selective attention is the brain function that modulates ongoing processing of retinal input in order for selected representations to gain privileged access to perceptual awareness and guide behavior. Enhanced analysis of currently relevant or otherwise salient information is often accompanied by suppressed processing of the less relevant or salient input. Recent findings indicate that rewards exert a powerful influence on the deployment of visual selective attention. Such influence takes different forms depending on the specific protocol adopted in the given study. In some cases, the prospect of earning a larger reward in relation to a specific stimulus or location biases attention accordingly in order to maximize overall gain. This is mediated by an effect of reward acting as a type of incentive motivation for the strategic control of attention. In contrast, reward delivery can directly alter the processing of specific stimuli by increasing their attentional priority, and this can be measured even when rewards are no longer involved, reflecting a form of reward-mediated attentional learning. As a further development, recent work demonstrates that rewards can affect attentional learning in dissociable ways depending on whether rewards are perceived as feedback on performance or instead are registered as random-like events occurring during task performance. Specifically, it appears that visual selective attention is shaped by two distinct reward-related learning mechanisms: one requiring active monitoring of performance and outcome, and a second one detecting the sheer association between objects in the environment (whether attended or ignored) and the more-or-less rewarding events that accompany them. Overall this emerging literature demonstrates unequivocally that rewards "teach" visual selective attention so that processing resources will be allocated to objects, features and locations which are likely to optimize the organism's interaction with the surrounding environment and maximize positive outcome.

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1. Visual selective attention and its adaptability

Efficient goal-directed behavior is crucially mediated by visual selective attention. We are constantly exposed to a bombardment of sensory input, including from the retina; however, processing resources are inherently limited, and therefore only a small part of the incoming information can reach perceptual awareness and play a role in guiding behavior. All the available stimuli in a given context compete with one another to gain access to further processing, and visual selective attention is instantiated when the competition is resolved in favor of one or a few items of information that are deemed more relevant or are otherwise conspicuous (e.g., Chelazzi et al., 2011; Desimone & Duncan, 1995; Reynolds & Chelazzi, 2004). Through a twofold mechanism, visual selective attention aids goal-directed behavior by boosting the representation of stimuli that are salient or otherwise relevant given the current context and the goals of the individual, and by weakening the representation of the less relevant and potentially distracting items, whose processing may harm the execution of the intended behavior (e.g., Chun, Golomb, & Turk-Browne, 2011; Desimone & Duncan, 1995; Egeth & Yantis, 1997; Pashler, 1998; Reynolds & Chelazzi, 2004). The probability for different visual objects to be selected by attentional mechanisms may depend on properties that are perceptual in nature (in bottom-up, Theeuwes, 1992; Yantis & Jonides, 1984), such as their luminance or color contrast, or their sudden appearance, but also on strategic settings, for instance when an observer is searching for a specific feature or object in a cluttered display (Chelazzi, 1999; Egeth & Yantis, 1997; Wolfe, 1994). Moreover, selection may depend on the significance that certain objects have gained over time through experience, suggesting that visual selective attention and memory mechanisms work in close functional synergy (e.g., Awh, Belopolsky, & Theeuwes, 2012; Chun, Golomb, & Turk-Browne, 2011; Desimone, 1996; Kristjánsson, 2006; Kristjánsson & Campana, 2010; Logan, 2002).

This view of visual selective attention is supported by a vast literature showing that its deployment is flexibly adapted depending on the situation, with the result of increasing fitness to the

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environment and maximizing the outcomes of behavior. Not surprisingly, then, attentional selection mechanisms are particularly sensitive to the regularities offered by the situation, showing typical learning effects. These functional adjustments may occur on a trial-by-trial basis (in the short term), indicating that the setting of attentional priority is affected by a running evaluation of the events that immediately precede each attentional episode, as well as in the long term, indicating that prolonged experience with specific stimuli, contexts and tasks may give rise to enduring selection biases. For instance, on-line adjustments of attentional selection have been well documented in pop-out visual search tasks and more demanding, conjunction search tasks. Here the stability of target and distracters defining features across consecutive trials leads to marked improvements in search performance, even when the repeated features are not critical for the task at hand (Maljkovic & Nakayama, 1994, 1996, 2000; see Awh, Belopolsky, & Theeuwes, 2012; Kristjánsson, 2006; Kristjánsson & Campana, 2010, for reviews). Analogous priming mechanisms have been shown to affect orienting of transient, cue-driven attention, strengthening the notion that reflexive attention is not impermeable to the influence of memory (Kristjánsson, Mackeben, & Nakayama, 2001; Kristjánsson & Nakayama, 2003).

Similar rapid adjustments can be specifically found in relation to the attentional processing of distracting items. For instance, when a stimulus that has been shown as a distracter in the immediately preceding trial (and was therefore ignored) is then displayed as the target in the current trial and needs to be selected and processed, responses are slower and less accurate, giving rise to the negative priming effect (e.g., Tipper, 1985, 2001).

To account for the above findings, in particular the observation that inter-trial priming effects can aid the rapid orienting of attention to task-relevant and task-irrelevant items, the proposal has been made that attentional deployment is constantly supported by an implicit, primitive memory system (Kristjánsson, 2006; Kristjánsson & Campana, 2010; Kristjánsson & Nakayama, 2003). The fundamental role of the system would be to allow an individual to readily select information in the environment that has been perceived and attended in the recent past, capitalizing on the fact that the world around us rarely undergoes instantaneous changes. Key properties of this mechanism would be that it mainly operates at the level of individual stimulus features, it intervenes automatically, and it entirely escapes voluntary control. Moreover, increasing understanding of its neural underpinnings indicates that such memory system operates at multiple processing levels of the perceptual hierarchy, including nodes along the extrastriate cortical visual pathways, and brain regions in parietal and frontal cortex that are traditionally assumed to play a key role in attentional control (Kristjánsson & Campana, 2010).

Fine tuning of attention also occurs in the long term, showing that prolonged practice with given stimuli and contexts can alter attentional priorities for considerable lapses of time. In visual search paradigms such lasting effects have been observed both in relation to the selection of visual targets and to the suppression of distracters, in all cases leading to a more efficient processing of stimuli that have been repeatedly subject to attentional treatment. Long term benefits on selection have been found for items that were repeatedly used as targets for a number of trials (Kyllingsbæk, Schneider, & Bundesen, 2001; Shiffrin & Schneider, 1977; Sireteanu & Rettenbach, 2000), for targets bearing features that, although non task-relevant, were frequently associated to target items (Tseng, Gobell, & Sperling, 2004), for targets consistently shown in specific spatial positions within the display (e.g., Ciaramitaro, Cameron, & Glimcher, 2001; Geng & Behrmann, 2002; Hoffman & Kunde, 1999; Miller, 1988), and for targets consistently displayed together with specific distracters or arranged according to repeatedly used target-distracter spatial configurations (Chun, 2000; Chun & Jiang, 1998, 1999; Conci & Müller, 2012; Jiang & Chun, 2001). The latter effect, known as "contextual cueing", has been obtained also for targets embedded within naturalistic scenes, supporting the notion that the underlying mechanisms are likely to play a crucial role in guiding our attention to relevant objects within complex, natural environments (Becker & Rasmussen, 2008; Brockmole & Henderson, 2006; Stokes et al., 2012; Summerfield et al., 2006; Torralba et al., 2006). Moreover, if certain stimuli are used extensively as targets in visual search tasks, large interference effects are found when the same items are subsequently displayed in the role of distracters (Shiffrin & Schneider, 1977). This effect has been explained assuming that the repetitive search for a given item will increase its attentional priority, rendering it gradually more perceptually salient over consecutive trials. Consequently, when these objects with high priority are available among other stimuli, they will automatically attract attentional resources even when their selection is not required or beneficial (Kyllingsbæk, Schneider, & Bundesen, 2001).

Recent work has further demonstrated that the efficiency of attentional deployment to task-relevant information can be specifically aided by enhanced ability to filter-out distracting information as a result of extended practice (Dixon et al., 2009; Gál et al., 2009; Kelley & Yantis, 2009; Vidnyánszky & Sohn, 2005). For example, in one elegant study it was found that prolonged ignoring of a task-irrelevant and potentially interfering visual motion stimulus led to elevated thresholds for that stimulus, in the long run and this was paralleled by attenuated fMRI responses for the same stimulus in a number of cortical visual areas, including MT+ (Gál et al., 2009).

A special case of long term memory influence on attention is given by semantic associations, or the associations at the conceptual level between a sought target and any visual item displayed within a multi-element array (Moores, Laiti, & Chelazzi, 2003). It has been demonstrated that, in the context of a visual search task, objects associated to the target are both recalled more readily and chosen more often in a forced-choice recency judgment procedure. Moreover, under appropriate conditions, the presence of an associated object renders search slower and less accurate, owing to its ability to summon attention automatically. Finally, objects associated to the sought target tend to attract gaze more potently than unrelated items. Overall it appears that objects semantically associated to the object of search have privileged access to working memory, perceptual awareness and decision mechanisms (Moores, Laiti, & Chelazzi, 2003; see also Belke et al., 2008; Telling et al., 2010).

