How is value processed in the brain to inform decision making? A plethora of studies describe how preferences are shaped by experience with external reinforcements. While research on this reinforced pathway is well established, far less research has explored the neural pathways promoting preference change in the absence of external reinforcements. Here, we review behavioral paradigms linking nonreinforced preference change with manipulations of stimulus exposure, response, and gaze position. Based on this work, we propose that several brain regions traditionally associated with selective attention constitute a pathway for nonreinforced preference change. Together, this nonreinforced pathway (termed here the dorsal value pathway; DVP) and the more famously studied reinforced pathway (ventral value pathway; VVP), interface with prefrontal regions of the primate brain to guide value-based decisions.

Two Paths for Preference Change

How are preferences constructed in the brain to guide value-based decisions? The most common way to assign value to goods is through rewarded experience, a framework that has been formalized by reinforcement learning (see Glossary) [1,2]. Within the reinforcement learning framework, choices that lead to positive outcomes are reinforced whereas those that lead to negative outcomes are avoided. Usage of external reinforcement has been described by learning theories as the association between a stimulus, either with or without a response, and an outcome (for review, see [3]). The repeated association between a stimulus, response, and positive outcome, for example, leads to a positive change in preference towards that stimulus (Figure 1A). However, there are other paths for preference change that do not rely on external reinforcements. In many situations, preferences towards stimuli (or goods) are changed in the absence of external reinforcement (Figure 1B). While decades of research have elucidated the neural mechanisms underpinning preference change due to external reinforcement [4–6], relatively little is known about the neural substrates related to preference change that occurs in its absence, despite the paramount importance of both in guiding value-based decisions.

What are the factors that drive nonreinforced preference change? In this Opinion, we attempt to uncover the factors governing nonreinforced preference change and their underlying mechanisms. We review behavioral studies linking nonreinforced preference change with manipulations of exposure, response, and gaze position. We synthesize behavioral and neuroimaging studies in humans with neurobiological investigations in macaques to inform a framework within which a neural pathway exists for nonreinforced preference change, centered on areas traditionally associated with selective attention. We put forth that this pathway, together with the more famously studied pathway governing reinforced preference change [7], interfaces with prefrontal regions of the primate brain to guide value-based decisions.
Reinforced preference change

Nonreinforced preference change

Behavioral Evidence of Nonreinforced Preference Change

Glossary

Attentional drift diffusion model (aDDM): a computational model that describes how overt attention (gaze position) biases preference towards one of two or more stimuli over time.

Choice-induced preference change: a behavioral paradigm in which the mere act of making a choice in one instance influences preferences towards subsequently presented stimuli.

Covert attention: in covert attention, stimuli are selected for processing in the absence of orienting movements.

Cue-approach training: a nonreinforced behavioral change paradigm whereby the mere association of a stimulus with a neutral cue and speeded button press leads to preference changes towards the stimulus.

Gaze-dependent preference change: general term for preference changes that occur following manipulations of gaze towards stimuli, independent of external reinforcement.

Nonreinforced preference change: change in preference towards a stimulus that occurs in the absence of external reinforcement. This is in contrast to reinforced preference change, in which preference to a stimulus may increase due to a positive outcome associated with the stimulus.

Overt attention: in overt attention, stimuli are selected for processing through an overt orienting event (e.g., eye movement).

Reinforcement learning: an area of machine learning that has been successfully applied to both behavior and the brain and has implicated the dopaminergic system as being involved in it. Reinforcement learning serves to explain how organisms use the outcome of a certain behavior to adjust future behavior.

Selective attention: a process by which behaviorally relevant stimuli are selected for processing over another or others.
reinforcement does not guarantee the absence of internal reinforcement, but current experimental designs lack the resolution to address this directly.

