

## Opinion

## A Neural Pathway for Nonreinforced Preference Change

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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.

## Highlights

Subjective preferences can be changed even in the absence of external reinforcement.

Neural evidence from humans suggests that nonreinforced preference change involves areas in the visual cortex, parietal cortex, striatum, and prefrontal regions.

We suggest that areas related to nonreinforced preference change promote the change in preference through mechanisms related to selective attention.

We put forth a framework in which nonreinforced preference change takes place through attention-related areas in a circuit we term the dorsal value pathway (DVP).

The DVP is complementary to the extensively studied pathway promoting externally reinforced preference change through dopamine signals, which we term the ventral value pathway (VVP). The DVP and VVP may operate in tandem to shape the unified representation of value in the brain.

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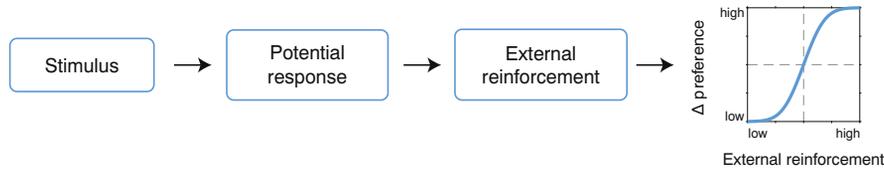
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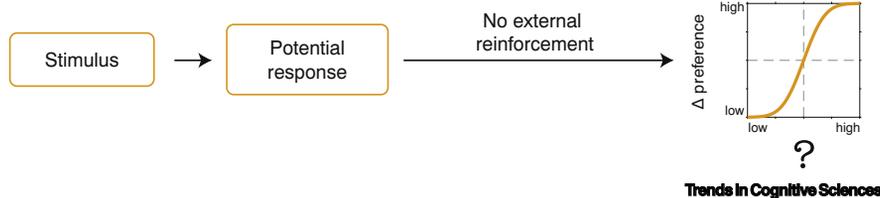
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## (A) Reinforced preference change



## (B) Nonreinforced preference change



**Figure 1. Conceptual Paths for Preference Change.** (A) Reinforced preference change: a stimulus, either with or without a response, is repeatedly associated with an external outcome that varies in its degree of reinforcement. The magnitude of reinforcement serves to shape the change in preference ( $\Delta$  preference) towards the stimulus. (B) Nonreinforced preference change: a stimulus, either with or without a response, does not result in an external reinforcement. Nonetheless, preference towards the stimulus is changed ( $\Delta$  preference) due to some factors (? on abscissa) that we aim to elucidate in this Opinion.

## Behavioral Evidence of Nonreinforced Preference Change

### Manipulations of Behavior Influence Preference

Preferences can be manipulated in the absence of external reinforcement using several methods. Early evidence of nonreinforced preference change was reported by Zajonc [8,9], who experimentally manipulated exposure levels to Chinese-like calligraphy and unfamiliar faces, and found that stimuli presented more frequently were deemed more favorable. The effect was dubbed the mere-exposure effect, used to describe the positive attitude developed by people towards stimuli previously exposed to [8,9]. Indeed, marketing research had long linked exposure to favorable familiarity [10]. A general framework suggested that preferences could be described in terms of memory [11], and indeed, the speed and ease of processing or remembering (fluency) have been tied to positive preference [12–15], as well as to a wide class of decisions [16].

Nonreinforced preference change has also been linked to the act of making a choice, in and of itself. In **choice-induced preference change** paradigms, the mere act of choosing a stimulus or item (as opposed to receiving it, for example) was found to influence subsequent preference towards it [17–19]. The effect of choice on subsequent preference, similar to the effect of exposure, has also been suggested to involve memory mechanisms [20,21], and in the context of perceptual decision making, has been suggested to recruit mechanisms for selective attention [22].

