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The attention habit: how reward learning shapes attentional selection

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There is growing consensus that reward plays an important role in the control of attention. Until recently, reward was thought to influence attention indirectly by modulating task-specific motivation and its effects on voluntary control over selection. Such an account was consistent with the goal-directed (endogenous) versus stimulus-driven (exogenous) framework that had long dominated the field of attention research. Now, a different perspective is emerging. Demonstrations that previously reward-associated stimuli can automatically capture attention even when physically inconspicuous and task-irrelevant challenge previously held assumptions about attentional control. The idea that attentional selection can be value driven, reflecting a distinct and previously unrecognized control mechanism, has gained traction. Since these early demonstrations, the influence of reward learning on attention has rapidly become an area of intense investigation, sparking many new insights. The result is an emerging picture of how the reward system of the brain automatically biases information processing. Here, I review the progress that has been made in this area, synthesizing a wealth of recent evidence to provide an integrated, up-to-date account of value-driven attention and some of its broader implications.

Keywords: selective attention; attentional capture; reward learning; reinforcement; incentive salience; basal ganglia

Introduction

The landscape of attention research has changed dramatically in recent years. Early work on the topic of selective attention established a framework within which selection was held to be the product of goal-directed (i.e., top-down, endogenous) factors related to the task relevance of stimuli on the one hand, and stimulus-driven (i.e., bottom-up, exogenous) factors related to the physical salience (feature contrast) of stimuli on the other hand.[1–7] This dichotomy provided the framework for prominent theories of attentional control over the decades to come,[2,8–13] and, at times, sharp debate arose as to which of the two served as the default mechanism of selection along with the conditions under which goal-directed control was and was not possible.[6,7,13–18]

Interest in the effects of reward on attention is not new, although studies on this topic have, until recently, represented only a small minority of research on human attention. In keeping with the aforementioned theoretical framework, however, reward was often employed in such studies as a means of manipulating task-specific motivation.[19–25] Search for a particular target stimulus either was or was not incentivized by extrinsic rewards, with the aim of describing the consequence of this incentive on selection. In parallel with this important work on motivated attention, however, a more direct influence of reward on the attention system was beginning to become apparent.

The first evidence suggesting that reward processing might have a direct influence on selective attention was provided by Della Libera and Chelazzi in 2006.[26] Using a priming task, they showed that the ability to select a target was impaired if participants were highly rewarded for ignoring that stimulus on the previous trial. A few years later, a compelling demonstration of reward-mediated priming showed that rewarding the selection of a stimulus on

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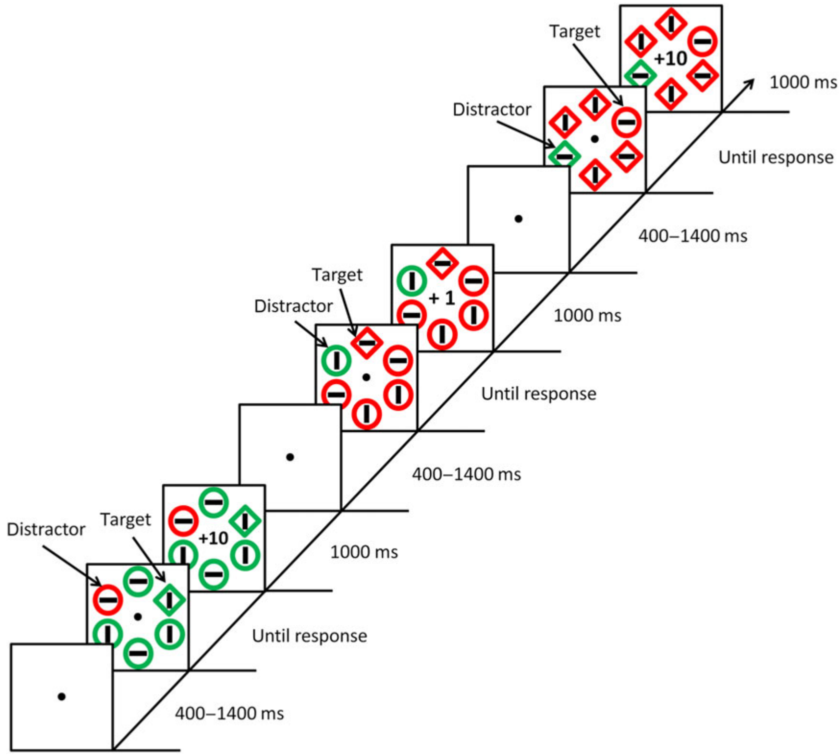

Figure 1. The reward-mediated priming paradigm. The task is to report the orientation of the bar (vertical or horizontal) within the uniquely shaped target. Either a high or low reward (points, which are converted to money at the end of the experiment) is delivered after each correct response, the magnitude of which is randomly determined from trial to trial. The color of the target and distractor (if present) either remains the same or swaps across consecutive trials. The sequence shown is for three trials. Value-mediated priming is demonstrated by an interaction between color swap and prior reward, such that attentional capture by the distractor is especially strong if participants were highly rewarded on the prior trial and the colors swapped. Adapted from Ref. 27.

one trial made that stimulus more difficult to ignore when presented as a distractor on a subsequent trial (Fig. 1), an effect that was robust for competing goals.[27–29] At about the same time, studies began to reveal that the tendency to preferentially select a reward-associated target, which was previously attributed to motivation-mediated processes, was a persistent effect that could continue even well after the reward schedule was discontinued.[30–33] These latter studies provided the first evidence that reward learning might shape attentional priority to favor selection of reward-associated stimuli in the future.