Measures of neural activity with a variety of methods, both in humans and animals, are consistent with some of the above behavioral reports (e.g., see Kristjánsson & Campana, 2010; for review). Just to cite an example, recordings of single unit activity from the inferotemporal cortex of the macaque suggest that the enhanced behavioral relevance of frequently attended stimuli, as well as the reduced relevance of consistently ignored stimuli, is directly linked to robust changes in their representation at the neural level. In one study it was found that, following extensive training, neuronal responses are increased for items repeatedly used as targets, while they are progressively reduced for those repeatedly displayed as distracters to be ignored (Jagadeesh et al., 2001). Fully compatible observations have been obtained by recording activity in the macaque frontal eye field within the context of visual search tasks (Bichot & Schall, 1999; Bichot, Schall, & Thompson, 1996).

As the above literature indicates, visual selective attention mechanisms are shaped and refined through short- and long-term learning and this property is likely crucial for allowing an efficient guidance of behavior. In fact, all the above adjustments share the common property of adaptively meeting specific environmental regularities and contingencies.

Based on its remarkable flexibility, the ultimate role of visual selective attention is that of providing behavioral planning processes with the most efficient and relevant representation of the outer world (see e.g., Gottlieb, 2012, for an interesting discussion on this general point). Access to the limited central processing resources must be granted to the objects that have the highest priority, given the current behavioral goals, and the knowledge accumulated over the past in similar contexts (including through evolution). Therefore, what has to be taken into account during attentional selection cannot be a simple memory of the past encounters with objects and situations, but most importantly, the effects (or outcomes) experienced in the past by selecting or inhibiting those objects within specific situations. Explicitly, if attentional selection of a certain object has led to positive consequences in the past, the same object ought to more likely win the attentional competition against alternative items when again encountered in the future in similar contexts. The same could be conceived of attentional suppression, assuming that if suppressing a specific object has previously been advantageous, a tendency to suppress the same object in the future may come about more readily. In this review we will present and discuss the main findings from a recent and quickly growing body of literature – coming in part from our own laboratory – which offers a groundbreaking perspective on experience-dependent attentional flexibility, suggesting that it may be dramatically influenced (if not even primarily controlled) by the delivery of rewards. However, before we address the main subject of this review – namely, a collection of reward-dependent attentional learning phenomena, we will present and discuss recent work investigating a related, yet -we argue- clearly distinct, type of influence exerted by reward on attentional deployment. It is well known that the prospect of reward can act as a form of incentive motivation, which mobilizes cognitive resources for the achievement of the reward at stake, including through the more effective deployment of attention towards task-relevant input (Aarts, Custers, & Marien, 2008; Pessoa, 2009; Shen & Chun, 2011). In the following section we will discuss this form of influence of reward on attentional processing.

2. Biased reward affecting attention through incentive motivation

Rewards, including monetary ones, have been often used as means to affect the motivational engagement of subjects taking part in behavioral experiments (Pessoa, 2009; Pessoa & Engelmann, 2010; Sarter, Gehring, & Kozak, 2006; Watanabe, 2007). Typically, subjects are informed prior to each trial that a certain (monetary) outcome is at stake for responses that meet a predetermined criterion on both speed and accuracy, so that there may be the possibility to earn some money with successful responses, or alternatively to lose money in case of poor responses. In all cases, money therefore acts as an incentive for optimal performance, directly increasing subjects' motivation and effort to deliver correct and fast responses in order to achieve the desired outcomes. A recent report further indicates that changes (increases) in the expected reward from one trial to the next are especially potent to enhance cognitive flexibility, as it can be measured with a number of task paradigms, including task switching (Shen & Chun, 2011).

A number of studies have further demonstrated that the availability of reward, and especially differential reward in relation to different spatial locations or objects, can exert a profound influence on the deployment of attention. Specifically, evidence supports the notion that the prospect of earning larger amounts of reward in relation to a given location or visual item leads to preferential deployment of attention towards the corresponding location or item. It should be stated immediately that these effects of reward

do not necessarily reflect explicit, or conscious processing, although in general they do; nevertheless in our opinion they invariably reflect changes in cognitive strategy in order to maximize the earning of reward during the course of the experiment. A key feature of these studies is that effects of reward on attention are measured while rewards are available and the participants are likely doing their best to harvest as much as possible of the available reward.

In most cases the possible outcomes of each trial are signaled in advance, so that the level of motivational engagement can be manipulated prior to the presentation of the experimental stimuli, and independently of their perceptual properties. Small et al. (2005) were the first to use monetary incentives to investigate whether the attentional processing of a given visual stimulus could be affected by subjects' motivation, and they applied varying monetary incentives for performance in a typical attentional orienting task, i.e. the Posner task (Posner, 1980). Subjects were asked to maintain central fixation and a target stimulus was displayed either on the left or on the right of the center. The task required the discrimination of the shape of the target by delivering the appropriate behavioral response. Before target onset, a cue was shown at fixation, which could either point to a possible target location, or be neutral. When the cue was directional, trials could be valid, with targets appearing at the cued position (80% of cases), or invalid, with targets appearing on the opposite side (the remaining 20%). Since directional cues are assumed to trigger attentional orienting, valid trials are usually associated with marked performance benefits due to the fact that targets appear in a location already in the focus of attention, and invalid trials to significant performance costs due to the fact that attention must be reoriented towards the target in order to allow its processing (Posner, 1980). In their study, Small and colleagues showed that when monetary outcomes were at stake for optimal performance, responses were significantly faster, and that the effects of incentives were particularly evident in trials which entailed attentional orienting towards a given region of space (i.e., valid and invalid trials, with no significant modulation of performance in neutral trials). The neural correlates of these effects were found in an incentive-dependent modulation of the overall activity in early visual areas, as well as in areas involved in the orienting of visuo-spatial attention, such as the posterior parietal cortex, including the inferior parietal lobule. Moreover engagement of posterior cingulate cortex was specifically related to the motivational aspect of the task (Small et al., 2005).

In a subsequent study, the relationship between the subjects' motivational state and attentional performance was investigated by administering target stimuli that were either related or unrelated to food, and participants were tested while hungry or satiated (Mohanty et al., 2008). The results showed that hungry subjects oriented their attention more quickly towards food related stimuli, in line with the fact that these items were more relevant given the subjects' current motivational state. This effect was found to correlate with activity in a number of brain regions, including portions of the parietal cortex, such as the intraparietal sulcus, the amygdala, the posterior cingulate cortex, the locus ceruleus and the substantia nigra. Interestingly, the activation levels in these regions were selectively modulated by the motivational relevance of the target stimuli: activity was increased in hungry subjects who were orienting their attention towards food-related items, while it was decreased both in hungry subjects orienting their attention towards non-food items, and in satiated subjects orienting their attention to food-related stimuli, whose motivational salience was low (Mohanty et al., 2008).

Beneficial effects of motivation on attentional performance have also been reported in a series of studies by Engelmann and Pessoa (Engelmann et al., 2009; Engelmann & Pessoa, 2007; Pessoa & Engelmann, 2010). These researches showed that the

performance improvements determined by incentive motivation are directly linked to an increased perceptual sensitivity for the critical stimuli. The neural mechanisms underlying this increased sensitivity have been identified in motivation-induced changes in activity in a distributed neuronal network, involving areas already associated with attentional processing of sensory stimuli, including the ventral precentral sulcus, the anterior insula, the caudate, and the fusiform gyrus, in addition to nodes of the reward-processing network (Engelmann et al., 2009).

By using a different approach, the effect of incentive motivation on the detection of a given target stimulus has also been investigated by Navalpakkam, Koch, and Perona (2009). They showed that the performance benefits associated to motivation might not only derive from an improved perceptual/attentional stimulus processing, but also from a response optimisation process that has the effect of maximizing the possible behavioral outcomes (Navalpakkam, Koch, & Perona, 2009). Evidence further indicates that the perceptual and the motivational relevance of visual objects can be integrated at early stages of sensory input processing, giving rise to a moment-to-moment complete representation of the expected reward in each trial. Attentional resources have access to this overall priority map and can be systematically oriented towards the spatial locations that are associated to the maximum expected reward in the current trial (Navalpakkam et al., 2010).

Another way of studying the effects of incentive motivation on visual processing consists in the administration of experimental tasks in which subjects are asked to choose between alternative stimuli, which are ultimately associated to different outcomes. Typically, the participants' pattern of performance demonstrates that they have learned the link between a stimulus and the associated reward probability by increasing the frequency with which they prefer stimuli with more successful outcomes. Recent evidence (Serences, 2008) has shown that this learned preference for highly valued stimuli may have a neural correlate in brain areas involved in the processing of visual input, indicating that the learned value of a visual stimulus can directly influence its neural representation throughout large portions of the visual cortex, at both early and late stages of the hierarchy (see also Shuler & Bear, 2006). Modulations of activity related to stimulus value were found in portions of retinotopically organized visual areas, including V1, extrastriate visual cortex, intraparietal sulcus and frontal eye fields, as well as in areas involved in the processing of both attentional and motivational information, such as the inferior and medial frontal gyri, left superior frontal sulcus, medial frontal cortex, posterior cingulate cortex, and inferior parietal lobe (Serences, 2008). Further evidence obtained with fMRI has shown that the incentive value associated with a given stimulus may also affect and sharpen the activity of functional systems involved in the processing of its critical features, such as for instance its orientation, a type of modulation that may eventually lead to an improved discrimination of the motivationally relevant stimuli with respect to other, less valued items (Serences & Saproo, 2010; see also Baldassi & Simoncini, 2011; for a related psychophysical observation). Interestingly, in the work of Serences and Saproo (2010) sharper tuning of neuronal representations in visual cortex (notably V1) for valuable stimuli was found even when the valuable stimulus was not selected by the subject, and therefore was presumably outside the focus of endogenous attention. However, unlike what suggested by the authors, we do not take this to imply that the reported effects are independent of attention; rather, we would suggest that they likely reflect a form of attentional control which depends on learning and acts regardless of strategic control (see Della Libera & Chelazzi, 2009).