**Manipulations of Gaze Influence Preference**

In one of the first studies to link gaze to the formation of preferences in the absence of external reinforcement, subjects freely viewed pairs of stimuli and selected the one they preferred [29]. Within a single trial, the stimulus gazed upon more often tended to be preferred by the subjects, demonstrating a correlation between gaze and preference. A causal demonstration then followed, whereby manipulations of the duration of stimulus presentation (and duration of subject gaze at the stimulus) influenced subjects’ preference. The authors proposed that preferences are enhanced towards stimuli at the center of gaze by virtue of a gaze cascade, in which gaze directed towards an appetitive stimulus leads to increased attention towards it, which in turn, leads to the attraction of gaze. This line of work was followed by studies that manipulated the position of gaze position directly, which also influenced preference [29,30]. One study found that the effect of gaze manipulations on preference was positive for appetitive items and negative for aversive items [29], suggesting that the manipulation operates as a gain on value: amplifying the preference regardless of sign. Together, studies linking gaze with preference have suggested that the root of the observed *gaze-dependent preference change* effects is based on the deployment of *overt attention* [29–32].

Following the experimental approaches linking overt attention with preference change, a computational model termed the *attentional drift diffusion model* (aDDM) was developed whereby attention is proposed to guide valuation [31]. The aDDM is based on the extensively studied drift diffusion model [33,34] and describes how a relative decision value evolves over time, and crucially, how it is biased by overt attention such that ultimately, one item is valued more highly and preferred over another. The approach has influenced a number of groups [35–37], but it should be noted that the locus of attention in the model is determined by overt attention (i.e., gaze position) and not by controlling for *covert attention*, which might sometimes be deployed elsewhere [38]. Whether or not manipulations of covert attention influence preference similarly to manipulations of overt attention is an important open question.

The relationship between gaze and preferences extends beyond studies that manipulate gaze explicitly, and is also evident in the aforementioned choice-induced preference change and CAT. For example, a recent study of choice-induced preference change found that subject gaze was preferentially allocated towards items that were subsequently preferred [21]. In fact, fixation duration was predictive of the magnitude of preference change. In CAT, unchosen Go items were found to attract gaze more than unchosen NoGo items during the test phase [23]. However, these experimental designs lack the resolution to determine whether the manipulation caused a preference change which biased gaze, or a bias in gaze which led to a preference change. The underlying mechanisms across paradigms likely differ, but a commonality amongst them emerges downstream, where changes in both preference and gaze are observed.

**Short-Term versus Long-Term Preference Change**

Notably, the timescale of preference change can vary considerably across paradigms. Gaze manipulations operate within a single trial, influencing preference on the order of seconds. In contrast, preference change induced by mere exposure, by choice, and by CAT, occur outside the duration of a trial and are thought to take place on substantially longer timescales. Indeed, the behavioral consequences of CAT last for months [26], and those of choice-induced preference change, for years [19]. Thus, it is possible that these long-term effects of preference change
rely more heavily on memory-related mechanisms for value assignment [21,39], while short-term effects avail other mechanisms, potentially related to selective attention [22,31]. However, it is also possible that the differences in timescale are a consequence of task design. For example, the CAT design does not lend itself to within-trial manipulations, and, as far as we know, the effects of within-trial gaze manipulations have not been tested beyond the scope of the manipulated trial. Thus, it is currently unclear whether differences in timescale of effect across paradigms are indicative of underlying mechanism, or of differences in experimental design.

Neural Regions Implicated in Preference Change

Reinforced Preference Change
The neural basis of preference change has been extensively studied and continues to be elucidated, but almost exclusively in response to external reinforcement and with reinforcement learning models [1,4,7,40]. The brain regions involved in externally reinforced preference change constitute a pathway which we denote here as the ventral value pathway (VVP), due to the ventral location of the dopaminergic nuclei in the midbrain and their innervation to the ventral and dorsal striatum [41,42]. The representation of subjective value assigned to a stimulus or response has been extensively linked to activity in the ventromedial prefrontal cortex (vmPFC) and orbitofrontal cortex (OFC), which have been posited to represent value in a unified and common currency [43,44]. The vmPFC and OFC are considered late in the VVP hierarchy, and are thought to be read out by downstream areas that guide value-based choices and actions, such as the anterior cingulate cortex and related regions in the frontoparietal network [45–50].