Compelling evidence for a direct influence of reward history in the guidance of attention was provided by Anderson and colleagues.[34] In their study, participants first learned associations between color targets and reward in a training phase, and in a subsequent test phase, these same color stimuli served as distractors during search for a shape-defined target (Fig. 2). Critically, the previously reward-associated distractors were neither physically salient nor task relevant and thus should not be attended by virtue of either a stimulus-driven or goal-directed attention mechanism. The results demonstrated robust attentional capture by the previously reward-associated distractors, thereby establishing a distinctly value-driven mechanism of attentional selection.

The last several years have seen a concentrated effort to understand and characterize value-driven attention, and a number of studies both replicating and extending the value-driven capture of attention have been reported. Current theoretical accounts of value-driven attention, however, lag behind and are largely limited to a description of the phenomenon—that reward history plays a direct role in the control of attention. The limitations

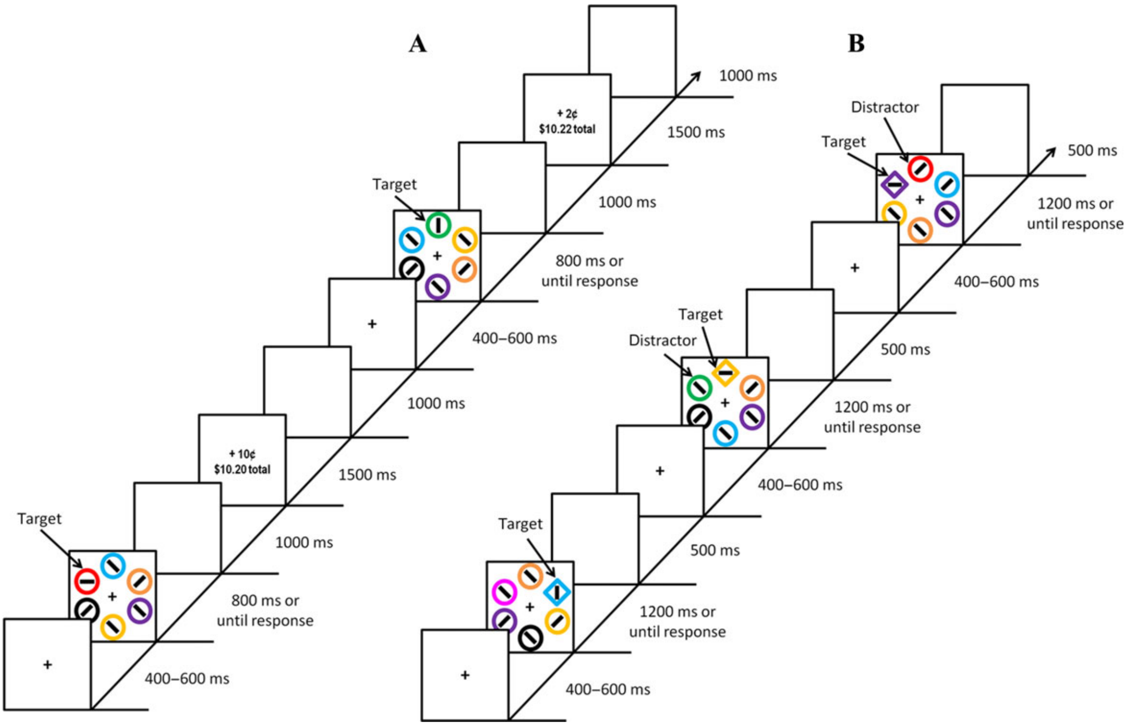

Figure 2. The value-driven attentional capture paradigm. (A) Training phase in which color-defined targets are associated with different amounts of monetary reward. The task is to report the orientation of the bar within the target (vertical or horizontal). The sequence shown is for two trials. (B) Unrewarded test phase in which color is a task-irrelevant feature, and critical distractors are rendered in the previously reward-associated colors. The sequence shown is for three trials. Value-driven attentional capture is measured as the slowing of response time associated with the presence of the previously reward-associated distractors. Adapted from Ref. 34.

of the top-down versus bottom-up theoretical dichotomy,[13] the distinction between reward influencing attention directly (associative learning) and indirectly (by modulating goals and motivation),[35,36] and a conceptual framework for the principle of value-driven attention[37] are discussed elsewhere. Here, I seek to unpack the influence of reward history on attention, synthesizing a large number of recent studies in this burgeoning area of investigation, many of which were published after these earlier reviews were written. What emerges is an integrative account of the mechanisms by which the reward system of the brain biases information processing.

Decomposing value-driven attentional priority

When associated with a reward outcome, stimuli acquire heightened attentional priority such that they become capable of competing for attention even when inconspicuous and task irrelevant.[34,37] Such a change in attentional priority is the result of an interaction between value signals and corresponding sensory signals. An important first step in understanding value-driven attention, then, is to characterize these two individual components that jointly contribute to the development of a selection bias. This has been a major focus of recent studies investigating value-driven attention.