Similar effects of reward biases acting as incentives which affect the participants' motivation to select specific visual stimuli have been obtained within the context of pop-out search (Kiss, Driver, & Eimer, 2009). Here subjects were engaged in a simple visual search task where on each trial they had to first locate a color singleton target among distracting items, and secondly discriminate its shape by delivering the appropriate motor response. Importantly, subjects were informed that targets in different colors would be associated with different reward probabilities, so that the incentive properties of the visual stimuli used were defined a priori and were entirely transparent to the participants (Kiss, Driver, & Eimer, 2009; see also Kristjánsson, Sigurjónsdóttir, & Driver, 2010; for an extension of these findings to a condition in which subjects were apparently never aware of the a priori associations between target features and potential reward). Highly valued targets led to marked benefits in performance, and were associated to an earlier and larger N2pc component in the corresponding ERP signal, suggesting that their increased motivational saliency was indeed accompanied by changes in neural activity at relatively early stages of cortical visual processing (Kiss, Driver, & Eimer, 2009).

In another brilliant study, the delivery of unbalanced rewards has been introduced within the classical Stroop task (Krebs, Boehler, & Woldorff, 2010), in which the stimuli displayed are color-words shown in colored print, such as the word YELLOW printed in blue color. Subjects are required to name the print color of each stimulus, and typically performance is slower and more error-prone when the print color and the word meaning are conflicting with respect to when they coincide (i.e. the word YELLOW written in yellow color). In their study, Krebs and collaborators delivered biased rewards in return for correct performance in the Stroop task, so that some print colors were associated with monetary incentives (and resulted in gains or losses, on the basis of actual response parameters), while other print colors were not. The results of this and a related study showed that the Stroop-like conflict can be significantly affected by the motivational relevance associated to target and distracting information. In particular, performance improved in trials where the motivationally significant information was task-relevant, while it was impaired when the same information appeared as part of the distracter to be ignored (Krebs et al., 2011; Krebs, Boehler, & Woldorff, 2010). Using fMRI, the later study observed that the prospect to obtain reward engaged the nucleus accumbens – a region known to play a key role in reward processing, together with dorso-lateral prefrontal cortex and the inferior frontal gyrus on the right, and frontopolar cortex on both sides – regions known to participate in executive control functions. Furthermore, enhanced activity was found in the inferior parietal cortex bilaterally, as well as in the fusiform gyrus. Overall, these results indicate that the prospect of earning money engages essentially three component brain systems: the one involved in processing reward, the one crucially responsible for exerting cognitive control and maintaining task goals, and finally, portions of extrastriate cortex that are responsible for processing the task-relevant stimuli. The same study also explored the neural underpinnings of performance costs due to implicit, or accidental, reward associations with the task-irrelevant dimension (word meaning), whose influence on behavior cannot depend on strategic effects of monetary incentives on attentional control. Here, in contrast, enhanced activity was found in lateral and medial frontal cortex, including the pre-supplementary (pre-SMA) region, as well as in the fusiform area bilaterally. It was proposed that the pre-SMA activation may be specifically responsible for countering prepotent response tendencies elicited by the reward-associated, yet task-irrelevant, stimulus information. Finally, enhanced activity within the fusiform gyrus was shared between task-relevant and task-irrelevant stimulus-reward associations and was proposed to mediate increased processing and attention (whether strategically deployed or reflexively engaged) for reward-associated input in object-representation areas (Krebs et al., 2011).

In the present section we have jointly discussed the behavioral effects and neural underpinnings of motivationally driven influences of reward prospect on attentional control. What we intend to emphasize here is that rewards motivating individuals to deploy attention in order to maximize success engage the same neuronal mechanisms that are normally important for exerting cognitive control. It has been argued before that, under conditions where rewards act as a form of incentive motivation to mobilize resources for more efficient control of attention, the effects of reward on attention are hardly separable from those that can be elicited by any other cue or instruction instigating attentional deployment in a strategic fashion (Hickey, Chelazzi, & Theeuwes, 2010a; Maunsell, 2004; but see Krebs et al., 2011). To be more explicit, whenever individuals are presented with stimuli that predict different amounts of reward, or different reward probabilities, it is obvious that they will allocate attentional resources according to those differences in a strategic fashion, owing to the diverse motivational significance of the competing stimuli. The motivational significance associated with each stimulus in a set can immediately translate into more effort to deploy attention towards the stimulus which predicts higher gains. These notions, which are confirmed by the results summarized in the foregoing paragraphs, are strongly reminiscent of the principles captured by the well-known "matching law". In simple terms, the matching law states that when organisms are confronted with a choice situation, they allocate their behavior to competing options in proportion to the distribution of reinforcers (Baum, 1974, 1979; Herrnstein, 1961; Sugrue, Corrado, & Newsome, 2004, 2005). The notion can be easily transferred to the domain of attentional allocation, by simply assuming that the attentional priorities of a number of competing stimuli will reflect the differential in reward prediction associated with the various stimuli (see Shahan & Podlesnik, 2006, 2007, for compatible findings in the pigeon). Unlike what we have discussed so far, in the following sections we shall address forms of reward-mediated attentional control that are not accounted for by the notion that reward prediction mobilizes cognitive resources in a purposive manner and instigates deployment of attention accordingly in order to maximize benefit. Instead, we will focus on forms of reward-mediated effects on attention that crucially depend on learning and memory.

3. Effects of reward on the immediate deployment of visual selective attention

The long standing research on the mechanisms and brain circuits underlying reward processing in general has shown that they play a fundamental role in the monitoring of performance, by operating a continuous evaluation of the outcomes of behavior and of their desirability (O'Doherty, 2004; Schultz, 2006; Schultz, 2007a, 2007b). During performance in typical paradigms used in psychophysical and cognitive psychology experiments, both the feedbacks often provided to inform participants of their response accuracy or the acknowledgment by the participant (in the absence of an external feedback) that a correct response or an error has just been made, evoke specific activations in brain structures that are also sensitive to the delivery of reward, including portions of the cingulate cortex (Holroyd & Coles, 2002; Miltner, Braun, & Coles, 1997). Moreover, when the tasks entail the win of variable amounts of reward in return for correct performance, the same structures also show differential activations for rewards of different entities, so that lower rewards are usually associated with patterns of activation that are quite similar to those normally associated with error feedbacks (e.g., Gehring & Willoughby, 2002). These results hint at the possibility that even in standard conditions (i.e., in the absence of explicit rewards), performance is continuously subject to an internal evaluation of its efficacy, which eventually leads to the selective reinforcement and consolidation of patterns of neural activity that led to the more advantageous behavior (Holroyd & Coles, 2002).

In the studies carried out in our laboratory, considered below, participants were engaged in attention demanding tasks, and while error responses received a corresponding error signal, correct responses were followed by a reward feedback which signaled the delivery of a variable monetary win. Importantly, highly and poorly rewarded responses were equally correct from a formal point of view, as the assignment of high and low rewards was always predetermined and unrelated to performance parameters (e.g., rewards were not related to response time). As it will be noted, although the different studies report different effects of reward on selective attention, they all reveal reward-dependent attentional adjustments tending to increase the future probability of obtaining more successful – and highly rewarding – outcomes.

Some years ago we pioneered the study of the relationship between reward and visual selective attention. In particular, in our first study we set out to investigate whether rewards had an impact on the immediate aftereffects of attentional deployment (Della Libera & Chelazzi, 2006). The experimental protocol allowed us to investigate the influence of reward on two well known intertrial effects, such as positive (Rabbitt & Vyas, 1973; Tipper, 1985) and negative priming (e.g., Tipper, 1985, 2001). Within this context, positive priming consists of a marked facilitation in performance, i.e. faster reaction times and lower error rates, in trials where the current target has also served as the target in the previous trial, indicating that perceptual processing and attentional selection of a given stimulus (as well as response selection) is facilitated over repeated encounters with the same stimulus. Symmetrically, as briefly described above, negative priming refers to deteriorated performance when the target stimulus in the current trial matches the item that had served as the distracter to be ignored in the previous trial. It is generally agreed that negative priming arises from traces of lingering inhibition applied to a distracter's internal representation, which perhaps in combination with other perceptual and/or mnemonic mechanisms hampers the selective processing of information that has previously been actively suppressed (May, Kane, & Hasher, 1995; Neill & Valdes, 1992; Neill et al., 1992; Tipper, 2001; Tipper & Milliken, 1996). Both these effects can be taken to indicate that any episode of attentional processing leaves specific memory traces that outlive the current episode and impact the ability to select and ignore specific items in the immediate future (also see Kristjánsson, 2006).