Nonreinforced Preference Change
While the VVP is one of the most actively researched circuits in neuroscience, research into the neural basis of preference change that is not externally reinforced is scarce. One functional magnetic resonance imaging (fMRI) study found that manipulating overt attention by restricting gaze position to one of two appetitive food items influenced subjects’ preference towards the items [30]. A link was identified between the induced preference change and activity in ventral striatum, vmPFC, and visual regions. The vmPFC has also been implicated in the CAT paradigm across multiple different stimuli [23,27,51]. Such fMRI results add an important dimension to the behavioral findings but were obtained only after the preference had already changed, during the choice phase. Thus, it is unclear whether the areas implicated in these studies are related to a change in nonreinforced preference specifically, or to a change in preference at large, irrespective to how it was formed.

To uncover brain regions related to preference shaped by nonreinforced manipulations specifically, a recent fMRI study compared brain activation to snack-food items before versus after CAT, independent of choice [28]. The study found that parietal regions decreased in fMRI signal following training, while the vmPFC and visual areas in the lateral occipital cortex increased. The modulation of visual areas is reminiscent of value-based modulations observed in early visual cortex [30,52]. A second CAT study showed a correlation between fMRI signals in the striatum during training to the subsequent preference change, implicating the striatum in nonreinforced preference change [27]. Similar brain regions were implicated in choice-induced preference change studies with the addition of the hippocampus [17,39], and in one instance, the preference change could be decoded from activity in dorsolateral PFC and precuneus, even before it had behaviorally manifest [21]. A recent study [53] explored the response of value-encoding OFC neurons in freely-viewing monkeys where, while individual trials were associated with a reward, individual eye movements were not. Value encoding in OFC neurons was strongly modulated by gaze position, providing a neural-based explanation to the link between gaze position and value observed previously as reviewed earlier [29,31,54].
In summary, the set of brain regions involved in nonreinforced preference change is gradually being uncovered, but it is still unclear whether the highlighted regions play a causal role in driving the change in preference itself or whether they reflect the end product of a process that has taken place elsewhere. In the following section we propose a number of mechanisms that might play a causal role in propagating the changes in preference observed during nonreinforced paradigms.

**Proposed Mechanisms for Nonreinforced Preference Change**

It is unlikely that the various behavioral manipulations reviewed earlier are all supported by the exact same set of underlying mechanisms. However, the links between overt attention and preference change in multiple studies across paradigms lead us to hypothesize that certain neural architectures may be common across paradigms. We propose a number of neural mechanisms through which nonreinforced manipulations might influence preference, based on mechanisms involved in selective attention. The proposed mechanisms differ in functional architecture but might operate in conjunction to best guide behavior. While we are unaware of studies that have manipulated covert attention to influence preference, we suspect that the architectures we discuss later apply to these manipulations as well.

**Changing Preference through Gating**

First, we draw inspiration from the classical view of attention as a filter (or gate), proposed to cope with the limited resources available for processing information in the brain [55,56]. In this view, selective attention is supported by a mechanism that gates the information content of neural representations in support of perceptual decision making by either increasing signal or suppressing noise [57,58]. In a similar vein, we propose that such a mechanism may gate the relative valuation of signals that guide value-based decision making (Figure 2A). Such a mechanism would rely on areas causally related to the deployment of overt attention. Causal roles have been demonstrated for the macaque lateral intraparietal (LIP) cortex [59,60], the frontal eye fields (FEF) [61], and the superior colliculus (SC) [62]. In addition to influencing behavior in tasks requiring selective attention, the FEF and SC have been shown to exert control over sensory cortices, although at different stages of the visual processing hierarchy [63,64]. Such neurobiological routes may be used to regulate the flow of value information associated with goods to downstream valuation regions such as the OFC.