A related means with which to influence preference towards stimuli in the absence of external reinforcement was recently developed using **cue-approach training** (CAT) [23]. In CAT, stimuli such as food items that vary in subjective value are presented on the screen one after the other. A neutral cue (e.g., sound) appears after the presentation of some of the stimuli, and participants are instructed to respond (press a button) as fast as they can following the cue, without any feedback or external reinforcement to the response. Several studies found that the association of a cue and speeded response to an item (termed the Go item) led to pronounced preference changes in favor of the Go item, consistent across multiple stimulus categories and cue modalities [24–26], and lasting for months [23,26–28]. Importantly, the absence of external

## 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 to 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.

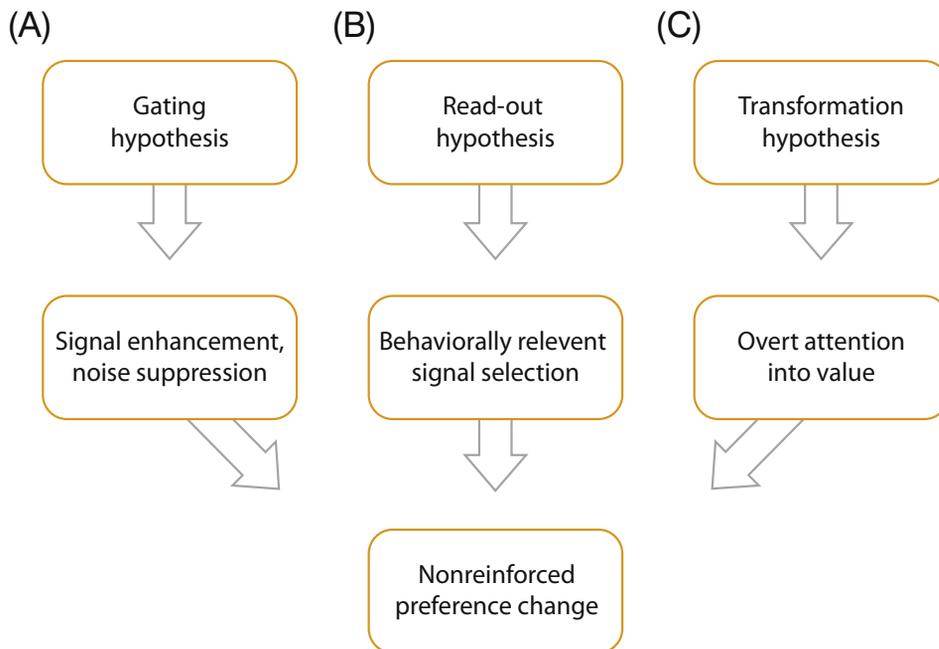
### Proposed Mechanisms for Nonreinforced Preference Change

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.

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**Figure 2. Potential Mechanisms for Nonreinforced Preference Change.** (A) In the gating hypothesis, an enhancement of signal or suppression of noise lead to stronger representation of value associated with a stimulus. (B) In the readout hypothesis, behaviorally relevant information is selectively read out by downstream areas to modulate the value associated with a stimulus. (C) In the transformation hypothesis, neural signals associated with overt attention are transformed into value, shaping subsequent preference.

### Changing Preference through Readout

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

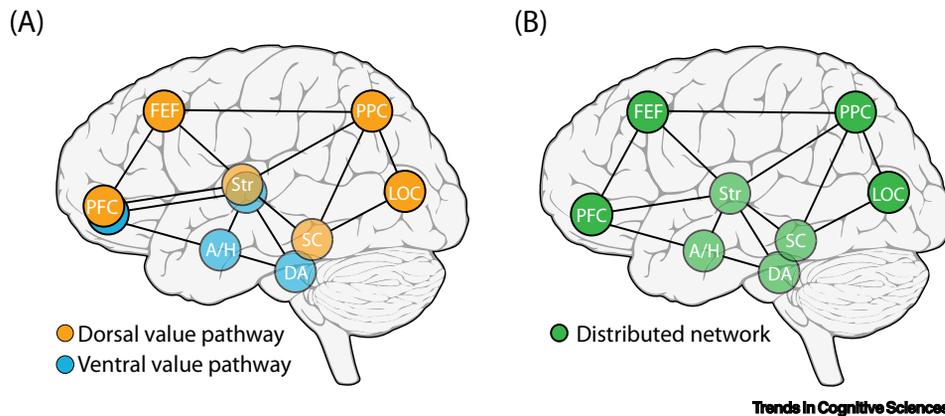
the efficient readout hypothesis are the basal ganglia, which are extensively implicated in reward signaling [71], and are proposed to govern state estimation during tasks that require attention [67]. The basal ganglia may similarly govern the preference changes surveyed here, especially if internal 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]. Amygdalostriatal 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.