Characterizing the underlying sensory signals

There is now strong evidence that early visual representations for specific stimulus features provide sufficient information for value-driven attentional biases to occur. When only color[34,38,39] or orientation[40,41] is sufficient to differentiate a reward-predictive target from other nontarget stimuli, subsequent attentional biases for stimuli possessing the specific reward-associated feature are robust. Interestingly, value-driven attentional biases appear to be, at least to some degree, dissociated from the level of representation that is used to localize the reward-associated stimulus during learning. When the target is defined as a feature singleton, selection of the target is known to occur on the basis of its relative salience (i.e., singleton detection mode) without regard to specific feature information.[14,42] When a rewarded target is a salient feature singleton, however, value-driven attentional biases are still specific to the reward-predictive feature,[43] suggesting that the perceptual representations, rather than the goal-directed selection processes used to localize a reward-associated stimulus, become prioritized. This conclusion fits with work demonstrating that reward can drive perceptual learning even when the reward-predictive stimulus is rendered subliminal.[44]

At first glance, these findings seem to suggest that value-driven attentional priority is established early in visual processing and then cascades forward through the visual system. Indeed, early accounts of the influence of reward on attention seemed to suggest that this was the case, likening this influence to a change in the low-level salience of the reward-associated features.[27,45] Although there is evidence that prior reward associations can have a rapid influence on early visual processing, as will be discussed later, it is clear that more complex visual representations are also subject to value-driven attentional bias.

Early investigations on the influence of reward on attention demonstrated selection biases for previously reward-associated shapes,[30,46] faces,[31,47] and even semantic information in a Stroop task.[32,48] However, because such stimuli were always included in the target set and thus task relevant, it was difficult to determine the degree to which these biases reflected reward interacting with search goals and selection strategies.[49] More recent demonstrations have confirmed that objects[50,51] and scenes,[52] when paired with reward, can subsequently serve as potent distractors even when specific visual features are insufficient to distinguish such rewarded stimuli from other, unrewarded stimuli. Intriguingly, as will be further discussed later, previously reward-associated distractors are preferentially represented in object-selective cortex (lateral occipital complex) even when they are only identifiable on the basis of their color,[53] suggesting an integrated priority signal across different levels of the visual system.

Recent evidence also suggests that information about stimulus position is reflected in value-driven attentional priority. The ability of reward to bias selection of the location of a rewarded stimulus is immediately evident on the subsequent trial,[54] extending earlier reports of reward-mediated priming of stimulus feature.[27,28] When a target is consistently more highly rewarded when it appears in a particular location in the search array, a persistent bias to preferentially process information at the location develops.[55] Value-driven attentional biases for a particular feature (in this case, color) have also been shown to be modulated by position information when position determines whether the feature is predictive of reward.[56] In the temporal domain, priming of a visual stimulus on the basis of its time of presentation relative to the start of the trial has also been shown to be modulated by reward information,[57] echoing earlier findings that neural responses in early visual cortex (V1) are sensitive to the predicted time of reward signaled by a visual stimulus.[58] These findings demonstrate that visual signals representing a variety of stimulus properties are subject to modulation on the basis of reward history.

Up to this point, evidence for value-driven attention has been restricted entirely to the visual system. This leaves open the question of the extent to which value-driven attention reflects a broad principle of information processing that extends across sensory systems, and whether value-based attentional priority can influence crossmodal stimulus competition. Evidence in the affirmative was recently provided by a study in which auditory targets were associated with reward during training and later served as task-irrelevant distractors during visual search for a shape-defined target. Target detection was impaired by the presentation of a previously reward-associated sound,[59] suggesting that the mechanisms underlying value-driven attention are not domain specific and instead operate across multiple sensory systems.

Characterizing the underlying value signals

Early investigations of value-driven attention used monetary reward to modulate attentional priority.[26–32,34,38] More recent studies have begun to reveal the domain generality of the value signals that give rise to value-driven attentional biases. Stimuli associated with food reward subsequently capture attention,[60] and the same holds true for stimuli associated with positive social feedback (social reward), even though such feedback is unrelated to task performance.[61] These studies suggest that a sort of "common neural currency"[62] used to represent value is responsible for influencing the attention system. Consistent with this notion, stimuli associated with a substance of abuse selectively capture attention in individuals addicted to that substance,[63–68] which can be explained by drug reward influencing value-driven attention.

Recent evidence suggests that the value of a stimulus is represented regardless of whether that value is meaningful to the current task.[69] This automatic value signal, rather than the value signals that are computed during decision making, predict attentional processing of a stimulus.[69] As will be later discussed, value signals can give rise to attentional biases for reward-predictive stimuli even when selection of those stimuli is itself never rewarded.[70–73] These findings suggest that automatically generated signals representing the experience of reward, rather than cognitive appraisals of value, influence the attention system. Such a relationship helps to explain why the receipt of reward modulates stimulus priming when the underlying reward structure is completely random.[26–29,45,50,54,57,74]

Although never directly manipulated in a single experiment, it has become clear that relative or normalized value, rather than associated value in an absolute sense, biases attention. Comparatively high (within the context of the experiment) reward values have ranged from $US 0.05[34,38] to $0.25[53] to $1.50,[75] and the magnitude of value-driven attentional capture across studies has been similar and clearly does not scale with absolute value. However, differences in the magnitude of attentional capture between stimuli associated with comparatively high and low value within the same experimental context has been observed (e.g., Refs. 38, 41, 52, 56, 61, 70–73). It would seem, therefore, that the reward signals that drive attention are normalized relative to expectations concerning the amount of reward available within the current context, which fits nicely with formal models of reward learning.[76,77] In line with this, the value associated with a stimulus is anchored to beliefs about how much reward is available to other participants for performing the same task.[78] Stimuli associated with comparatively small rewards often produce attentional biases as well, and the difference in attentional bias between high- and low-value stimuli typically does not scale with the magnitude of the difference in reward value between the two.[34,39,40,53] As such, it appears that non-zero reward is sufficient to bias attention, but that greater rewards can strengthen that bias.