In our experiments, each correct response led to the gain of a reward that could be high or low (10 or 1 Eurocents, respectively), and participants were deceitfully told that this amount would be determined by an algorithm on the basis of their performance. Specifically, incorrect responses would receive only an error feedback and no reward, while correct responses would receive a high reward when performance was deemed optimal, or a low reward when it was deemed less than optimal (Fig. 1a). Contrary to this instruction, reward values were selected independently from the subject's performance in the current trial, and could be high or low with the same overall probability (50%). The key finding of the study was that in conditions that normally lead to negative priming effects (i.e., when the current target is identical to the previous distracter, relative to a control condition) robust negative priming was found exclusively if response to the preceding trial had led to high reward, and therefore performance was deemed especially successful (Fig. 1b). In contrast, the attentional selections that, albeit correct, had been followed by a low reward (and were therefore considered unsuccessful) not only failed to give rise to negative priming, but in some cases even led to a paradoxical facilitation in responses – or a positive priming effect,
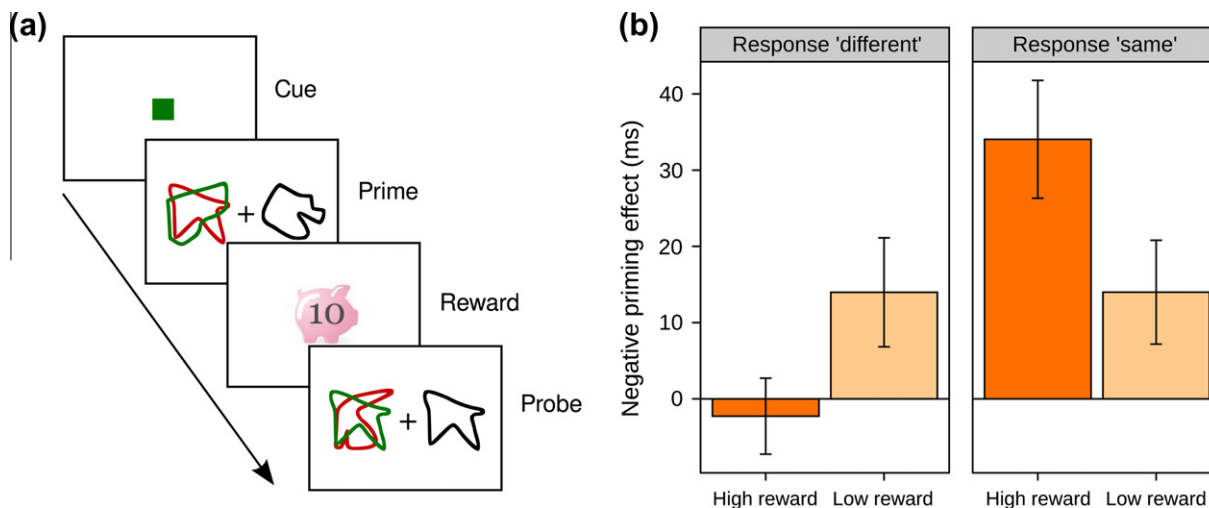
Fig. 1. Methods and results of Experiment 2 described in Della Libera and Chelazzi (2006). (a) Experimental paradigm: Two overlapping shapes, one red and one green, appeared on the left of fixation, while a black shape appeared on the opposite side. A green or red central square cued the relevant color in the sequence. Subjects had to perform a same/different judgment between the shape in the relevant color on the left and the black one on the right. (b) Main results: The negative priming effect observed in probe responses was significantly modulated by the reward delivered following responses to the previous prime. In particular, the effect was only statistically reliable for probes requiring a 'same' judgment and following highly rewarded primes. Error bars denote SEM.

probably due to the nude beneficial effect of stimulus repetition across consecutive trials in the absence of an inhibitory tag (Della Libera & Chelazzi, 2006). Thus, the monetary feedback delivered after each behavioral response appeared to play a key role in strengthening the memory traces established by the attentional suppression of distracting information during successful trials, or in clearing up these traces whenever the attentional episode was classified as unsuccessful. These results demonstrated for the first time that the memory trace left in place by each selection episode can be modulated by a post-hoc appreciation of its adaptive value, so that attentional selections with more desirable consequences, including higher monetary gains, leave behind stronger and/or longer-lasting traces compared to less rewarded selections.

Differently from what emerged relatively to the negative priming effect, the reward-dependent modulations of positive priming seemed weaker and less consistent in this experiment (but see below), suggesting that the facilitatory inter-trial effect that was present in the data might reflect primarily the automatic consequences of stimulus repetition, and be less sensitive to outcome-based adjustments (Schacter & Buckner, 1998).

On the basis of the above observations, notably the absence of any negative priming effect following low reward, it is actually tempting to speculate that in standard experiments of this kind, where reward is not typically involved, the occurrence of negative priming may be dependent on some form of internal reward, acting in a similar way to external reward feedback. In this vein, the shared belief that negative priming tends to be a highly erratic phenomenon under usual circumstances may be due to the variable and ill-controlled impact of internal reward signals in most experiments. Similar ideas can of course be put forward in relation to different kinds of attentional learning phenomena, as previously discussed, where learning is normally investigated in the absence of any explicit reward, except sometimes for the delivery of feedback to inform the participants of their correct vs. wrong performance. As we will see in later sections, we now know that long-term attentional learning is also critically gated by reward.

Other studies have subsequently extended the above observations within the context of the additional distracter, visual search paradigm (Theeuwes, 1992), showing that robust reward-based effects can also be obtained relatively to the attentional mechanisms underlying target selection in these paradigms (Hickey, Chelazzi, &

Theeuwes, 2010a, 2010b, 2011). Here participants performed visual search tasks in which the target, bearing a distinctive visual feature, had to be first detected among a number of nontarget stimuli, and then categorized according to a task relevant stimulus property. Importantly, on some trials, one of the nontargets was rendered especially salient relative to the other nontargets, acting as a singleton distracter (e.g., a green singleton item amongst an array of red items). As shown in prior work, the salient distracter impaired performance, owing to its ability to capture attention in a reflexive manner. More importantly, when the color that distinguished the target from the salient singleton distracter remained stable across consecutive trials, a significant performance benefit was observed with respect to when it was changed, leading to the well known facilitatory effect of inter-trial repetition priming in this sort of task (Hickey et al., 2011; Maljkovic & Nakayama, 1994). However, such repetition benefit was much stronger in trials following highly rewarded responses with respect to trials following poor rewards. This indicates that processing of reward-associated features is facilitated, such that attention is deployed to objects characterized by these features in subsequent trials (see Kristjánsson, Sigurjónsdóttir, & Driver, 2010; for a compatible finding). One should note that also in these studies reward values were completely decoupled from actual response parameters. Nonetheless, low rewards, acting as a deceitful indicator of poor performance, appeared to impede the establishment of strong attentional aftereffects, even when the prior selection episode had been perfectly adequate. Of crucial interest, the data also showed that these effects of reward persisted even when strategic deployment of attention acted in opposite direction, revealing a form of enhanced and irresistible automatic capture of attention by reward-associated features. The latter property – namely that reward-associated features enjoy higher attentional priority even in opposition to strategic attentional setting, is reminiscent of what is known of the memory system that mediates priming of pop-out and related phenomena (e.g., Kristjánsson, 2006). It is therefore plausible that at least some of the influence exerted by reward on inter-trial priming effects is mediated by the same memory system.

More recent research (Hickey & van Zoest, 2012) has extended these initial observations to overt oculomotor behavior, showing that reward-associated features influence saccade trajectory even

when they are entirely task-irrelevant and the observer is asked to ignore them, with a detailed pattern of eye movements that is highly similar to what previously observed with salience-based manipulations (Godijn & Theeuwes, 2004).

Additional important observations emerged from the recent work of Hickey and colleagues. One study demonstrated that reward signals directly affect the perceptual salience of stimulus features that have just been processed (Hickey, Chelazzi, & Theeuwes, 2010a). Specifically, the analysis of scalp-recorded electroencephalographic signals obtained from a group of participants revealed that the event-related potentials (ERPs) recorded from posterior recording sites in relation to the attentional selection of the target stimuli (i.e., the P1 and N2pc) had a significantly larger amplitude in target feature-repetition trials following high rewards. This suggested that the salience of target-defining properties, which is normally enhanced when these properties are repeated across consecutive trials, could be further boosted by an intervening reward.