**Figure 3. Proposed Pathways for Preference Change in the Brain.** (A) Areas constituting the dorsal value pathway (DVP) are identified by orange nodes. Areas proposed to constitute parts of the ventral value pathway (VVP) are identified by blue nodes. Nodes from both pathways are presented on a human brain cartoon. Transparency denotes areas that lie beneath the neocortex. (B) In the unified view, the same areas constitute a single distributed network. Abbreviations: A/H, amygdala and hippocampus; DA, midbrain dopamine neurons; FEF, frontal eye field; LOC, lateral occipital cortex; PFC, prefrontal cortex; PPC, posterior parietal cortex; SC, superior colliculus; Str, striatum.

Tasks of different nature may recruit a different set of areas (e.g., manipulations of model-free vs. model-based decisions [96]). Thus, the extent of DVP and its constituent regions is still under active investigation, but at least within the framework considered here, includes areas that play key roles in the allocation of selective attention.

While we use monikers to refer to the VVP and DVP pathways in isolation, there is considerable overlap between them, especially in the involvement of striatal, hippocampal, and prefrontal regions. Other regions might also overlap. For example, it is unknown whether dopamine signals accompany nonreinforced preference change. Thus, the degree of overlap between the VVP and DVP is unclear, despite clear distinctions between behaviors that include external reinforcement versus those that do not. Accordingly, distinctions drawn by experimenters with regard to external reinforcement versus no reinforcement (or potential internal reinforcement) may not manifest as separate neural structures and instead recruit a network that is unified and distributed (Figure 3B). Future experiments with targeted experimental designs will shed light on the differential function of the pathways proposed here, on the neural architecture constituting each, and on the nature of their interaction.

### Concluding Remarks

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

### Outstanding Questions

How do behavioral manipulations lead to changes in preference in the absence of external reinforcement? What are the computational principles governing such changes, and what are the underlying mechanisms?

Are differences in timescale of preference change effects indicative of different underlying mechanisms, or alternatively, due to differences in task design?

Do description-based manipulations to preference (e.g., via framing) differ from the item-based manipulations to preference presented here? How?

Would manipulations to covert attention influence preference similarly to manipulations of overt attention? What would their differential effect tell us about mechanism?

Do nonreinforced attentional manipulations change preference through similar mechanisms to those proposed for selective attention? How would the preference change process be influenced by causal perturbations to attention-related regions such as LIP, FEF, and SC? Nuclei of the basal ganglia?

To what degree is nonreinforced preference change in fact not reinforced? Is it possible that subjects are reinforced in ways that are not readily apparent with current methodologies? Could more refined experimental protocols be developed to detect and discern the types of reinforcement that may be taking place?

What is the degree of overlap (or lack thereof) between DVP areas recruited during nonreinforced preference change and VVP areas recruited during standard reinforcement learning? Is preference change promoted by the pathways independently, or do they work in tandem? Does the level of cooperation depend on factors such as behavioral context and internal goals?

How does the DVP circuitry contribute to the representation of value in prefrontal cortex? What are the anatomical projections and functional relations between areas within the DVP from which signal propagates to influence the final perception or calculation of value?

**Box 1. Clinical Applications of Nonreinforced Behavioral Change**

The inability to behave in accordance with internal goals has devastating outcomes and can manifest as addiction, mental illness, and eating disorders. While such maladaptive behaviors are pervasive worldwide, behavioral change can have a dramatic positive effect. Many interventions that rely on self-control or external reinforcements have positive effects. However, these effects are often short lived, and tend to fail in the long run [99–102]. Thus, new interventions and approaches need to be used. The behavioral paradigms reviewed in this article are simple and do not rely on self-control or external reinforcements, but on basic behavioral mechanisms. These types of tasks have the potential to be transformed into clinical applications by adapting them to specific areas of interest such as depression, whereby some gamified version of a task may be used to enhance preferences towards positive stimuli. In anorexia nervosa patients, the approach may enhance preference towards particular foods. CAT, for example, can be considered under the attentional bias modification (ABM) approach, that had been widely applied to anxiety disorders [103]. In ABM, diverting attention away from negative stimuli or enhancing preferences to positive stimuli has been shown to prevent the recurrence of maladaptive behaviors such as depression [104] or social anxiety [105]. The importance of cognitive training in psychiatric disorders has been highlighted [106] as a potentially effective avenue of treatment for mood disorders like anxiety or depression.