When a reward is devalued, attentional biases for stimuli associated with the devalued reward are no longer evident,[60] consistent with a link between the orienting of attention and the incentive salience of a stimulus.[79–81] This finding is not well explained by an influence of the hedonic aspects of reward processing on the attention system and instead suggests a role for the motivational aspects of reward in modulating attentional bias. In further support of this idea, simply pairing a stimulus with a reward outcome during training is alone insufficient to give rise to value-driven attentional capture if the stimulus is not useful for predicting the reward.[82]

It is important to distinguish between the influence of learned value on attentional selection from the influence of selection history more broadly. With sufficient practice, the selection of a specific stimulus will become automatic even without explicit rewards being given.[83,84] Therefore, evidence above and beyond attentional capture by previously rewarded targets is necessary to support the idea that reward learning influences attention. One source of such evidence comes from demonstrations that attentional capture by former targets is either not observed or is significantly weaker following otherwise equivalent training in which explicit reward feedback is removed.[34,53,82,85,86] More compelling is evidence that the magnitude of attentional capture is greater for stimuli associated with high compared to low reward,[38,41,52,56,59,61,70–73] as, in this case, the motivational context of training is matched between conditions. Such findings provide clear and convincing evidence that value associations can modulate the attentional priority of a stimulus.

Studies have also begun to examine whether value-driven attentional biases are specific to reward learning, or whether punishment learning can similarly bias attention. Stimuli associated with monetary loss,[85,87] electric shock,[85,88,89] and aversive noise[90,91] automatically capture attention. Monetary loss and gains also appear to bias attention to a similar degree.[87] Although electric shock appears to have an especially potent effect on attentional selection,[85,88,89] direct comparison to the effects of

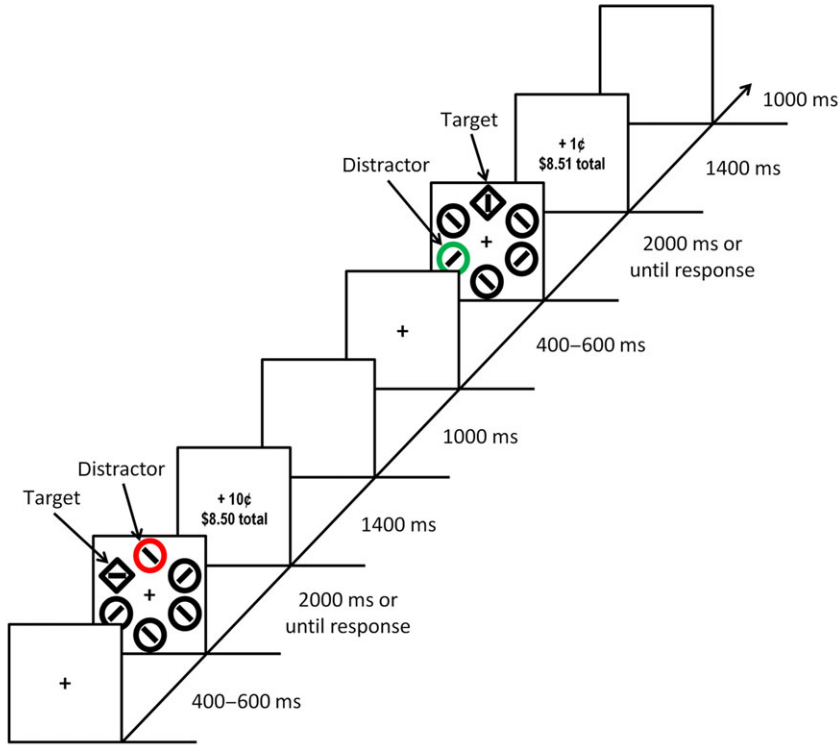

Figure 3. The task-irrelevant reward cue paradigm. The task is to report the orientation of the bar (vertical or horizontal) within the diamond-shaped target. Either a high or low reward is delivered after each correct response. The reward is always high when one color distractor is present and always low when the other color distractor is present. Value-driven attentional capture is reflected in greater interference from the distractor associated with higher value, even though its value is contingent upon correct report of the shape target. The sequence shown is for two trials. Adapted from Ref. 70.

monetary outcomes on attention is difficult as these sources of feedback differ in many respects. As will be further discussed, the extent of the similarity in the neural mechanisms underlying the effects of reward and punishment on attention remains to be shown; however, these findings make it clear that value in a bivalent sense is reflected in attentional priorities. Claims about reward-driven attention should therefore be made carefully, as similar principles may also apply to cases of aversive conditioning. As the dynamics of attentional biases arising from punishment learning are poorly described relative to those arising from reward learning, punishment-driven attention reflects an important area for future investigation.

