ELSEVIER

Available online at www.sciencedirect.com

ScienceDirect

Current Opinion in Psychology

Neurobiology of value-driven attention

Brian A Anderson

What we pay attention to is influenced by reward learning. Converging evidence points to the idea that associative reward learning changes how visual stimuli are processed in the brain, rendering learned reward cues difficult to ignore. Behavioral evidence distinguishes value-driven attention from other established control mechanisms, suggesting a distinct underlying neurobiological process. Recently, studies have begun to explore the neural substrates of this value-driven attention mechanism. Here, I review the progress that has been made in this area, and synthesize the findings to provide an integrative account of the neurobiology of value-driven attention. The proposed account can explain both attentional capture by previously rewarded targets and the modulatory effect of reward on priming, as well as the decoupling of reward history and prior task relevance in value-driven attention.

Address
Texas A&M University, United States

Corresponding author: Anderson, Brian A (brian.anderson@tamu.edu)

Current Opinion in Psychology 2019, **29**:27–33

This review comes from a themed issue on **Attention and perception**

Edited by **Sarah Shomstein**, **Andrew Leber** and **Joy Geng**

https://doi.org/10.1016/j.copsyc.2018.11.004

The representational capacity of the brain's perceptual system is limited, and attention serves as the mechanism by which organisms select which input receives representation at later stages of information processing [1]. One of the most fundamental questions that can be asked in the study of attention concerns the factors that determine which information is attended and which is ignored. Substantial evidence points to the role of current task goals (goal-directed attention) [2,3] and the physical salience of stimuli (stimulus-driven attention) [4,5] in the selection process, each of which has been linked to a dedicated network of brain regions responsible for signaling the corresponding priority [6–8].

More recently, selection history has emerged as a third factor governing the control of attention that is distinguishable from goal-directed and stimulus-driven influences [9,10]. One component of selection history that has received substantial research interest is reward history. Previously reward-associated stimuli are afforded heightened attentional priority [11–13], even when they are physically non-salient, currently task-irrelevant, and no longer predictive of reward [13]. Such evidence has led to the idea that attention can be *value-driven*, in a manner that is dissociable from goal-directed and stimulus-driven factors [13].

The principle of value-driven attention, along with its cognitive and learning profile, have been extensively reviewed [e.g. in Refs. 9,10,14,15]. Missing from these reviews has been in-depth discussion of the neural structures and processes subserving value-driven attention, which is critical for the argument that value-driven attention reflects a dedicated selection mechanism. Newly emerging research has resulted in substantial progress on this issue, and I synthesize these findings here to provide an integrative account of the neurobiology of value-driven attention. The proposed account can accommodate a variety of neuroimaging data in addition to behavioral findings with neurobiological implications.

Value-based plasticity in the visual system

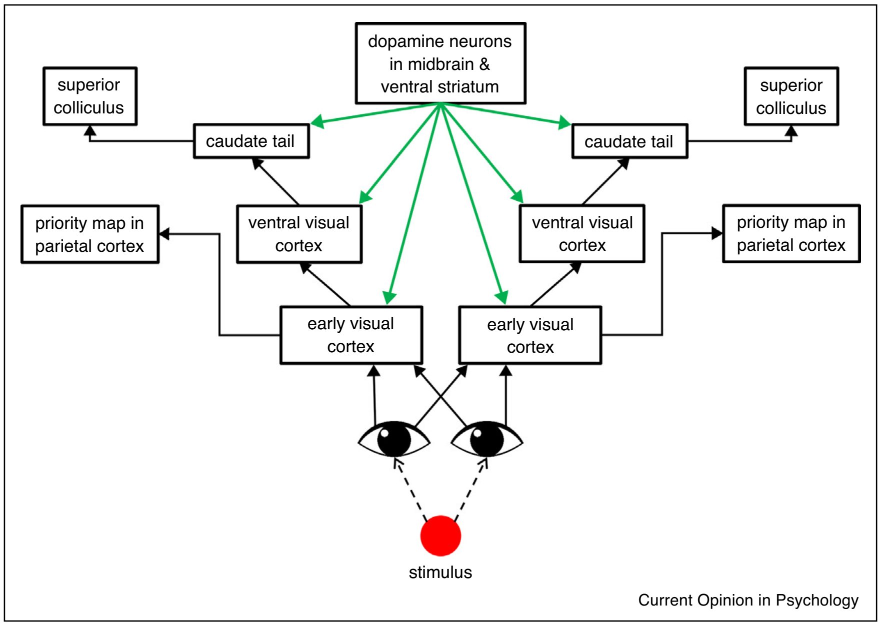
Compared to previously unrewarded or less valuable stimuli, stimuli previously associated with high reward produce stronger visually evoked responses in the brain. Such elevated priority signals have been frequently observed in the ventral (object-selective) visual cortex and caudate tail [16,17••,18•,19•,20••,21•,22,23], in addition to early visual cortex [24–26]. The caudate tail projects to the superior colliculus via the substantial nigra pars reticulata and is involved in the generation of value-guided eye movements [27], with neural responses reflecting stable, well-trained object values rather than more immediate reward considerations [22,23]. Interestingly, elevated responses in the ventral visual cortex and posterior caudate have been observed even when the stimuli during reward training differ only in a single feature dimension (color) [16,17••,28•], suggesting that biased representation at the level of object identity reflects a futprintndamental organizational principle rather than a function of task demands [see Refs. 18•,19•,20••,21•,22,23]. A causal role for the caudate tail in biasing eye movements was evident following neuronal stimulation in non-human primates [27], and a causal role for early visual representations in value-driven attention was provided by a study in which transcranial random noise stimulation was applied to the occipital lobe during reward training [29•].