Interestingly, across individual participants, the extent to which reward influenced stimulus salience and search performance was highly correlated with the extent to which high vs. low reward feedback itself elicited differential activity at the level of an anterior and medial frontal region, including the anterior cingulate cortex (ACC), a region which is commonly associated with the processing of stimulus value and rewarding content (e.g., Gehring & Willoughby, 2002). The higher the ACC sensitivity to the different reward magnitudes, the largest the reward-dependent modulation of performance for stimulus features that had been recently associated with high vs. low rewards (Hickey, Chelazzi, & Theeuwes, 2010a). Moreover, and quite amazingly, the attentional sensitivity to reward signals could be reliably predicted by specific measures of personality traits that are commonly used to estimate a subject's reward sensitivity in the context of their daily activities (Hickey, Chelazzi, & Theeuwes, 2010b). Overall, based on the above evidence, the authors proposed that rewards modulate activity within the mesocorticolimbic dopaminergic system, including the ACC, which then broadcasts signals towards posterior visual cortical areas, directly modulating stimulus representations at this level (Hickey, Chelazzi, & Theeuwes, 2010a), a notion that finds direct support in other work (Weil et al., 2010).

## 4. Reward-dependent attentional learning

The evidence that highly rewarded attentional selections leave stronger traces and exert a greater impact on the immediately subsequent performance raises the obvious possibility that their influence might also be longer lasting, so that the more successful selections should have a higher probability of affecting behavior in the long term. We investigated this possibility through a general approach whereby participants underwent a training phase, followed some days later by a test phase (Della Libera & Chelazzi, 2009). During training, which consisted of three experimental sessions on consecutive days, subjects were engaged in a task requiring selective processing of task-relevant information and concurrent suppression of distracting information (Fig. 2a). Correct performance was immediately signaled by the delivery of reward, which could be high or low. Crucially, and unknown to the subjects, during training the reward values were systematically biased depending on the specific stimuli displayed as target to be selected or distracter to be ignored (Fig. 2c). When four out of the sixteen total stimuli in the set were displayed, each correct response had an 80% probability of leading to a high reward, and a 20% probability of leading to a low reward. Four other items were instead associated with a high reward in 20% of cases, and to a low reward in the remaining 80%. Orthogonally to this classification, for four of

these stimuli (two for each probability level) the bias was applied only to trials where they were the target to be selected, while for the remaining four stimuli the bias was only applied when they were the distracter to be ignored. Importantly, each of the stimuli used in the experiment was displayed the same number of times as target and distracter, therefore the perceptual and attentional experience gained with all the items in the stimulus set was equal. The experimental paradigm was designed so that the global probability of either reward value was 50%, and for each of the participants different visual stimuli were assigned to the different categories. It is important to underscore that, when queried at the end of the experiments, none of the tested participants reported any intuition of the reward schedule in relation to the different stimuli.

The effects of the unbalanced reward delivery applied during the training phase were assessed in a separate experimental session (test), which took place 5 days after training, and during which no rewards were delivered. Participants were divided in two groups, and tested by means of two different experimental paradigms (Experiments 1 and 2 in Della Libera & Chelazzi, 2009) which tapped distinct aspects of attentional processing (Fig. 2b and d). In both cases subjects had to perform a task requiring selection and filtering of visual shapes, and the stimuli were the same as those used during the training phase. In spite of the considerable delay between training and test, we observed marked differences in performance to stimuli falling in the different categories of reward bias (Fig. 3a and b). Across paradigms, which provided complementary results, items associated with higher rewards when selected as targets during the training phase led to facilitated responses when they were the target to be selected in the test task. On the other hand, when the same stimuli were presented as distracters at test, their suppression was harder, leading to slower and less efficient behavioral performance. Symmetrical results were obtained for stimuli that during training were systematically associated with reward biases when playing the role of distracters. If the test task required to ignore a stimulus that previously (during training) led to higher gains when correctly ignored, then performance was more efficient, whereas it was more difficult to select the same stimuli if they were displayed as targets in the test trials (Della Libera & Chelazzi, 2009). In other words, we gathered evidence to indicate that reward delivery led to especially robust attentional learning, which included both the increased efficiency of target selection and of distracter suppression.

There are several important observations to be made in relation to the above findings. First and foremost, the observation that under appropriate conditions we could detect an effect of our reward-based manipulation in relation to the distracting item presented during the test task is especially informative, as it indicates that in our paradigm the influence of reward history on performance was not mediated by any change in deliberate strategy. Of course a change in strategy might be expected to affect performance, if at all, in relation to the target item one is instructed to select, not in relation to the distracter. Therefore, the demonstration that a distracter that had been associated with high reward during training (when playing the role of target) is harder to ignore compared to a distracter that had been associated with low reward during training (again, when playing the role of target) suggests that the effect is due to the attentional priority acquired by the item during training, and that such priority affects performance regardless of strategy. Moreover, it is also highly unlikely that our reward-based manipulation influenced performance through an incentive motivation mechanism, of the type we have discussed previously, since it is important to remember that no rewards were involved during the test phase.

A second important point to make concerns the nature of the underlying learning mechanism. As we will further elaborate
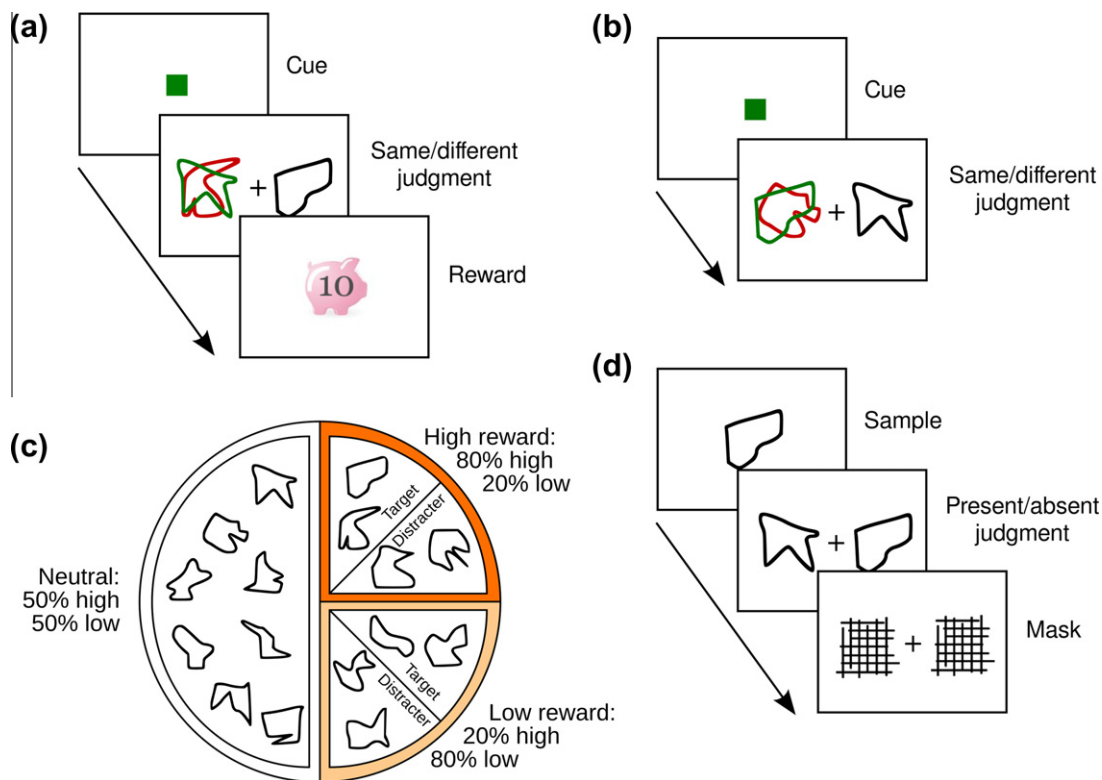
Fig. 2. Methods described in Della Libera and Chelazzi (2009). (a) Experimental paradigm adopted during the training sessions with reward in both Experiments 1 and 2: Subjects performed a same/different judgment between the shape on the left shown in the previously cued color (red or green), and the black shape displayed on the right. Each correct response was followed by a reward feedback indicating a high or low monetary win. (b) Experimental paradigm adopted in the test session of Experiment 1: The task was identical to the one used during training, except that no reward was involved. (c) Sample sorting of stimulus shapes into biased reward categories for one example subject. (d) Experimental paradigm adopted in the test session of Experiment 2: A sample shape was shown at the beginning of each trial. Then two shapes appeared briefly, one to the left and the other to the right of fixation, and were immediately hidden by a pattern mask. Subjects had to decide as quickly and accurately as possible whether the sample was present or absent in the stimulus array. Samples were present in 50% of cases.

below, we do not believe that the above findings can be adequately understood in terms of value learning, or the acquired value of stimuli stemming from their consistent association with rewarding events during training. If this were the case, then one would be led to predict that stimuli consistently associated with high reward when shown in the role of distracters during training, should either remain unaffected or should have also become valuable items, and therefore should be relatively easy to select and hard to ignore during the test phase. But we obtained exactly the opposite pattern of results. To reiterate, when the task at test measured the ability to ignore a stimulus that previously (during training) led to higher gains when correctly ignored, we found that filtering of such distracter was more efficient, whereas it was more difficult to select these stimuli if they were displayed as targets in the test trials. Therefore, it appears that the association with high reward during training enhanced the ability to select stimuli presented as targets as well as the ability to ignore stimuli presented as distracters. Again, this is unlike what one might expect as the consequences of value learning, whereby items imbued with higher value should have higher attentional priority and should therefore be easier to select and harder to ignore.