Mechanisms of learning

Having explored the stimulus and value signals that contribute to the development of a selection bias, an important next question concerns the mechanisms by which these signals are integrated via learning. With regard to this issue, several recent studies have focused on exploring the role of top-down goals and motivation in value-driven attention. As described earlier, reward can bias attention to an associated stimulus feature even when that feature is not used to localize the target during reward training,[43] suggesting that it is the predictive stimulus, not the corresponding search goals, that become prioritized. Compelling evidence for this dissociation between search goals and value-driven attention comes from studies demonstrating that stimuli that are always task irrelevant, but nonetheless predict the reward that will be received for selecting a different stimulus (the target), become prioritized with experience in the task (Fig. 3).[70–73] Even though participants never voluntarily select the reward-predictive stimulus and are in fact motivated by reward (which is contingent upon correct target identification) to ignore it and all other distractors in these studies, value-driven attentional biases are still observed. Importantly, such attentional biases also persist through periods in which the stimulus is no longer rewarded, even when the task changes.[73] These findings are consistent with an associative learning mechanism by which stimuli that co-occur with high rewards acquire heightened attentional priority regardless of their task relevance.

Further evidence for the role of prediction-based learning in value-driven attention was provided by Sali and colleagues,[82] who showed that when participants are provided with a predictable reward for selecting a color-defined target, or when target selection is incentivized by a random reward that is unrelated to the target color, value-driven attentional biases do not develop. Subsequent attentional biases were observed only when the color of the target predicted the magnitude of reward, even though participants were reinforced for selecting the target during training in all cases.[82] Thus, providing an extrinsic reward for target selection is insufficient for the target stimulus to acquire heightened attentional priority, which depends on mechanisms of prediction-based associative learning.

Another important question concerns the generalizability of reward learning in biasing attention to particular stimulus features. How does the attention system keep track of which stimulus–reward associations are pertinent to a particular situation, both during learning and in the subsequent expression of that learning? Recent evidence suggests that contextual information can play a powerful role in the modulation of value-based attentional priority. When context is manipulated by using a task-irrelevant background image, the stimulus–reward associations that bias attention are specific to the reward that was experienced within that context.[92] Similar gating of reward learning by context occurs when context is manipulated by spatial position,[56] in a manner that is not reducible to combined spatial[55] and feature[34,38,39] biases. However, such contextual dependencies are only observed when the information provided by context provides predictive information about reward, in this case indicating which stimulus–reward associations apply. When stimulus–reward associations are not contextually dependent, generalization of reward learning to a new context can be observed.[73,86]

Value-driven attentional biases can be learned fairly rapidly. For example, a single instance of high reward is sufficient to bias attention to the rewarded stimulus on the subsequent trial.[27–29,45,50] Such reward-mediated priming might facilitate the development of more enduring attentional biases when rewards are consistently paired with a stimulus. Although early studies on the effect of reward learning on attention employed a long training procedure involving over 1000 trials and sometimes multiple sessions,[30,33,34,38,46] persistent value-driven attentional biases have been shown to develop after fewer than 200 training trials,[82] and studies of value-driven attention now frequently employ 300 or fewer trials of training (e.g., Ref. 34, experiment 3; Refs. 39, 41, 53, 61, 86). Associations with aversive shock can establish a persistent attentional bias after a mere 20 trials of training.[88]

No study to date has provided a rigorous examination of the role of awareness of the reward contingencies in value-driven attention. However, the weight of the current evidence suggests that awareness is not necessary for value-driven attentional biases to develop. Value-driven attentional biases for task-irrelevant but reward-predictive stimuli have been shown to be similar across cases in which participants are and are not informed of the reward structure.[71] When participants are later queried about their knowledge concerning the reward structure, value-driven attentional biases do not depend on whether the participants correctly identified the actual reward contingencies.[41,56,92,93] In light of demonstrations that value-driven attentional biases can occur toward stimuli that never serve as a target,[70–73] it would appear that the processes linking reward to stimulus features can proceed automatically, tracking their co-occurrence and updating attentional priorities accordingly.

Representation and neural basis

Early work on value-driven attention established robust spatial specificity underlying value-based distraction effects, clearly implicating spatially specific stimulus representations.[34,39,41,47] However, nonspatial information at the level of scene semantics can also be subject to value-driven attentional bias.[52] This latter finding suggests that value-driven attentional priority signals are not limited to the level of spatially specific representations and can instead bias information processing broadly in the face of competition for representation.

As described earlier, value-driven attentional priority appears to rely on implicit learning and memory,[41,56,71,92,93] the influence of which is sensitive to contextual information.[56,92] Value-based attentional priority is also enduring, being evident weeks[34] and even months after learning has occurred, in the absence of explicit memory for the previously learned stimulus–reward associations that are biasing selection.[94] This suggests an influence of cortically distributed memory representations that contain value information linked to particular stimulus properties. When these associative memory representations are activated, attentional priorities shift to favor the selection of stimuli that have proven rewarding in similar situations in the past.