The aforementioned evidence points to two different mechanisms by which learned reward cues are afforded elevated priority in the visual system (Figure 1). The first is through elevated stimulus-evoked responses arising in the visual perceptual system, which include feature-selective responses in early visual cortex [24–26,28•] but may also arise in object-selective cortex for category-level representations that are particularly diagnostic of value [18•,19•,20••,30]. These value-modulated signals propagate through the visual system, influencing activity in the spatial priority map in the parietal cortex [16,20••,28•,31,32] and competition in the visual system more broadly. Here in the parietal cortex, value-based attentional priority competes with other sources of priority reflecting stimulus-driven input from the visual cortex and goal-dependent modulation from the frontal cortex [6–8]. With respect to the priority map, value-driven attentional priority is analogous to the bottom-up influence of physical salience, with biased activity arising earlier in the visual system and feeding forward. To the degree that feature-specific responses in the visual cortex are modulated in this way, the consequence for the priority map should be similar to that of a situation in which the actual intensity of the stimulus was correspondingly increased through a change in brightness or feature contrast. Such a feedforward account of value-driven attention helps to explain why previously reward-associated stimuli can robustly outcompete goal-directed influences on the control of attention [13,14,16,17••,29•,31] that rely on feedback signals from the frontal cortex [5–7,10].

The second mechanism concerns competition within the oculomotor system, with value-modulated responses in the caudate tail exerting an immediate impact on reflexive eye movements via the superior colliculus [16,17••,22,23,27,28•]. Through this second signaling pathway, value-modulated information processing bypasses goal-directed influences within the priority map of parietal cortex, which may help explain why learned value can in some situations overpower both stimulus-driven and goal-directed influences [13,16,17••,33••]. Dopamine plays an important role in this signaling pathway, with the release of dopamine as measured using position emission tomography (PET) predicting behavioral measures of value-driven attentional capture [17••,33••].

The oculomotor pathway through the caudate tail could explain why elevated responses in object-selective cortex are observed [16,18•,19•,20••,21•,28•] even when distinguishing early visual features is sufficient to predict reward [16,28•]. Neural responses within the caudate tail are distinctly object-selective, which is evident even

Figure 1



Current Opinion in Psychology

Schematic of the proposed neural mechanism underlying value-driven attention. When more reward than expected is received (i.e. positive reward prediction-error), dopamine signals from the midbrain and ventral striatum serve as teaching signals to the visual system (green arrows), potentiating the visual representation that preceded the reward. Over multiple exposures with the same reward-predictive cue, these teaching signals will sensitize the visual system to the specific visual representation(s) that reliably differentiate the cue from non-predictive stimuli. The resulting plasticity within the visual system will result in stronger signals evoked by the cue (solid black arrows), which originate in the area(s) in which stimulus-evoked responses were predictive of reward. Note that the schematic is not intended to represent all regions and connections involved in the proposed circuit, but rather to provide an integrative account of known key components.