A final important notion which can be derived from the above study concerns the degree to which the effects of our reward-based manipulation require that the task be the same between training and test, or whether instead they can generalize across different tasks. Evidence obtained in one of the tested groups (Experiment 2 in Della Libera & Chelazzi, 2009) clearly indicates that effects generalize easily to a different task from that used during training. This strengthens the notion that such effects do not reflect the lingering consequences of a deliberate strategy developed during training in relation to the various stimuli within the context of a given task, because if that were the case then one would expect that no effect should be found when the task changes between training and test, but this was not the case. Therefore, we can conclude that the reported effects depend on attentional learning phenomena occurring in relation to the specific stimuli shown during training, and the effects are bound to the specific stimuli but are independent from the given task.

A growing literature from recent years provides converging evidence to support the notion that rewards exert an especially strong influence on attention and attentional learning. In the study by Raymond and O'Brien (2009) subjects were initially involved in a value learning protocol, in which they (implicitly) learned that different visual stimuli (in this case human faces) had a different probability of leading to more or less positive outcomes. Subsequently, the same stimuli appeared in a rapid visual serial presentation (RSVP) task where subjects had to discriminate the shape of a simple geometrical figure, and then to categorize a subsequently presented face stimulus as old or new with respect to the faces seen in the previous phase of the experiment. It is well established that, in RSVP paradigms, when the time lag between the two targets is within a critical range (typically between 100 and 500 ms) a significant decrement in performance is observed in relation to the second target, provided that the first is correctly identified – an effect termed "attentional blink" (e.g., Dux & Marois, 2009; Olivers & Meeter, 2008; Raymond, Shapiro, & Arnell, 1992). Interestingly, it was found that when highly rewarded faces were used as the second target, these were more likely to be correctly identified with respect to less rewarded items, therefore showing a marked resistance of valuable items to the attentional blink effect
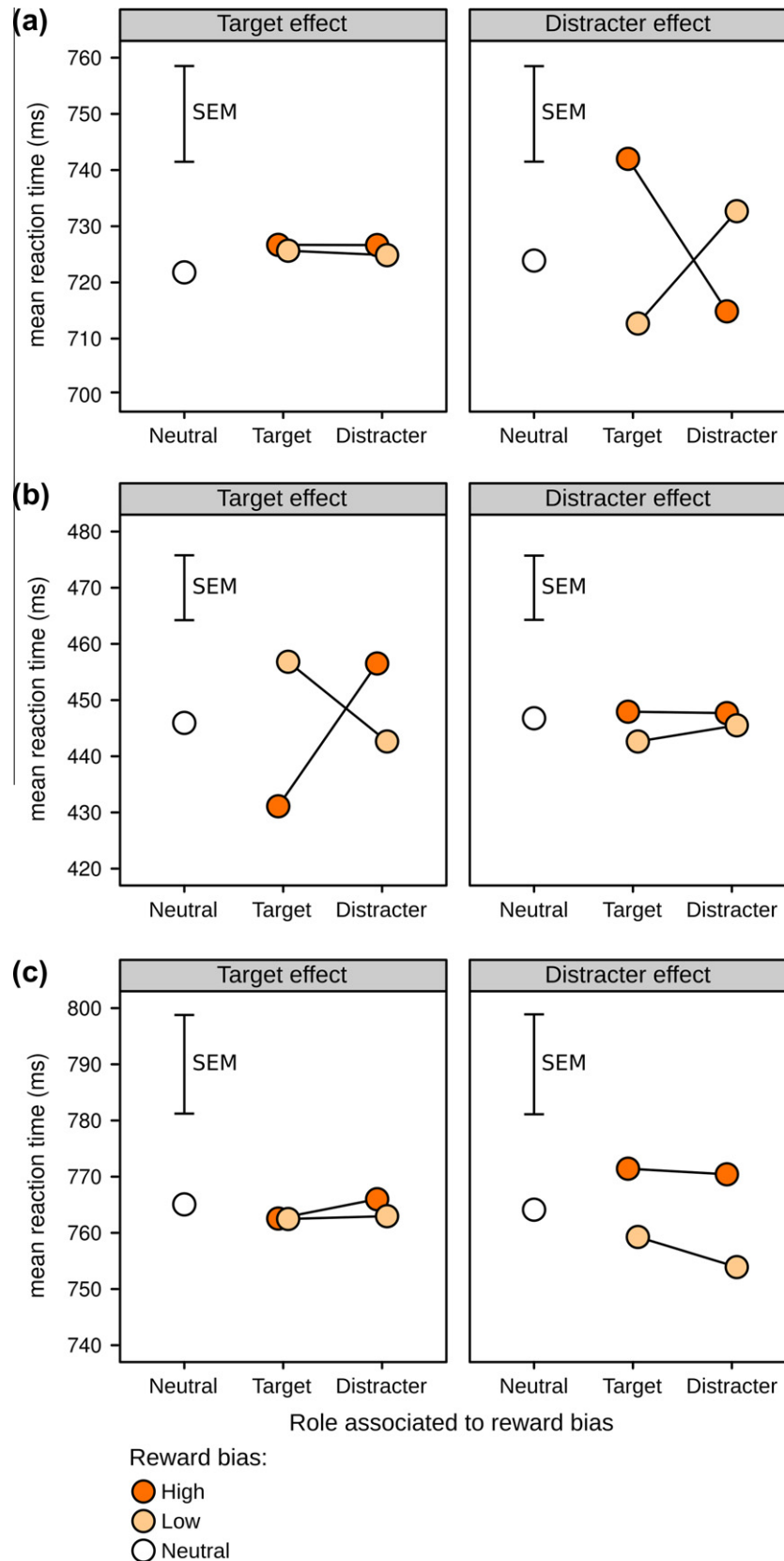
Fig. 3. Long term effects of reward. (a) Results from Experiment 1 in Della Libera and Chelazzi (2009). (b) Results from Experiment 2 in Della Libera and Chelazzi (2009). (c) Results described in Della Libera, Perlato, and Chelazzi (2011). In all panels the effects associated with the current target item are depicted on the left, while those associated with the current distracter are depicted on the right. Error bars denote SEM for the data presented in each panel.

(Raymond & O'Brien, 2009). These authors have subsequently shown that value association of stimuli affects not only the

deployment of attention in the time domain, as the effect on the attentional blink suggests, but also in the spatial domain

(Rutherford, O'Brien, & Raymond, 2010). When the same stimuli were used as uninformative cues in a typical probe task, responses were slower for probes appearing in positions previously occupied by highly valued stimuli. Assuming that attention is automatically captured by the initial appearance of highly rewarded objects, the subsequent presentation of a task relevant item (the probe) in the same spatial position might have led to the typical cost in performance associated with inhibition of return (e.g., Klein, 2000), suggesting that the reward-related stimuli are capable of strong capture of visuo-spatial attention.

A direct test that stimuli imbued with value, as a result of stimulus-reward associations established during a training phase, can exert attentional capture – termed value-driven attentional capture – has been performed by Anderson and colleagues with a series of experiments using variants of the visual search task (Anderson, Laurent, & Yantis, 2011a, 2011b). Similarly to the procedure that we have adopted in our study (Della Libera & Chelazzi, 2009), here again subjects completed a training and a test session, although unlike what we did in our work, here both sessions took place on the same day. Rewards were delivered only during training and the probability of receiving a high or low reward was biased according to the specific target-defining color. During training participants were to search for a color defined target presented amongst an array of colored nontargets. Target color was constant and defined in advance, and it could be either red or green with equal probability, with one color associated with high reward on most trials, ant the other color associated with low reward on most trials (Anderson, Laurent, & Yantis, 2011a, 2011b). During the test session, which took place immediately after training, colors were never task relevant, and subjects had to find a uniquely shaped target, to then discriminate the orientation of a line segment that appeared inside it. In one study (Anderson, Laurent, & Yantis, 2011b), on half the trials all the stimuli were displayed in black against a white background, while on the other half one of the nontargets was made more salient and shown in one of the colors that during training was associated with high or low rewards. The presence of a salient distracter during the test strongly hampered task performance, as previously shown (Theeuwes, 1992); however, this effect was magnified when the salient distracter was shown in the color linked to higher rewards during training, indicating that highly rewarded target features engendered especially strong and involuntary capture of attention (Anderson, Laurent, & Yantis, 2011b). Interestingly, in a previous study (Anderson, Laurent, & Yantis, 2011a) it was shown that capture can be induced by a valuable distracter even when this is not an intrinsically salient element, thus for the only reason that value has enhanced its salience relative to that of the other nontargets.

In summary, the above studies provide converging evidence that reward delivery affects attentional priority through forms of learning, which leads to substantial changes in performance depending on the reward history associated with specific stimuli. Importantly, as we noted earlier, while some findings lend themselves to a relatively simple interpretation in terms of value learning (Anderson, Laurent, & Yantis, 2011a, 2011b; Raymond & O'Brien, 2009), others require more articulated explanations, presumably calling into play different forms of learning and a more specific learning-mediated influence on selection and suppression mechanisms (Della Libera & Chelazzi, 2009), as discussed in the following section.