Identifying the neural substrates of mood disorders and maladaptive behaviors has been a long-standing goal of translational neuroscience. Determining the similarities and differences between neural circuits underlying reinforced versus nonreinforced preference change (such as the VVP and DVP, respectively) may prove important for informing the development of neurobiological interventions based on either pharmacology or direct stimulation of the brain. These may be coupled with appropriate behavioral manipulations to target either reinforced or nonreinforced preference change to best alleviate specific abnormalities and achieve long lasting behavioral change.

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).

**Acknowledgments**

Tom Schonberg was supported by the European Research Council (ERC) under the European Union's Horizon 2020 Research and Innovation Programme (grant number 715016) and the Israeli Science Foundation (grant number 2004/15); The authors would like to thank Drs. Richard Krauzlis, Russell Poldrack, Alex Huk, Jacob Yates, Akram Bakkour, Rotem Botvink Nezer, Nathaniel Daw, for comments on earlier versions of this manuscript. The authors would like to thank Tom Salomon for assistance with preparation of Figure 3 and comments on an earlier version of this manuscript.

**References**

- Rangel, A. *et al.* (2008) A framework for studying the neurobiology of value-based decision making. *Nat. Rev. Neurosci.* 9, 545–556
- Sutton, R. and Barto, A. (2018) *Reinforcement Learning: An Introduction*. MIT Press
- Balleine, B.W. *et al.* (2009) Multiple forms of value learning and the function of dopamine. In *Neuroeconomics*, pp. 367–387, Elsevier
- Gershman, S.J. and Uchida, N. (2019) Believing in dopamine. *Nat. Rev. Neurosci.* 20, 703–714
- Glimcher, P.W. (2011) Correction for Glimcher, Understanding dopamine and reinforcement learning: the dopamine reward prediction error hypothesis. *Proc. Natl. Acad. Sci.* 108, 17568–17569
- Niv, Y. (2009) Reinforcement learning in the brain. *J. Math. Psychol.* 53, 139–154
- Schultz, W. (2015) Neuronal reward and decision signals: from theories to data. *Physiol. Rev.* 95, 853–951
- Zajonc, R.B. (1968) Attitudinal effects of mere exposure. *J. Pers. Soc. Psychol.* 9, 1–27
- Zajonc, R.B. (2001) Mere exposure: a gateway to the subliminal. *Curr. Dir. Psychol. Sci.* 10, 224–228
- Grimes, A. and Kitchen, P.J. (2007) Researching mere exposure effects to advertising - theoretical foundations and methodological implications. *Int. J. Mark. Res.* 49, 191–219
- Weber, E.U. and Johnson, E.J. (2006) Constructing preferences from memory. In *The Construction of Preference* (Lichtenstein, S. and Slovic, P., eds), pp. 397–410, Cambridge University Press
- Winkielman, P. *et al.* (2003) The hedonic marking of processing fluency: implications for evaluative judgment the psychology of