Recent research on value-driven attention implicates dopamine signaling within the basal ganglia in mediating the value signals that guide selection. In nonhuman primates, cells within the posterior caudate (tail) respond preferentially to previously reward-associated stimuli and are related to corresponding eye movements.[95–97] This same brain area is similarly more active when humans process previously reward-associated but currently task-irrelevant distractors,[53] suggesting its role in the value-driven capture of attention. Evidence implicating dopamine signaling specifically in the value-driven capture of attention has been provided using positron emission tomography.[75] In that study, the magnitude of distraction caused by previously reward-associated stimuli across participants was predicted by individual differences in distractor-evoked dopamine release within the right caudate and posterior putamen.[75] Similar patterns of elevated dopamine release have been observed in drug-dependent patients viewing drug-related stimuli.[98,99]

Representations in the posterior caudate clearly reflect stable object values built up through experience that are distinguishable from current expected value,[97] and dopamine signaling within the dorsal striatum more broadly is thought to play a key role in habitual responses[100] and drug craving.[98,99] In contrast to these stable representations of value in the dorsal striatum, dopamine signaling in the ventral tegmental area, substantia nigra, and ventral striatum represents reward prediction errors that are thought to reflect the teaching signals that underlie associative reward learning.[76,77,100] Interestingly, attentional capture by currently reward-associated stimuli is predicted by the strength of activity in the ventral tegmental area and substantia nigra pars compacta,[51] suggesting that, in addition to stable representations of value in the dorsal striatum,[53,75,96,97] current reward predictions can also influence attentional selection; such a mechanism could play a role in reward-mediated priming.[27] Also consistent with a distinction between current and prior value representations in the control of attention is that value-driven attentional capture by previously reward-associated stimuli remains robust when the current target is itself associated with reward.[101]

The posterior caudate is well connected to visual cortical representations through the visual corticostriatal loop and also projects to the superior colliculus,[97,102] which is known to play an important role in both attention modulation and eye movements.[103] Consistent with this important link to visual information processing, value-driven attentional priority is strongly represented in the lateral occipital complex,[53] and prior studies of value-driven attention have provided clear evidence for associated value modulating extrastriate representations in visual cortex.[51,53,104–106] Feedback from the dorsal striatum to the visual cortex and superior colliculus reflects one potential signaling pathway by which value representations bias stimulus competition (Fig. 4A). Given its connections and strong role in habit learning,[100,102] feedback from the basal ganglia reflecting value information likely influences vision more rapidly than feedback concerning task relevance associated with the frontal cortex,[9,107,108] which would help to explain why previously reward-associated stimuli can compete for selection even when inconspicuous and currently task irrelevant.[34] Interestingly, biasing signals arising from the associated value and current task relevance of stimuli in extrastriate visual cortex appear to be additive in nature,[106] further suggesting a distinctly value-driven contribution to visual information processing.

Object representations within the posterior basal ganglia are strongly location dependent,[53,95–97] preferentially responding to stimuli within the contralateral hemifield even when unassociated with reward,[95] and thus contain the spatial information necessary to guide attention. Interestingly, the amygdala response to valent stimuli is similarly

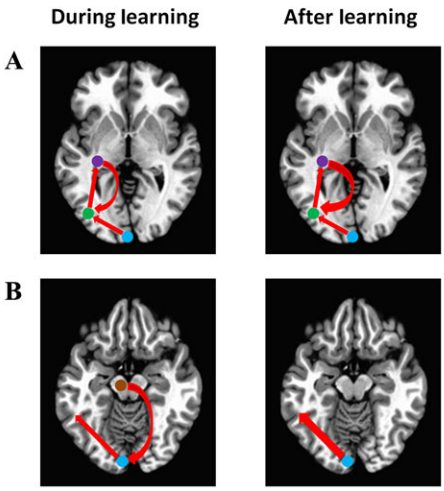

Figure 4. Conceptual schematic of proposed feedback (A) and feedforward (B) mechanisms for signaling value-based attentional priority. Blue = primary visual cortex, green = lateral occipital cortex, purple = caudate tail, brown = midbrain (ventral tegmental area and substantia nigra). Thicker lines symbolize stronger signals; curved lines symbolize feedback signals. Not shown in A are signals from the caudate tail to the superior colliculus. Schematic is depicted in the left hemisphere, as if the stimulus was presented in the right visual field; the same principles should also apply to the other hemisphere/visual field. Positions of the region markers are approximated from Refs. 51 and 53.

location dependent,[109–112] although the relationship between this spatially specific response and the capture of attention remains unclear. Such location specificity, however, highlights a direct and likely important relationship between value information and corresponding visual information.

In addition to the proposed feedback mechanism, there is some evidence that associated value can modulate early visual representations more directly.[113] Neurons representing particular stimulus features may come to generate stronger signals when their activation is reinforced by associated reward feedback (Fig. 4B). There is some evidence that reward prediction and reward prediction error signals are reflected in early visual cortical activity,[58,114] which could serve as a teaching signal that modulates future visually evoked responses. Reward-associated targets are preferentially processed as early as V1,[115,116] and subliminally pairing reward with a particular orientation can give rise to perceptual learning.[44] Preferential processing of an irrelevant but previously reward-associated stimulus is reflected in the early P1 component of the event-related potential over occipital electrodes using electroencephalography,[117] and value-driven attentional capture can influence the early visual processing of a target as reflected in the N1 component.[118] Although consistent with the value-based modulation of early visual processing in a bottom-up fashion, the role of feedback in these modulations is difficult to assess, and more direct tests of value-modulated perceptual learning are needed.