5. Underlying mechanisms of reward-based attentional plasticity

The controlled delivery of reward has become an elective method to unveil how our neuro-cognitive systems can flexibly adjust in order to increase fitness with the environment and its unfolding transformations. The literature on reward-dependent modifications of overt behavior plays a fundamental role within psychology and behavioral sciences in general. Starting at the beginning of the twentieth century, with Thorndike's formulation of the Law of Effect (Thorndike, 1911), the evidence that reinforced behaviors tend to be more easily incorporated in the repertoire of the individual and more frequently reinstated has paved the way to the development of the well known learning theories based on operant conditioning (Skinner, 1938, 1953, 1981). On the other hand, the natural sensitivity to reward signals can determine significant changes in behavior even when reward delivery bears no relationship with a specific behavioral pattern, but happens to be temporally contiguous to the perceptual processing of a given sensory event. Hence, stimuli whose processing has been systematically followed by a reward may become favorite over other competing objects (Pessiglione et al., 2008), can be more easily discriminated (Seitz, Kim, & Watanabe, 2009), and are more vigorously represented in cortical visual processing areas (Frankó, Seitz, & Vogels, 2010). Interestingly, these effects occur even when reward signals are displayed below the threshold of perceptual awareness (Pessiglione et al., 2008), and in tasks that require a minimal or null deployment of attentional resources towards the given perceptual stimuli (Frankó, Seitz, & Vogels, 2010; Seitz, Kim, & Watanabe, 2009). The latter evidence is in line with the phenomenon of evaluative conditioning, which consists in a change in the valence of a stimulus (initially neutral) resulting from its pairing with another stimulus (that usually has a specific emotional valence) (De Houwer, Baeyens, & Field, 2005; De Houwer, Thomas, & Baeyens, 2001). Just like other types of Pavlovian associative learning (Hall, 1994), this type of reward-based learning involves the mere association between a given sensory input and the more or less pleasurable events that accompany it. In conclusion, it is likely that the attentional processing of visual stimuli be shaped by reward signals both in conditions where the implementation of an efficient behavioral response is instrumental for the obtainment of the given reward (as in operant conditioning), and in conditions where rewards are garnered fortuitously, and irrespectively of behavior (as in Pavlovian conditioning).

Previous research has pointed out that associative learning in humans can be influenced both by the type of instructions received by participants upon entering an experiment, as well as by their beliefs and hypotheses on the relationship between their performance and the resulting outcome (Dickinson, Shanks, & Evenden, 1984; Rosenfarb et al., 1992). Therefore, an aspect that should not be overlooked when studying reward-based manipulations in human participants is the type of instructions conveyed to the participants at the start of any experiment as well as the type of information conveyed by reward signals obtained during the course of the experiment. In the studies reviewed in previous sections, exploring reward-based effects on visual selective attention, the information given to the participants about the criteria underlying reward delivery was quite variable. In some cases rewards were delivered within a passive viewing task that did not require any behavioral responses (Seitz, Kim, & Watanabe, 2009); therefore the coupling between rewards and visual stimuli only occurred on the basis of temporal contiguity between the two. In others instead rewards were delivered in turn for a correct response within the context of the given task, and thus the association between rewards and stimuli implied an instrumental type of associative learning. Still, among these latter cases, the relationship between reward values and perceptual stimuli could be completely transparent, so that subjects were fully debriefed that correct responses to some stimuli would yield higher rewards (Kiss, Driver, & Eimer, 2009; Krebs, Boehler, & Woldorff, 2010; Krebs et al., 2011; Pessiglione et al., 2008; Raymond & O'Brien, 2009; Rutherford,
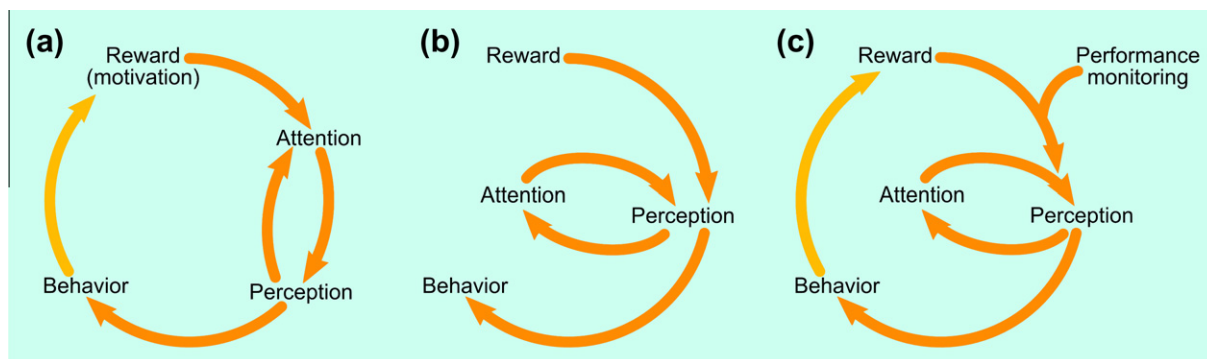
Fig. 4. Conceptual representation of the different mechanisms through which reward can affect attentional deployment. (a) Rewards as incentives for motivation. The prospect of earning reward in return for optimal performance triggers cognitive effort and the deployment of top-down attention towards stimuli with a higher motivational salience. Attention then impacts on perceptual processes (which in turn influence attention in bottom-up), allowing enhanced representation of valuable input; the selected input is the target of behavioral performance. Behavior is guided towards the achievement of reward. (b) Rewards as accidental events, leading to forms of Pavlovian conditioning: The rewarding signal is passively associated with the perceptual representation of the current input stimuli, which leads to their enhanced representation (to note that perception and attention entertain a two-way interaction, as in panel a); the selected input representation has privileged access to behavioral control. Lack of a link between behavior and reward is meant to highlight that here reward is not acting as a motivational drive of behavior. (c) Rewards as feedbacks on performance: When rewards are perceived to depend on one's own performance, the information carried by reward signals is integrated with an internal evaluation of performance, and impacts on specific attentional processes applied to the perceptual representation of stimuli. Rewarding feedbacks thus affect stimulus salience through a selective modulation process, in which reward values are associated with the specific operations (selection or inhibition) that instrumentally led to them, impacting behavior accordingly.

O'Brien, & Raymond, 2010), or concealed, whereby subjects were led to believe that rewards would depend on their performance, so that the monetary gains were not only viewed as events with a certain rewarding value, but also conveyed feedback information on performance (e.g., Della Libera & Chelazzi, 2006, 2009).

Given that these different types of reward-based associative learning may be mediated by partially independent systems (Bjork & Hommer, 2007; Hakyemez et al., 2008; Tricomi, Delgado, & Fiez, 2004), understanding whether they can exert similar or different modulations of visual selective attention seems a crucial issue, in order to unveil the mechanisms underlying these effects. In a recent study we have specifically addressed this problem. We replicated one of our original experiments on long term effects of rewards (Experiment 1 in Della Libera & Chelazzi, 2009), but this time we informed subjects that the monetary wins following each correct response would be determined on a random, lottery-like basis (Della Libera, Perlato, & Chelazzi, 2011). As in the previous experiment, subjects took part in three training sessions with biased reward delivery, and in a test session 5 days later. The results were strikingly different from those previously gathered with the very same experimental paradigm but from a group of subjects who believed to earn their rewards on the basis of their performance level. In this new group, responses in the test task were solely affected by the overall reward bias associated to the given visual stimuli, so that in comparison to the less rewarded ones, items that had been more frequently followed by high rewards were more difficult to filter out when they were the distracters in the current trial, and this happened irrespectively of the role (target or distracter) that they played when the reward manipulation was applied during training (Fig. 3c).

The picture emerging by considering this result and those discussed in the previous sections indicates that, just as it happens for learning of overt behavior, reward-based attentional learning may follow different routes depending on the perceived link between performance and outcome. When performance is considered determinant for the achievement of rewards, then plasticity is observed at the level of the specific processes that enabled it (i.e., target selection and distracter inhibition), and learning takes the form of an instrumental type of adaptation (Della Libera & Chelazzi, 2009). Differently, when rewards are viewed as random, fortuitous events, then a direct and passive association takes place between the perceived stimuli and the rewards that follow them (Della Libera, Perlato, & Chelazzi, 2011).

According to the notion of Pavlovian-to-instrumental transfer (Lovibond, 1983), instrumental learning emerges following two consecutive phases: initially, a perceptual stimulus is associated with a contiguous reward in a Pavlovian fashion. Subsequently, subjects learn to act in response to this stimulus in order to evoke the associated reward. If this were also the case for the sort of attentional learning that we have induced, then we might conjecture that when rewards are viewed as unrelated to performance only the first – automatic – association is formed, and only the overall contingencies between stimulus representations and rewards will be learned (Della Libera, Perlato, & Chelazzi, 2011). If instead rewards are thought to depend on performance, then the process develops completely and learning modulates not just a generic stimulus representation, but specifically the attentional weighing (or prioritisation) process acting on this representation (i.e., selected as a target or inhibited as a distracter) (Della Libera & Chelazzi, 2009).