without reward manipulations [27]. Coupled with the fact that the caudate tail is a robust neural correlate of value-driven attentional capture even in feature-based attention tasks [16,17••,28•], and that current reward considerations are sufficient to modulate responses in feature-selective cortex [25,26] but insufficient to modulate responses in the caudate tail [22,23], it seems unlikely that the caudate tail is merely a passive recipient of value-based priority signals arising in early vision. Given the close connections between the caudate tail and the superior colliculus, plasticity within the caudate tail itself reflects a viable mechanism by which value-driven attention emerges in the oculomotor system. By this account, the elevated activity within the ventral visual cortex could reflect biasing signals arising within the caudate tail through the visual cortico-striatal loop [34]. However, an alternative possibility remains that both the spatial priority map of parietal cortex and the caudate tail are the recipient of a common source of value-dependent priority originating in early, feature-selective visual cortex, with this priority signal propagating along the dorsal and ventral visual pathway to culminate in these two regions.

Teaching signals from dopaminergic reward prediction-errors

Behaviorally, value-driven attentional capture is only evident following learning in situations in which reward is uniquely predicted by particular visual stimuli [35]. Simply providing an entirely predictable reward for orienting to a stimulus or incentivizing orienting with an entirely unpredictable reward is insufficient to give rise to value-driven attention [35]. Value-modulated attentional orienting has also been observed for a reward-predictive cue that never served as a target [36,37], suggesting that the learning of stimulus-reward associations rather than instrumental conditioning of the orienting response is responsible for value-driven attention. Once learned, value-dependent attentional priority can be further modulated by reward prediction-errors that co-occur with the previously reward-predictive stimulus [38]. Such evidence implies a critical role for reward prediction-errors in value-based plasticity within the visual system.

Reward prediction-errors are signaled through the dopamine system in the midbrain and striatum [39,40]. Direct evidence for the role of reward-evoked dopamine in the development of value-driven attention was provided by a PET study in which the behavioral effect of value-driven attentional capture was predicted by striatal dopamine release specifically attributable to the processing of reward feedback during training [33••]. Correspondingly, depressed individuals, who exhibit blunted neural responses to rewards, also exhibit blunted value-driven attentional capture [41,42]. After learning, the signaling of value-based attentional priority within the oculomotor pathway continues to rely on the transmission of striatal dopamine [17••], proving a clear link between teaching signals and subsequent biasing signals.

Findings such as these suggest that dopaminergic reward prediction-errors propagate to the visual system, which serve as teaching signals modulating the responsiveness of neurons representing reward-predictive stimuli. Reward prediction-error-like responses have been observed in early visual cortex [43,44], and are hypothesized to play a role in perceptual learning [45,46]. Consistent with such an account of value-driven attention, the receipt of high reward was found to evoke elevated responses in both early and ventral visual cortex and the caudate tail compared to the receipt of low reward [28•]. Importantly, the position and identity of the preceding target could be decoded from these reward responses in the visual system, as if the stimulus representation that predicted the reward was either reactivated or maintained for a longer period of time [28•]. Such reward-dependent visual responses could serve to ‘stamp in’ the responses predictive of high reward, tuning the neurons underlying this representation and producing the elevated responsiveness described in the prior section.

Midbrain and ventral striatal activation have also been observed as neural correlates of value-driven attentional orienting [18•,19•,20••,47], with activation within these regions correlating with behavioral measures of value-modulated distraction. However, in each of these cases, either the effect of reward on attention was measured in the context of inter-trial priming [19•,47] or when the reward-associated distractor could also appear as a target on different trials in the same task [18•,20••]. Consistent with the role of these regions in online reward prediction [39,40], and their role as the teaching signal for more enduring changes in the visual cortex and caudate tail as hypothesized here, such responses may reflect the strength of associative reward learning in the task and its more immediate impact on the visual system. The fact that such responses are evident in a reward priming paradigm in which there are no stable stimulus-reward associations [19•,47], whereas value-dependent caudate tail activation is only observed when stable long-term value associations have been trained [22,23], suggests two distinct time courses to the contributions of these regions to the orienting of attention.