- evaluation: affective processes in cognition and emotion. In *The Psychology of Evaluation: Affective Processes in Cognition and Emotion* (Musch, J. and Klauer, K.C., eds), pp. 189–217, Lawrence Erlbaum Associates
13. Johnson, E.J. *et al.* (2007) Aspects of endowment: a query theory of value construction. *J. Exp. Psychol. Learn. Mem. Cogn.* 33, 461–474
  14. Mantonakis, A. *et al.* (2015) Consumer memory, fluency, and familiarity. In *Handbook of Consumer Psychology*, Routledge
  15. Mandler, G. *et al.* (1987) Nonspecific effects of exposure on stimuli that cannot be recognized. *J. Exp. Psychol. Learn. Mem. Cogn.* 13, 646–648
  16. Shadlen, M.N. and Shohamy, D. (2016) Decision making and sequential sampling from memory. *Neuron* 90, 927–939
  17. Izuma, K. *et al.* (2010) Neural correlates of cognitive dissonance and choice-induced preference change. *Proc. Natl. Acad. Sci.* 107, 22014–22019
  18. Voigt, K. *et al.* (2017) Endogenous formation of preferences: choices systematically change willingness-to-pay for goods. *J. Exp. Psychol. Learn. Mem. Cogn.* 43, 1872–1882
  19. Sharot, T. *et al.* (2012) Is choice-induced preference change long lasting? *Psychol. Sci.* 23, 1123–1129
  20. Izuma, K. and Murayama, K. (2013) Choice-induced preference change in the free-choice paradigm: a critical methodological review. *Front. Psychol.* 4
  21. Voigt, K. *et al.* (2019) Hard decisions shape the neural coding of preferences. *J. Neurosci.* 39, 718–726
  22. Talluri, B.C. *et al.* (2018) Confirmation bias through selective overweighting of choice-consistent evidence. *Curr. Biol.* 28, 3128–3135.e8
  23. Schonberg, T. *et al.* (2014) Changing value through cued approach: an automatic mechanism of behavior change. *Nat. Neurosci.* 17, 625–630
  24. Chen, Z. *et al.* (2016) Changing food choice through cued approach: impulsive or deliberative response? *Appetite* 101, 229
  25. Zoltak, M.J. *et al.* (2018) Attention! Can choices for low value food over high value food be trained? *Appetite* 124, 124–132
  26. Salomon, T. *et al.* (2018) The cue-approach task as a general mechanism for long-term non-reinforced behavioral change. *Sci. Rep.* 8, 3614
  27. Salomon, T. *et al.* (2020) Enhanced striatal and prefrontal activity is associated with individual differences in nonreinforced preference change for faces. *Hum. Brain Mapp.* 41, 1043–1060
  28. Botvinik-Nezer, R. *et al.* (2020) Enhanced bottom-up and reduced top-down fMRI activity is related to long-lasting nonreinforced behavioral change. *Cereb. Cortex* 30, 858–874
  29. Armel, K.C. *et al.* (2008) Biasing simple choices by manipulating relative visual attention. *Judgm. Decis. Mak.* 3, 396–403
  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
  31. Krajbich, I. *et al.* (2010) Visual fixations and the computation and comparison of value in simple choice. *Nat. Neurosci.* 13, 1292–1298
  32. Krajbich, I. (2019) Accounting for attention in sequential sampling models of decision making. *Curr. Opin. Psychol.* 29, 6–11
  33. Ratcliff, R. *et al.* (2016) Diffusion decision model: current issues and history. *Trends Cogn. Sci.* 20, 260–281
  34. Smith, P.L. and Ratcliff, R. (2004) Psychology and neurobiology of simple decisions. *Trends Neurosci.* 27, 161–168
  35. Vaidya, A.R. and Fellows, L.K. (2015) Testing necessary regional frontal contributions to value assessment and fixation-based updating. *Nat. Commun.* 6, 10120
  36. Thomas, A.W. *et al.* (2019) Gaze bias differences capture individual choice behaviour. *Nat. Hum. Behav.* 3, 625–635
  37. Molter, F. *et al.* (2019) GLAMbox: a Python toolbox for investigating the association between gaze allocation and decision behaviour. *PLoS One* 14, e0226428
  38. Posner, M.I. (1980) Orienting of attention. *Q. J. Exp. Psychol.* 32, 3–25
  39. Chammat, M. *et al.* (2017) Cognitive dissonance resolution depends on episodic memory. *Sci. Rep.* 7, 41320
  40. Lee, D. *et al.* (2012) Neural basis of reinforcement learning and decision making. *Annu. Rev. Neurosci.* 35, 287–308