Interestingly, Dickinson, Shanks, and Evenden (1984) demonstrated that when participants are initially exposed to an experimental context in which outcomes are determined by external causes, they fail to acquire instrumental learning when outcomes are later rendered contingent on their own performance. We might speculate that in our recent study (Della Libera, Perlato, & Chelazzi, 2011) the explicit instruction that rewards were randomly delivered similarly *blocked* (Kamin, 1969; Kruschke & Blair, 2000) instrumental learning for the behaviorally relevant contingencies.

Recent research suggests that both types of reward-based attentional learning involve brain structures usually associated with attentional control, including posterior parietal cortex (Krebs et al., 2011; Peck et al., 2009), and the processing of rewarding information, including the striatum and the anterior cingulate cortex (Hickey, Chelazzi, & Theeuwes, 2010a; O'Doherty, 2004; Schultz, 2006; Weil et al., 2010). Moreover, and perhaps most interestingly, they can affect the neural representation of visual stimuli at the level of extrastriate visual cortex, including area V4 and the inferotemporal cortex (Frankó, Seitz, & Vogels, 2010; Hickey, Chelazzi, & Theeuwes, 2010a; Jagadeesh et al., 2001; Mogami & Tanaka, 2006; Pessiglione et al., 2008; Weil et al., 2010), and this can occur even outside the context of a task as the result of the shear association of a stimulus with reward (Frankó, Seitz, & Vogels, 2010). Furthermore, recent evidence suggests that specific subcortical structures, such as portions of the striatum (Bjork & Hommer, 2007; Hakyemez et al., 2008; Tricomi,

Delgado, & Fiez, 2004), might be crucially recruited only when rewards are perceived to depend on performance, giving rise to action-dependent instrumental learning. It would then be particularly interesting to explore whether training with different types of attentional learning protocols – including those where rewards are viewed as a form of feedback on performance and those where they are viewed as random events, recruits specific and dissociable patterns of brain activity, both at the cortical and subcortical level, highlighting the contribution of specific brain structures to distinct forms of reward-mediated attentional learning.

6. Reward-based attentional plasticity and its side-effects

The sensitivity of attentional mechanisms to reward-related signals has recently been recognized as one of the core factors underlying the development and the maintenance of dysfunctional behaviors observed in a number of psycho-pathological conditions. Such sensitivity is attested to by marked biases of attention towards certain items, or categories of items. One of these conditions is represented by the various forms of addiction, which develop after an initial exposure to a substance (e.g., cocaine, heroine, nicotine) or an activity (e.g., gambling, sex, video games) with immediately rewarding effects, and subsequently evolve as a strong and compulsive drive to obtain more reward, despite any negative consequences and at the expense of most other activities (Feltenstein & See, 2008; Wise, 1980). Abnormal biases of attention towards critical visual stimuli have also been uncovered in a variety of other clinical conditions, including eating disorders (Davis, 2010), forms of anxiety (Bar-Haim et al., 2007), phobias (Mogg & Bradley, 2006), and obsessive-compulsive disorders (Dobson & Dozois, 2004). As evidenced in a number of studies, addicted individuals show a strong and automatic tendency to focus attentional resources onto addiction-related objects when they are available in the visual environment (for a recent review, see Field & Cox, 2008). According to one influential theory, the Incentive Sensitisation Theory of addiction (Robinson & Berridge, 1993, 2000, 2008), these biases are determined by an exaggerate increase in the salience of certain classes of stimuli, in turn generated by the repeated association between the perceptual/attentional processing of these items and the enactment of rewarding (and addicting) behaviors. As this theory proposes, addiction may induce plastic changes in brain circuits and mechanisms mediating the incentive salience of visual stimuli, so that their mere exposure may evoke in addicts strong craving and drive to re-enact their addictive habits. From a clinical point of view these biases represent one of the major obstacles to a full recovery from addiction, because they seem quite resistant to treatment and may cause relapse even in former addicts (Field & Cox, 2008). From our point of view, however, they are especially interesting because it is likely that they are generated through the same mechanisms that are tapped by the sort of reward-based manipulation that we and others have applied to study the influence of reward on attention and attentional learning in normal individuals. Therefore, we believe that the understanding of the neuro-cognitive mechanisms underlying reward-dependent attentional learning in normal individuals will ultimately prove of crucial importance also for the understanding of pathological biases of attention in specific groups of individuals, including but not limited to addicts.

7. Conclusions

To sum up, the studies on attentional processing of stimuli associated with biased rewards reveal that when highly rewarded stimuli are task relevant they may lead to faster and more accurate performance in visual search tasks (Della Libera & Chelazzi, 2009;

Kristjánsson, Sigurjónsdóttir, & Driver, 2010), and in the Stroop task (Krebs, Boehler, & Woldorff, 2010; Krebs et al., 2011); they also engender stronger inter-trial priming effects (Hickey, Chelazzi, & Theeuwes, 2010a; Kristjánsson, Sigurjónsdóttir, & Driver, 2010) and a higher resistance to the attentional blink phenomenon (Raymond & O'Brien, 2009). When the same stimuli act as distracters that need to be ignored they often lead to stronger effects of involuntary attentional capture (Anderson, Laurent, & Yantis, 2011a, 2011b; Rutherford, O'Brien, & Raymond, 2010) and greater interference effects (Della Libera & Chelazzi, 2009; Krebs, Boehler, & Woldorff, 2010; Krebs et al., 2011). However, it should be recalled that while some of the above results could all be reconciled with the notion of value learning, and the ensuing influence on attentional priority, some other results require a different explanation, namely one where rewards cannot only increase the salience of certain visual stimuli, thus facilitating their selection, but also increase the efficiency with which other stimuli can be suppressed. We have proposed that the latter effects can only be accounted for by making reference to notions of instrumental conditioning, whereby the delivery of rewards in relation to the suppression of a certain stimulus will reinforce the tendency for attention mechanisms to suppress the same stimulus on future occasions, not unlike the influence of instrumental conditioning on motor performance.

We have also seen that attentional learning can occur through at least two distinct mechanisms, one involving active monitoring of performance and outcome (Fig. 4c), and a second one detecting the sheer association between objects in the environment (whether attended or ignored) and the more-or-less rewarding events that accompany them (Fig. 4b). In turn, these learning effects should not be confounded with effects obtained when the prospect of reward acts as a motivational drive to increase cognitive effort in relation to certain stimuli or locations (Fig. 4a).

In this article we have emphasized the importance of distinguishing among the different ways in which reward will influence attentional deployment and learning, depending on various characteristics of the given paradigm. However, it must be also recognized that in some of the studies reported so far the different mechanisms are often compounded, and the relative contribution of each individual mechanism is therefore hard to determine. For example, in studies (e.g., Kiss, Driver, & Eimer, 2009; Krebs, Boehler, & Woldorff, 2010; Kristjánsson, Sigurjónsdóttir, & Driver, 2010) where reward is primarily acting as a form incentive motivation, presumably driving attention in a deliberate, strategic manner (see Fig. 4a), it is very likely that learning mechanisms are also engaged during the course of the experiment (see Fig. 4b and c), with the overall pattern of reward-mediated effect at the performance level reflecting a combination of both mechanisms. Specifically, in the work of Krebs, Boehler, and Woldorff (2010) and Krebs et al. (2011), it is likely that rewards mainly acted through enhanced motivation in relation to task-relevant information, while their effect in relation to task-irrelevant information was presumably mediated by learning (see also Serences, 2008). However, even the effect obtained in relation to the task-relevant information was partly aided by learning-dependent mechanisms, as indicated by data obtained under the extinction regime (Krebs, Boehler, & Woldorff, 2010, Experiment 2), when rewards were no longer delivered.

Given the role of selective attention in guiding behavior, and given that behavior itself has long been known to be largely influenced by the delivery of rewards, it might seem logical to predict that selective attention is also sensitive to rewards. However, no research had ever been conducted to explore this possibility until a few years ago. Now a rapidly growing body of literature is reporting fascinating discoveries in this realm, enabling a rapid progress in our understanding of the different ways in which rewards shape

the ongoing deployment of attention and, especially, attentional learning phenomena affecting processing in the long term. Interestingly, as we alluded to earlier, it could be argued that every episode of attentional selection might be subject to some kind of internal efficiency check process, which may induce continuous adjustments of attentional deployment with the aim of maximizing fitness to the given context. In the absence of explicit, external feedback on performance, such as the rewarding feedbacks introduced *ad-hoc* in some of the studies reviewed here, neural signals underlying attentional selections that are internally recognized as being successful might be accordingly strengthened, giving rise to the standard attentional inter-trial effects and longer lasting attentional learning effects, as we know them.

In conclusion, it may seem rather paradoxical that learning principles once developed to explain overt behavior within a theoretical framework that was skeptical about the hidden and impalpable intricacies of cognition now appear to be perfectly suited to account for reward-based changes in attentional priority in the short and in the long term. It takes very little imagination to suspect that analogous effects of reward-mediated learning might impact all kinds of other cognitive activities.

Acknowledgment

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