Towards a unifying account

The proposed neural account of value-driven attention can accommodate a variety of observations in the literature, and offers specific hypotheses concerning their neural basis. The hypothesized feedback signals from the reward system to the visual system, which occur at the time of reward feedback and are stimulus-specific [19•,28•,48], provide a single mechanism that can account for both persistent biasing effects of protracted training [11,13,16,17••,22–24,29•,31,33••,35–38,41,42] as well as immediate trial-by-trial effects seen in reward-mediated priming [12,19•,47]. Such feedback is linked to stimulus representations (that in turn bias visually guided action), rather than to visually guided action plans themselves, and thus can proceed independently of whether orienting to the reward-predictive stimulus was ever goal-directed. This representational basis allows for attentional biases towards reward-predictive distractors to develop [36,37], dissociating the learning from the motivations of the observer.

The dual-mechanisms hypothesis, reflecting increased competition in the spatial priority map of parietal cortex on the one hand and increased competition in the oculomotor system of the basal ganglia on the other hand, lends potential insight into an interesting dissociation between value-driven attention and stimulus-driven attention. Value-driven attentional capture has been shown to occur even when attention is spatially focused [49,50], which contrasts with the effects of physical salience on attention [51]. Value-driven and stimulus-driven attention are hypothesized to similarly influence the spatial priority map of parietal cortex, which is subject to strong modulation by the goal-directed allocation of spatial attention [6], but value-driven attention uniquely recruits the caudate tail, which provides an additional source of priority that may be less subject to top-down spatial biasing signals. More broadly, the dual-mechanisms hypothesis lends potential insight into why value-driven attention can at times overpower both goal-directed and stimulus-driven attention [13,16,17••,31,33••,38,41,42], with more than one value-modulated visual signal biasing selection, allowing value-driven attentional priority to bypass competition in the spatial priority map.

In situations where a stimulus feature is only predictive of reward when appearing in a particular region of space, this feature selectively captures attention when appearing in the region in which it was rewarded [52]. The proposed neural account intuitively captures this spatial specificity by virtue of the retinotopic nature of the stimulus representations that are modified through reward feedback-mediated plasticity [28•]. Value-driven attentional capture by a previously reward-associated feature has also been shown to be specific to the context in which that feature was rewarded [53]. Speculatively, connections between the caudate tail and adjacent medial temporal lobe [34], which supports a variety of memory functions, could facilitate the context-dependent weighting of priority signals based on the binding of stimuli to context and the association of this bound representation with reward. Such contextual specificity would be difficult to account for if value-driven attention were limited to neural populations involved in the perception of early visual features, which would imply a more direct influence of context on perception itself. At the same time, plasticity in early visual areas can account for graded feature-similarity effects in value-driven attention [54], given the feature tuning functions characteristic of these representations [55].

Outstanding issues

In this review, I offer a neural framework for understanding value-driven attention. Although this framework can account for a wide variety of findings in the literature, it also has multiple shortcomings. The proposed account is likely too simplistic, accounting for only a subset of the neural processes by which reward-associated stimuli gain priority. For example, both the amygdala [56,57] and the anterior insula [58] have been implicated in value-driven attention, although our understanding of their contribution to the learning and expression of value-based attentional priority is not as well developed. The proposed framework is also particular to visual attention, although value-driven attention has more recently been demonstrated in the auditory domain as well [59,60]. Given that the superior colliculus plays a role in multisensory integration [61] and receives input from the caudate tail [27], it is possible that the caudate tail might be involved in signaling value-driven attentional priority in more than one sensory modality.

Reward learning has also been shown to bias spatial attention [62–64], but the neural mechanisms underlying this dimension of value-driven attention have not been investigated. One possibility would be contextually-dependent weighting of the spatial priority map [52,62]. However, the degree to which such biases are ‘purely’ spatial in nature or recruit object-selective or feature-selective representations in a spatial context is debatable [62–66]. Value-driven attentional biases can be strongly modulated by context [53], but the neural mechanisms underlying such contextual modulation remain to be studied.