Although previously reward-associated stimuli are capable of capturing attention even when inconspicuous and task irrelevant,[34,39,40] and even when the target competing with the previously reward-associated stimulus also has high attentional priority (by virtue of its affective valence),[119] goal-directed attentional control has been shown to modulate the effect of learned value on attention. Attentional capture by previously reward-associated stimuli is stronger when such stimuli also possess a task-relevant feature.[117,120] Attentional biases for reward-associated stimuli are also stronger when they can appear as a rewarded target,[121] and expectations concerning the target location can modulate the attentional processing of reward-associated stimuli.[117,120,122] Mindfulness training, which requires intense attentional focus, has been shown to reduce the impact of reward-associated distractors on performance.[123] It is tempting to hypothesize the existence of a common priority map to which value-driven, goal-directed, and stimulus-driven influences contribute to the competition for selection. This idea has previously been suggested,[13] although it has never been formally tested. One potential candidate for this common priority map is retinotopically organized regions of the parietal cortex, which have separately been shown to represent the task relevance,[9,107,108] learned value,[34,53] and physical salience[124–127] of stimuli.

The influence of value-driven attentional orienting on information processing extends beyond the level of perception. In a Stroop task, for example, irrelevant reward information can give rise to competition for response selection both behaviorally[32] and neutrally.[48] Value-driven attentional orienting affects the execution of goal-directed action in a reaching task.[128,129] Attentional processing of reward-associated stimuli predicts related economic risk taking,[130] and value-driven attentional capture can interfere with the process of value-based decision making.[118] In the domain of working memory, irrelevant reward associations have been shown to bias the storage of information, with previously reward-associated stimuli receiving privileged access.[131,132] The presence of reward-associated stimuli has also been shown to provide a general boost in working memory,[133] suggesting that this benefit may not be entirely stimulus specific. In the domain of long-term memory, the ability of contextual cues contained within scenes to facilitate target search is enhanced for scenes within which target localization was rewarded.[134] These findings suggest a broad role for value-driven attentional processing in human cognition, affecting the storage of information in memory and overt behavior.

Translational implications

Studies have begun to explore the potential role of value-driven attention in information-processing biases known to underlie certain psychopathologies. Attentional biases for stimuli associated with drug reward have been well characterized in addiction.[63–68] Recent evidence indicates that drug-dependent patients[93] and even currently nondependent individuals with a history of substance dependence[135] are especially distracted by stimuli previously associated with nondrug (monetary) reward. This suggests the possibility that drug-related attentional biases might reflect a more general sensitivity to the influence of reward history on attentional selection. Similarly, value-driven attentional capture is positively correlated with impulsiveness[34,135] and is more pronounced in adolescence, a period of life marked by increased risk taking.[136]

On the other end of the spectrum, value-driven attentional capture has been shown to be blunted in depressed individuals.[137] Coupled with findings from drug-dependent patients, this suggests that abnormal sensitivity to the influence of reward history on attentional selection may contribute to psychopathology. If attention is abnormally biased by certain types of information in psychopathology, training attention with rewards may be useful in curbing those attentional biases. For example, in social anxiety disorder, associating neutral faces with reward has been shown to modulate attentional biases toward faces exhibiting threatening expressions.[138]

Some limitations and outstanding issues

The proposed framework for value-driven attention emphasizes mechanisms by which stimuli that predict reward gain elevated priority. Although stimuli that predict reward when appearing as task-irrelevant distractors can come to capture attention,[46,70–73] there are at least some situations in which these same conditions can lead to facilitated ignoring.[26,30] Such facilitated ignoring of distractors that predict reward is not directly addressed by the proposed framework. One possibility is that stimuli that predict reward as distractors come to automatically capture attention, but can be more quickly rejected when rejection is associated with reward outcome. There is some evidence for selection preceding inhibition in the context of strategic attentional control.[139] Another possibility is that fundamentally different mechanisms underlie the influence of reward on stimulus rejection. The learning of value-based attentional priorities has been shown to be sensitive to contextual information,[56,92] and the context of learning might also play an important role in determining the manner in which reward is linked to stimulus processing, with value-driven attentional capture being specific to situations in which orienting to a stimulus is emphasized over the suppression of irrelevant information (such as when objects are superimposed as in Refs. 26 and 30).

The proposed framework posits a specific role for subcortical reward signals in the shaping of attentional priority. In this regard, value-driven attention might differ from other influences of selection history on attention,[13] such as intertrial priming,[140–142] statistical regularities,[143–146] and status as a former target (under conditions without explicit reward).[83,84] However, to the extent that successful identification of a target generates an internal reward signal, similar learning principles might apply in these circumstances. On the other side of the reward and attention equation, reward feedback can give rise to biases in working memory,[131–133] response competition,[32,48] and goal-directed action.[128,129] The extent to which such biases reflect downstream effects of attentional processing is unclear, although it seems unlikely that the totality of these biases is reducible to value-driven attention. The influence of reward history on other domains of information processing is beyond the scope of this review.