  41. Haber, S.N. *et al.* (2000) Striatonigrostriatal pathways in primates form an ascending spiral from the shell to the dorsolateral striatum. *J. Neurosci.* 20, 2369–2382
  42. Haber, S.N. and Knutson, B. (2010) The reward circuit: linking primate anatomy and human imaging. *Neuropsychopharmacology* 35 (1), 4–26
  43. Bartra, O. *et al.* (2013) The valuation system: a coordinate-based meta-analysis of BOLD fMRI experiments examining neural correlates of subjective value. *Neuroimage* 76, 412–427
  44. Levy, D.J. and Glimcher, P.W. (2012) The root of all value: a neural common currency for choice. *Curr. Opin. Neurobiol.* 22, 1027–1038
  45. Kennerley, S.W. *et al.* (2006) Optimal decision making and the anterior cingulate cortex. *Nat. Neurosci.* 9, 940–947
  46. Gluth, S. *et al.* (2012) Deciding when to decide: time-variant sequential sampling models explain the emergence of value-based decisions in the human brain. *J. Neurosci.* 32, 10686–10698
  47. Hare, T.A. *et al.* (2011) Transformation of stimulus value signals into motor commands during simple choice. *Proc. Natl. Acad. Sci.* 108, 18120–18125
  48. Rodriguez, C.A. *et al.* (2015) The neural basis of value accumulation in intertemporal choice. *Eur. J. Neurosci.* 42, 2179–2189
  49. PISAURO, M.A. *et al.* (2017) Neural correlates of evidence accumulation during value-based decisions revealed via simultaneous EEG-fMRI. *Nat. Commun.* 8, 15808
  50. Rich, E.L. and Wallis, J.D. (2016) Decoding subjective decisions from orbitofrontal cortex. *Nat. Neurosci.* 19, 973–980
  51. Bakkour, A. *et al.* (2017) Neural mechanisms of cue-approach training. *Neuroimage* 151, 92–104
  52. Serences, J.T. (2008) Value-based modulations in human visual cortex. *Neuron* 60, 1169–1181
  53. McGinty, V.B. *et al.* (2016) Orbitofrontal cortex value signals depend on fixation location during free viewing. *Neuron* 90, 1299–1311
  54. Shimojo, S. *et al.* (2003) Gaze bias both reflects and influences preference. *Nat. Neurosci.* 6, 1317–1322
  55. Broadbent, D.E. (1958) *Perception and Communication*, Pergamon Press
  56. Carrasco, M. (2011) Visual attention: the past 25 years. *Vis. Res.* 51, 1484–1525
  57. Desimone, R. and Duncan, J. (1995) Neural mechanisms of selective visual attention. *Annu. Rev. Neurosci.* 18, 193–222
  58. Serences, J.T. and Kastner, S. (2014) *A Multi-level Account of Selective Attention*, Oxford University Press
  59. Wardak, C. (2006) Contribution of the monkey frontal eye field to covert visual attention. *J. Neurosci.* 26, 4228–4235
  60. Liu, Y. *et al.* (2010) Intention and attention: different functional roles for LIPd and LIPv. *Nat. Neurosci.* 13, 495–500
  61. Squire, R.F. *et al.* (2013) Prefrontal contributions to visual selective attention. *Annu. Rev. Neurosci.* 36, 451–466
  62. Lovejoy, L.P. and Krauzlis, R.J. (2010) Inactivation of primate superior colliculus impairs covert selection of signals for perceptual judgments. *Nat. Neurosci.* 13, 261–266
  63. Moore, T. and Armstrong, K.M. (2003) Selective gating of visual signals by microstimulation of frontal cortex. *Nature* 421, 370–373
  64. Bogadhi, A.R. *et al.* (2019) Midbrain activity supports high-level visual properties in primate temporal cortex. *bioRxiv* Published online November 15, 2019. <https://doi.org/10.1101/841155>
  65. Pestilli, F. *et al.* (2011) Attentional enhancement via selection and pooling of early sensory responses in human visual cortex. *Neuron* 72, 832–846
  66. Baruni, J.K. *et al.* (2015) Reward expectation differentially modulates attentional behavior and activity in visual area V4. *Nat. Neurosci.* 18, 1656–1663
  67. Krauzlis, R.J. *et al.* (2014) Attention as an effect not a cause. *Trends Cogn. Sci.* 18, 457–464
  68. Lin, J.Y. *et al.* (2010) Enhanced memory for scenes presented at behaviorally relevant points in time. *PLoS Biol.* 8, e1000337
  69. Swallow, K.M. and Jiang, Y.V. (2010) The attentional boost effect: transient increases in attention to one task enhance performance in a second task. *Cognition* 115, 118–132
  70. Zénon, A. and Krauzlis, R.J. (2012) Attention deficits without cortical neuronal deficits. *Nature* 489, 434–437