The degree to which the neural mechanisms hypothesized here are particular to reward, or whether they are better described as valence-independent (driven by both reward and punishment learning), is unclear. Robust attentional biases have been observed for aversively conditioned stimuli [67,68]. The basolateral amygdala, which plays a critical role in representing fear, has projections to the caudate tail in non-human primates [69]. Furthermore, feature-dependent visual cortical plasticity has been observed following fear conditioning [70]. Findings such as these suggest similar neural principles may underlie punishment-driven attention, although direct comparisons between value-driven and punishment-driven orienting are lacking. Both financial losses and financial gains have been shown to influence attention to associated stimuli [67,71], although the neural mechanisms appear to be somewhat dissociable, with dopaminergic midbrain nuclei specifically predicting reward-based capture [20••].

More broadly, the concept of selection history in the control of attention encompasses not only reward and punishment, but also outcome-independent search history in which repeatedly orienting to a target-defined stimulus biases attention to repeat this orienting response in the future [72,73]. The role of reward prediction-errors in the development of value-driven attentional priority [28•,35,38], value-driven attentional biases for reward cues that never served as targets [36,37], the relationship between value-driven attentional capture and reward-related dopamine release [33••], and the finding that depressive symptoms blunt value-driven but not selection-driven attentional capture [42] are consistent with a direct role for reward signals in driving an attentional learning process rather than merely serving as a modulator of reward-independent learning processes. However, how different components of selection history relate to one another in the control of attention is not understood, and direct comparisons at the neural level are lacking.

Conflict of interest statement

Nothing declared.

Funding

The writing of this manuscript was supported in part by NARSAD Young Investigator Grant 26008 to BAA.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Desimone R, Duncan J: **Neural mechanisms of selective visual attention**. *Annu Rev Neurosci* 1995, **18**:193-222.
2. Wolfe JM, Cave KR, Franzel SL: **Guided search: an alternative to the feature integration model for visual search**. *J Exp Psychol: Hum Percept Perform* 1989, **15**:419-433.
3. Folk CL, Remington RW, Johnston JC: **Involuntary covert orienting is contingent on attentional control settings**. *J Exp Psychol: Hum Percept Perform* 1992, **18**:1030-1044.
4. Itti L, Koch C: **Computational modelling of visual attention**. *Nat Rev Neurosci* 2001, **2**:194-203.
5. Theeuwes J: **Top-down and bottom-up control of visual selection**. *Acta Psychol* 2010, **135**:77-99.
6. Corbetta M, Shulman GL: **Control of goal-directed and stimulus-driven attention in the brain**. *Nat Rev Neurosci* 2002, **3**:201-215.
7. Serences JT, Shomstein S, Leber AB, Golay X, Egeth HE, Yantis S: **Coordination of voluntary and stimulus-driven attentional control in human cortex**. *Psychol Sci* 2005, **16**:114-122.
8. Geng JJ, Mangun GR: **Anterior intraparietal sulcus is sensitive to bottom-up attention driven by stimulus salience**. *J Cogn Neurosci* 2009, **21**:1584-1601.
9. Awh E, Belopolsky AV, Theeuwes J: **Top-down versus bottom-up attentional control: a failed theoretical dichotomy**. *Trends Cogn Sci* 2012, **16**:437-443.
10. Theeuwes J: **Visual selection: usually fast and automatic; seldom slow and volitional**. *J Cogn* 2018, **1**:29 1-15.
11. Della Libera C, Chelazzi L: **Learning to attend and to ignore is a matter of gains and losses**. *Psychol Sci* 2009, **20**:778-784.
12. Hickey C, Chelazzi L, Theeuwes J: **Reward changes salience in human vision via the anterior cingulate**. *J Neurosci* 2010, **30**:11096-11103.
13. Anderson BA, Laurent PA, Yantis S: **Value-driven attentional capture**. *Proc Natl Acad Sci U S A* 2011, **108**:10367-10371.
14. Anderson BA: **The attention habit: how reward learning shapes attentional selection**. *Ann N Y Acad Sci* 2016, **1369**:24-39.
15. Chelazzi L, Perlato A, Santandrea E, Della Libera C: **Rewards teach visual selective attention**. *Vis Res* 2013, **85**:58-72.
16. Anderson BA, Laurent PA, Yantis S: **Value-driven attentional priority signals in human basal ganglia and visual cortex**. *Brain Res* 2014, **1587**:88-96.
17. •• Anderson BA, Kuwabara H, Wong DF, Gean EG, Rahmim A, Brasic JR, George N, Frolov B, Courtney SM, Yantis S: **The role of dopamine in value-based attentional orienting**. *Curr Biol* 2016, **26**:550-555.