Value-driven attention is argued to reflect an automatic attention mechanism that is functionally distinguishable from goal-directed attention. Once stimulus–reward associations have been learned, the orienting of attention to previously reward-associated stimuli is clearly not contingent on current task goals and priorities.[34,37] It is less clear the extent to which the learning of value-based attentional priorities is gated by goal-directed attention. The most compelling evidence for a dissociation between goal-directed and value-driven attention during learning comes from studies in which attention is captured by task-irrelevant distractors that nonetheless predict reward;[70–73] such value-based selection persists even when rewards are no longer available,[73] demonstrating that it is clearly nonstrategic. This suggests that the learning of value-based attentional priorities is capable of proceeding without the goal of attending to the reward-predictive stimulus. Furthermore, if value-driven attention is a reflection of the degree to which task-related attentional priorities are reinforced, then it should be better explained by the incentive provided by reward during training rather than its predictive relationship with target features. However, the opposite seems to be the case.[82]

In spite of this evidence, it would be premature to conclude that value-driven attention does not depend on the goal state of the organism during learning. Organisms presumably have an overarching goal of maximizing reward procurement, which gives reward-predictive stimuli a certain degree of task relevance. The voluntary tagging of a reward-predictive cue as a meaningful stimulus might therefore be a necessary ingredient for the development of more enduring value-dependent attentional biases. Indeed, in all studies examining value-driven attentional capture discussed here, the reward-associated stimulus was either a sought target or a highly conspicuous distractor during learning. The nature of the relationship between task-related attentional priorities and the development of value-driven attentional priorities has implications for how incidental the learning that underlies value-driven attention can be. Although perceptual learning can progress even without awareness of the presentation of a reward-predictive stimulus during learning,[44] whether the same holds true for value-driven attentional capture is not known.

The role of awareness of the reward structure in modulating attention is another area that would benefit from further investigation. Awareness of the stimulus–reward contingencies would be necessary to voluntarily modulate goal-directed attentional priorities, playing a clear role in motivated attention. Persistent value-driven attentional biases can occur without awareness of which stimuli predict higher value,[41,56,92,93] and at least under certain circumstances, informing participants of the reward structure does not affect the degree of subsequent capture.[71] However, our knowledge of the relationship between value-driven attention and awareness of the reward structure is still limited, as most of the reported studies neither assessed nor manipulated awareness. This is important, as value-driven attentional biases may have multiple inputs, with some of those inputs contingent on goal state (as motivated by rewards) during learning and others independent of goal state. Therefore, although certain aspects of value-driven attention seem to be unaffected by awareness, others might be affected.

The neural mechanisms underlying value-driven attention are only beginning to be understood. The contribution of a common neural currency for reward in the control of attention lacks direct empirical support, and the influence of multiple types of reward signals on attention remains a possibility. The relationship between subcortical representations of currently expected (ventral striatum and midbrain) and learned/stable (dorsal striatum) value in the control of attention is not well described, nor are the relative contributions from feedforward and feedback signaling mechanisms to value-driven attentional priority. Future research will add much needed clarity to these important issues.

Abnormal sensitivity to value-driven attentional capture has been demonstrated in addiction[93,135] and depression.[137] The extent to which value-driven attention may be implicated in other psychopathologies, such as obsessive–compulsive disorder and attention-deficit/hyperactivity disorder, poses an interesting question for future research. Whether such attentional biases play a causal role in addiction and depression or whether they instead reflect a consequence of drug- and mood-related changes in information processing, respectively, is also unknown. In this regard, it would be informative for future research to examine whether value-driven attentional biases can predict clinical outcomes.

Relatedly, the clinical benefits of using reward training to curb abnormal attentional biases, as in social anxiety disorder,[138] have not been established and should be investigated.

Conclusions

There is now substantial evidence supporting the idea that attention can be value driven, with reward history exerting a direct influence on selection. Over the past few years, progress has been made toward clarifying the mechanisms by which reward history shapes attention. When a reward is experienced, sensory representations that predicted the reward become prioritized. These sensory representations can reflect a variety of stimulus properties, from simple visual features[27,34,38–41] and locations[54–56] to complex objects[50,51] and scene semantics,[52] and span different sensory modalities.[59] The reinforcement of such sensory signals occurs automatically, even when they are irrelevant to the current task,[70–73] gated by prediction-based associative learning.[82] Such reward signals comply with formal models of reward learning, including reflecting a common neural currency for value[60–62] that scales with the amount of reward available in the current task,[34,38,53,75–77] likely reflecting mesolimbic dopamine.[75]

The effect of reward potentiating associated sensory signals is immediately apparent on the next trial, placing these signals in a privileged state.[27–29,45,50,54,74] As these sensory signals consistently predict the reward outcome (at least in the case of the visual system), an enduring representation of their associated value is built up in dopamine pathways through the posterior basal ganglia.[53,75,95–97] When these pathways become activated upon future encounters with learned predictors of reward, feedback to the visual system potentiates the underlying sensory signal.[53,102,106] A more direct, bottom-up effect of reward history on early visual processing is also possible,[44,115–118] affecting selection both directly and in concert with feedback mechanisms. Distributed memory representations reflecting the currently experienced context gate which value representations are activated.[92] The close connections[102] between the caudate tail, representing value-based attentional priority,[53,75,95–97] and the hippocampus, being critically involved in memory computations such as pattern separation,[147] could support such contextual modulation. Value-potentiated sensory signals compete more robustly for selection, allowing them to more effectively overcome competition from signals arising from physical salience and current task relevance.[34,39,53,56,92]

Through these mechanisms, organisms preferentially process information that has proven rewarding in the past, reflecting a habitual form of attentional selection. Such habitual attention contributes to behavior and decision making[32,48,118,128–130] and is abnormal in certain psychopathologies.[93,135,137] A more detailed mechanistic understanding of value-driven attention is therefore likely to have broad implications for our understanding of human cognition, with both theoretical and translational impact.

Conflicts of interest

The author declares no conflicts of interest.

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