While we believe the LIP, FEF, and SC play an important role in nonreinforced preference change, it is notable that they were not implicated in the fMRI studies reviewed earlier [21,23,27,28,51]. However, this does not necessarily constitute a mismatch given that our proposed mechanism is hypothesized to drive the change itself, while the fMRI findings may speak to a change that had already occurred. Attention-related areas may only be active during the propagation of the preference change, and not after. There exist several behavioral approaches that might test whether attention-related areas shape the representation of value during nonreinforced manipulations of attention. In humans, one could imagine developing tasks that have sufficient detection power to compare brain activation between trials in which gaze manipulation resulted in a preference change versus matched trials that did not. In macaques, the degree of preference change in response to attentional manipulations could be evaluated following causal manipulations to the aforementioned areas, directly evaluating their involvement in the process. No evidence to our knowledge currently argues in favor or against this hypothesized mechanism, at either early or late stages of attentional selection [58], but future experiments stand to determine whether attention-related areas play a regulatory role during nonreinforced change in preference.
In contrast to the view of attention as a filter, attention may be conceptualized as the consequence of efficient selection of sensory signals (i.e., readout) [58,65–67]. The underlying mechanism is not centered on the enhancement or suppression of neural representations but on the efficient readout of the signals most relevant for behavior at a particular moment given the agent’s environment, goals, and internal state. We propose that attention-based preference change may operate by a similar mechanism, whereby the value assigned to a stimulus is shaped as a consequence of behavioral relevance at that moment (Figure 2B). Such an explanation would be consistent with results from the CAT experiments where even though the cue-response was not associated with external reinforcement or feedback, its timely behavioral relevance (as in attentional boosting [68,69]) deemed the associated object more valuable. Stimuli frequently encountered, acted upon, or gazed at (as in the mere exposure effect, choice-induced preference change, and gaze manipulation paradigms, respectively), may similarly be deemed most relevant at that moment, leading to the modulated preference observed. The idea that selective attention is achieved by efficient readout as opposed to a modulation of sensory regions is supported by experimental data, where inactivation of the SC disrupted behavior in an attention task, without affecting early visual cortex [70] (but see [64]). It remains to be seen whether such a manipulation to SC (or related regions) would influence value assignment in nonexternally reinforced manipulations, and whether or not it would affect early sensory areas.

In human fMRI studies, BOLD activity was found to increase in the striatum following gaze manipulations [30], CAT [27], and choice-induced preference change [21]. Indeed, central to
the efficient readout hypothesis are the basal ganglia, which are extensively implicated in reward signaling [71], and are proposed to govern state estimation during tasks that require attention [67]. The basal ganglia may similarly govern the preference changes surveyed here, especially if internal reinforcement is gained despite the absence of external reinforcement. The primary input structure of the basal ganglia, the striatum, receives substantial input from gaze-related areas in the cerebral cortex [72], and is functionally linked to the SC [73,74]. The striatum also receives inputs from the amygdala and hippocampus [75–77], which likely hone the readout process in accordance with motivational states [78], aversive experiences [79], and remembered associations [16,80]. Amygdalo striatal projections could be related to the observed amplification of negative preference to aversive items during gaze manipulations [29], and hippocampal input to the long-term effects of CAT or choice-induced preference change [19,26,28].