Using positron emission tomography, this study demonstrated a correlation between distractor-evoked dopamine release in the human striatum and value-driven attentional capture as measured from behavior, providing direct evidence for the contribution of striatal dopamine to value-based attentional priority.

18. • Hickey C, Peelen MV: **Neural mechanisms of incentive salience in naturalistic human vision**. *Neuron* 2015, **85**:512-518.

Using multivariate pattern analysis of fMRI data, this paper shows that task-irrelevant examples of a high-value, real-world image category (people, cars, trees) are better represented in ventral visual cortex. The strength of this effect is linked to activity in dopaminergic nuclei in the midbrain and to reward-seeking personality traits, consistent with the idea of dopamine-driven value-dependent visual plasticity.

19. • Hickey C, Peelen MV: **Reward selectively modulates the lingering neural representation of recently attended objects in natural scenes**. *J Neurosci* 2017, **37**:7297-7304.

Using multivariate pattern analysis of fMRI data, the authors demonstrate that the representation of real-world object categories in ventral visual cortex is accentuated by reward, even when these objects are no longer present in the visual environment. This identifies a potential mechanism through which reward outcome might potentiate the representation of potential reward cue stimuli, sensitizing the visual system for similar objects in the future.

20. •• Barbaro L, Peelen MV, Hickey C: **Valence, not utility, underlies reward-driven prioritization in human vision**. *J Neurosci* 2017, **37**:10438-10450.

Uses multivariate fMRI to index neural representations of stimuli associated with reward or the evasion of loss. Results differentiate between the possibility that value-driven attentional selection reflects an economically normative mechanism versus an economically irrational mechanism driven by the valence of outcome. Shows that representations in ventral visual cortex are largely irrational, preferentially representing stimuli with positive valence, but that representations in parietal cortex are economically normative, with both positively valenced and negatively valenced stimuli represented equally when they are equally useful.

21. • Donohue SE, Hopf JM, Bartsch MV, Schoenfeld MA, Heinze HJ, Woldorff MG: **The rapid capture of attention by rewarded objects**. *J Cogn Neurosci* 2016, **28**:529-541.

Using magnetoencephalography, the authors demonstrated that exemplars of a high-value category automatically capture attention, with a similar N2pc profile to value-driven attentional capture by previously rewarded features observed in prior studies. This evidence suggests a rapid influence of prior reward learning on the selection of complex objects, consistent with value-dependent plasticity in the visual system.

22. Yamamoto S, Kim HF, Hikosaka O: **Reward value-contingent changes in visual responses in the primate caudate tail associated with a visuomotor skill**. *J Neurosci* 2013, **33**:11227-11238.
23. Kim HF, Hikosaka O: **Distinct basal ganglia circuits controlling behaviors guided by flexible and stable values**. *Neuron* 2013, **79**:1001-1010.
24. MacLean MH, Giesbrecht B: **Neural evidence reveals the rapid effects of reward history on selective attention**. *Brain Res* 2015, **1606**:86-94.

25. Serences JT: **Value-based modulations in human visual cortex**. *Neuron* 2008, **60**:1169-1181.

26. Serences JT, Saproo S: **Population response profiles in early visual cortex are biased in favor of more valuable stimuli**. *J Neurophysiol* 2010, **104**:76-87.

27. Yamamoto S, Monosov IE, Yasuda M, Hikosaka O: **What and where information in the caudate tail guides saccades to visual objects**. *J Neurosci* 2012, **32**:11005-11016.

28. • Anderson BA: **Reward processing in the value-driven attention network: reward signals tracking cue identity and location**. *Soc Cogn Affect Neurosci* 2017, **12**:461-467.

This study provided evidence that the receipt of reward evokes activity in visual areas that are known to play a role in the signaling of value-based attentional priority, from which the identity and position of the preceding reward-predictive cue can be decoded. This is consistent with the idea that reward signals serve as teaching signals to the visual system, driving value-dependent plasticity.

29. • van Koningsbruggen MG, Ficarella SC, Battelli L, Hickey C: **Transcranial random noise stimulation of visual cortex potentiates value-driven attentional capture**. *Soc Cogn Affect Neurosci* 2016, **11**:1481-1488.

Uses broadband electrical stimulation of cortex to test the idea that value-driven attentional capture reflects plasticity in visual cortex. Stimulation over visual cortex during training causes reward-associated stimuli to more strongly capture attention at test.

30. Hickey C, Kaiser D, Peelen MV: **Reward guides attention to object categories in real-world scenes**. *J Exp Psychol: Gen* 2015, **144**:264-273.

31. Qi S, Zeng Q, Ding C, Li H: **Neural correlates of reward-driven attentional capture in visual search**. *Brain Res* 2013, **1532**:32-43.

32. Lee J, Shomstein S: **The differential effects of reward on space- and object-based attentional allocation**. *J Neurosci* 2013, **33**:10625-10633.

33. •• Anderson BA, Kuwabara H, Wong DF, Roberts J, Rahmim A, Brasic JR, Courtney SM: **Linking dopaminergic reward signals to the development of attentional bias: a positron emission tomographic study**. *NeuroImage* 2017, **157**:27-33.

In this study, a behavioral indicator of value-driven attentional capture was predicted by reward-evoked dopamine release in the striatum measured during a preceding training phase, linking dopaminergic reward signals to value-dependent changes in attentional priority.

34. Seger CA: **The visual corticostriatal loop through the tail of the caudate: circuitry and function**. *Front Syst Neurosci* 2013, **7** 104.

35. Sali AW, Anderson BA, Yantis S: **The role of reward prediction in the control of attention**. *J Exp Psychol: Hum Percept Perform* 2014, **40**:1654-1664.

36. Le Pelley ME, Pearson D, Griffiths O, Beesley T: **When goals conflict with values: counterproductive attentional and oculomotor capture by reward-related stimuli**. *J Exp Psychol: Gen* 2015, **144**:158-171.

37. Bucker B, Theeuwes J: **Pavlovian reward learning underlies value driven attentional capture**. *Atten Percept Psychophys* 2017, **79**:415-428.

38. Anderson BA, Laurent PA, Yantis S: **Reward predictions bias attentional selection**. *Front Hum Neurosci* 2013, **7** 262.

39. Schultz W, Dayan P, Montague PR: **A neural substrate of prediction and reward**. *Science* 1997, **275**:1593-1599.

40. O'Doherty JP: **Reward representations and reward-related learning in the human brain: insights from neuroimaging**. *Curr Opin Neurobiol* 2004, **14**:769-776.

41. Anderson BA, Leal SL, Hall MG, Yassa MA, Yantis S: **The attribution of value-based attentional priority in individuals with depressive symptoms**. *Cogn Affect Behav Neurosci* 2014, **14**:1221-1227.

42. Anderson BA, Chiu M, DiBartolo MM, Leal SL: **On the distinction between value-driven attention and selection history: evidence from individuals with depressive symptoms**. *Psychon Bull Rev* 2017, **24**:1636-1642.

43. Shuler MG, Bear MF: **Reward timing in the primary visual cortex**. *Science* 2006, **311**:1606-1609.

44. Arsenault JT, Nelissen K, Jarraya B, Vanduffel W: **Dopaminergic reward signals selectively decrease fMRI activity in primate visual cortex**. *Neuron* 2013, **77**:1174-1186.

45. Roelfsema PR, van Ooyen A: **Attention-gated reinforcement learning of internal representations for classification**. *Neural Comput* 2005, **17**:2176-2214.

46. Sasaki Y, Nanez JE, Watanabe T: **Advances in visual perceptual learning and plasticity**. *Nat Rev Neurosci* 2010, **11**:53-60.

47. Meffert H, Penner E, VanThieghem MR, Sypher I, Leshin J, Blair RJR: **The role of ventral striatum in reward-based attentional bias**. *Brain Res* 2018, **1689**:89-97.

48. Schiffer AM, Muller T, Yeung N, Waszak F: **Reward activated stimulus-specific and task-dependent representations in visual association cortices**. *J Neurosci* 2014, **34**:15610-15620.

49. Munneke J, Belopolsky AV, Theeuwes J: **Distractors associated with reward break through the focus of attention**. *Atten Percept Psychophys* 2016, **78**:2213-2225.