Changing Preference through Transformation

In another view, we speculate that certain regions implicated in attentional control may reflect attention-related and value-related signals jointly (Figure 2C). The tight link between attention and reward has been described previously [81] and cannot be straightforwardly disentangled. Neurons in area LIP are of particular interest because they respond to manipulations of reward [82,83] and salience [84], in addition to their prominent role in overt and covert allocation of attention [60,85]. LIP has also enjoyed a wealth of studies linking its responses to the accumulation of evidence, but a picture is gradually emerging whereby LIP neurons appear less related to the accumulation of sensory evidence per se [86,87] and more reflective of sensorimotor facets of a task, attentional manipulations, and reward contingencies [88,89]. Thus, attention and reward signals in LIP neurons may be reflected jointly, multiplexed [90], or transformed from one to the other; similar to how sensory signals in LIP are transformed into motor actions [91]. Such functionality would be especially useful in explaining the relationship between gaze and preference, and may translate to paradigms using other effectors. Functionally connected areas such as FEF [92] may play a similar role given that neurons in FEF respond to manipulations of reward [93] and attention [61], and exhibit a flexible encoding repertoire [94,95]. In humans, parietal regions were implicated in nonreinforced preference change by exhibiting a modulation during choice-induced preference change [21] and during CAT [28]. However, the modulation associated with CAT was a decrease as opposed to an increase in activation, although this may be because fMRI scanning took place after the preference had already changed rather than during the change in preference itself. Additionally, attention-related regions in the frontoparietal network may be recruited in an effector specific manner and may only play a role in paradigms that require an oculomotor response (which was not required in the CAT studies). It would be especially useful then to adopt experimental approaches to nonreinforced preference change that stand to determine which areas are general to the process (or goods based), versus those that depend on sensorimotor facets of the task (or action based).

Two Neural Pathways for Preference Change?

We propose that there are two interrelated pathways for preference change in the brain, conforming to our conceptual framework (Figure 1). First, the well-known pathway that includes midbrain dopaminergic nuclei, the striatum, and prefrontal cortices [7], termed here the VVP. Second, a neural pathway promoting the preference change that occurs in the absence of external reinforcements. The regions implicated in imaging studies include the striatum, vmPFC, high level visual regions, and frontoparietal regions [21,27,28,30]. We hypothesize that the basal ganglia and attention-related regions play a crucial role in nonreinforced changes of preference, by one or some combination of the mechanisms proposed. Given the dorsal location of attention-related regions relative to the VVP, we refer to the circuit connecting them as the nonreinforced dorsal value pathway (DVP) (Figure 3A). It is likely that the set of areas proposed to constitute the DVP are but one set of many, depending on sensorimotor requirements and internal factors.
In this Opinion, we set out to determine the factors governing nonreinforced preference change in the brain. We described behavioral evidence linking behavioral manipulations with preference change in the absence of external reinforcement. We synthesized neuroimaging studies in humans with neurophysiological evidence in nonhuman primates to formulate a means by which attention-related regions could promote nonreinforced preference change. If this change relies on mechanisms related to attention, it likely involves visual areas, attention related structures of the basal ganglia, and prefrontal cortices, which play a role at different levels of the value assignment hierarchy. We put forth that attention-related areas are part of a network related to the subjective perception and shaping of value that we term the DVP. The DVP may play a regulatory role and gate which information enters the valuation system, or influence value through readout or signal transformation (Figure 2). The DVP and VVP may constitute two independent routes that influence the representation of value in prefrontal regions, or work in tandem as a readout or signal transformation.
function of context and behavioral goals (Figure 3). Such a framework is consistent with the idea that item values are not stored uniquely, but are dynamically shaped by a multitude of factors, in service of value-based decision making [97].

Further research is required to test the ideas put forth here and to address the many open questions that remain (see Outstanding Questions). Whether reinforced versus nonreinforced preference changes are shaped through distinct neural pathways or a unified network, it is important to consider the underlying neurobiology of both forms of preference change to more fully understand how value is represented and shaped in the brain. Such an understanding may advance models of learning and of value-based decision making under various contexts, both in humans and in machines [98]. Most importantly, a holistic understanding of how value is shaped may lead to an understanding of how value is mis-shaped, stimulating the development of interventions for maladaptive behaviors (Box 1).

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References

12. Winkielman, P. et al. (2003) The hedonic marking of processing fluency: implications for evaluative judgment the psychology of
Trends in Cognitive Sciences


30. Lim, S.-L. et al. (2011) The decision value computations in the vmPFC and striatum use a relative value code that is guided by visual attention. J. Neurosci. 31, 13214–13223


64. Bogadhi, A.R. et al. (2019) Midbrain activity supports high-level visual properties in primate temporal cortex. JNeurosci Published online November 15, 2019. https://doi.org/10.1101/841155