50. Munneke J, Hoppenbrouwers SS, Theeuwes J: **Reward can modulate attentional capture, independent of top-down set**. *Atten Percept Psychophys* 2015, **77**:2540-2548.

51. Yantis S, Jonides J: **Abrupt visual onsets and selective attention: voluntary versus automatic allocation**. *J Exp Psychol: Hum Percept Perform* 1990, **16**:121-134.

52. Anderson BA: **Value-driven attentional capture is modulated by spatial context**. *Vis Cogn* 2015, **23**:67-81.

53. Anderson BA: **Value-driven attentional priority is context specific**. *Psychon Bull Rev* 2015, **22**:750-756.

54. Anderson BA: **On the feature specificity of value-driven attention**. *PLoS One* 2017, **12**:e0177491.

55. Hubel DH, Wiesel TN: **Receptive fields, binocular interaction, and functional architecture in the cat visual cortex**. *J Physiol* 1962, **160**:106-154.

56. Peck CJ, Salzman CD: **Amygdala neural activity reflects spatial attention towards stimuli promising reward or threatening punishment**. *eLife* 2014, **3**:e04478.

57. Ousdal OT, Specht K, Server A, Andreassen OA, Dolan RJ, Jensen J: **The human amygdala encodes value and space during decision making**. *NeuroImage* 2014, **101**:712-719.

58. Wang L, Yu H, Hu J, Theeuwes J, Gong X, Xiang Y, Jiang C, Zhou X: **Reward breaks through center-surround inhibition via anterior insula**. *Hum Brain Mapp* 2015, **36**:5233-5251.

59. Anderson BA: **Value-driven attentional capture in the auditory domain**. *Atten Percept Psychophys* 2016, **78**:242-250.

60. Asutay E, Vastfjall D: **Auditory attentional selection is biased by reward cues**. *Sci Rep* 2016, **6** 36989.

61. Meredith MA, Stein BE: **Visual, auditory, and somatosensory convergence on cells in superior colliculus results in multisensory integration**. *J Neurophysiol* 1986, **56**:640-662.

62. Chelazzi L, Estocinova J, Calletti R, Lo Gerfo E, Sani I, Della Libera C, Santandrea E: **Altering spatial priority maps via reward-based learning**. *J Neurosci* 2014, **34**:8594-8604.

63. Anderson BA, Kim H: **Mechanisms of value-learning in the guidance of spatial attention**. *Cognition* 2018, **178**:26-36.

64. Hickey C, Chelazzi L, Theeuwes J: **Reward-priming of location in visual search**. *PLoS One* 2014, **9**:e103372.

65. Jiang VY, Li ZS, Remington RW: **Modulation of spatial attention by goals, statistical learning, and monetary reward**. *Atten Percept Psychophys* 2015, **77**:2189-2206.

66. Won B-Y, Leber AB: **How do magnitude and frequency of monetary reward guide visual search**. *Atten Percept Psychophys* 2016, **78**:1221-1231.

67. Wang L, Yu H, Zhou X: **Interaction between value and perceptual salience in value-driven attentional capture**. *J Vis* 2013, **13** 5.
68. Schmidt LJ, Belopolsky AV, Theeuwes J: **Attentional capture by signals of threat**. *Cogn Emot* 2015, **29**:687-694.
69. Giggs WS, Kim HF, Ghazizadeh A, Costello MG, Wall KM, Hikosaka O: **Flexible and stable value coding areas in the caudate head and tail receive anatomically distinct cortical and subcortical inputs**. *Front Neuroanat* 2017, **11** 106.
70. Thigpen NN, Bartsch F, Keil A: **The malleability of emotional perception: short-term plasticity in retinotopic neurons accompanies the formation of perceptual biases to threat**. *J Exp Psychol: Gen* 2017, **146**:464-471.
71. Wentura D, Muller P, Rothermund K: **Attentional capture by evaluative stimuli: gain- and loss-connoting colors boost the additional singleton effect**. *Psychon Bull Rev* 2014, **21**:701-707.
72. Sha LZ, Jiang YV: **Components of reward-driven attentional capture**. *Atten Percept Psychophys* 2016, **78**:403-414.
73. Grubb MA, Li Y: **Assessing the role of accuracy-based feedback in value-driven attentional capture**. *Atten Percept Psychophys* 2018, **80**:822-828.