71. Hikosaka, O. *et al.* (2014) Basal ganglia circuits for reward value-guided behavior. *Annu. Rev. Neurosci.* 37, 289–306
72. Selemon, L. and Goldman-Rakic, P. (1985) Longitudinal topography and interdigitation of corticostriatal projections in the rhesus monkey. *J. Neurosci.* 5, 776–794
73. Herman, J.P. *et al.* (2019) Attention-related modulation of caudate neurons depends on superior colliculus activity. *bioRxiv* Published online November 26, 2019. <https://doi.org/10.1101/843235>
74. Yasuda, M. and Hikosaka, O. (2015) Functional territories in primate substantia nigra pars reticulata separately signaling stable and flexible values. *J. Neurophysiol.* 113, 1681–1696
75. Averbeck, B.B. and Costa, V.D. (2017) Motivational neural circuits underlying reinforcement learning. *Nat. Neurosci.* 20, 505–512
76. Zorrilla, E.P. and Koob, G.F. (2013) Amygdalo-striatal projections in the neurocircuitry for motivation: a neuroanatomical thread through the career of Ann Kelley. *Neurosci. Biobehav. Rev.* 37, 1932–1945
77. Haber, S.N. (2016) Corticostriatal circuitry. In *Neuroscience in the 21st Century*, pp. 1721–1741. Springer, New York
78. Cunningham, W.A. and Brosch, T. (2012) Motivational salience. *Curr. Dir. Psychol. Sci.* 21, 54–59
79. Likhtik, E. and Paz, R. (2015) Amygdala–prefrontal interactions in (mal)adaptive learning. *Trends Neurosci.* 38, 158–166
80. Wimmer, G.E. and Shohamy, D. (2012) Preference by association: how memory mechanisms in the hippocampus bias decisions. *Science* 338, 270–273
81. Maunsell, J.H.R. (2004) Neuronal representations of cognitive state: reward or attention? *Trends Cogn. Sci.* 8, 261–265
82. Platt, M.L. and Glimcher, P.W. (1999) Neural correlates of decision variables in parietal cortex. *Nature* 400, 233–238
83. Sugrue, L.P. (2004) Matching behavior and the representation of value in the parietal cortex. *Science* 304, 1782–1787
84. Leathers, M.L. and Olson, C.R. (2012) In monkeys making value-based decisions, LIP neurons encode cue salience and not action value. *Science* 338, 132–135
85. Bisley, J.W. and Goldberg, M.E. (2010) Attention, intention, and priority in the parietal lobe. *Annu. Rev. Neurosci.* 33, 1–21
86. Katz, L.N. *et al.* (2016) Dissociated functional significance of decision-related activity in the primate dorsal stream. *Nature* 535, 285–288
87. Zhou, Y. and Freedman, D.J. (2019) Posterior parietal cortex plays a causal role in perceptual and categorical decisions. *Science* 365, 180–185
88. Huk, A.C. *et al.* (2017) The role of the lateral intraparietal area in (the study of) decision making. *Annu. Rev. Neurosci.* 40, 349–372
89. Forie, A.E. *et al.* (2010) Integration of sensory and reward information during perceptual decision-making in lateral intraparietal cortex (LIP) of the macaque monkey. *PLoS One* 5, e9308
90. Park, I.M. *et al.* (2014) Encoding and decoding in parietal cortex during sensorimotor decision-making. *Nat. Neurosci.* 17, 1395–1403
91. Zhang, M. and Barash, S. (2004) Persistent LIP activity in memory antisaccades: working memory for a sensorimotor transformation. *J. Neurophysiol.* 91, 1424–1441
92. Premereur, E. *et al.* (2012) Frontal eye field microstimulation induces task-dependent gamma oscillations in the lateral intraparietal area. *J. Neurophysiol.* 108, 1392–1402
93. Ding, L. and Hikosaka, O. (2006) Comparison of reward modulation in the frontal eye field and caudate of the macaque. *J. Neurosci.* 26, 6695–6703
94. Ebitz, R.B. *et al.* (2018) Exploration disrupts choice-predictive signals and alters dynamics in prefrontal cortex. *Neuron* 97, 475
95. Mante, V. *et al.* (2013) Context-dependent computation by recurrent dynamics in prefrontal cortex. *Nature* 503, 78–84
96. Daw, N.D. *et al.* (2011) Model-based influences on humans' choices and striatal prediction errors. *Neuron* 69, 1204–1215
97. Vlaev, I. *et al.* (2011) Does the brain calculate value? *Trends Cogn. Sci.* 15, 546–554
98. Botvinick, M. *et al.* (2019) Reinforcement learning, fast and slow. *Trends Cogn. Sci.* 23, 408–422
99. Wood, W. and Neal, D.T. (2007) A new look at habits and the habit-goal interface. *Psychol. Rev.* 114, 843–863
100. Christiansen, T. *et al.* (2007) Weight loss maintenance in severely obese adults after an intensive lifestyle intervention: 2- to 4-year follow-up. *Obesity (Silver Spring)* 15, 413–420
101. Jeffery, R.W. *et al.* (2000) Long-term maintenance of weight loss: current status. *Health Psychol.* 19, 5–16
102. Prochaska, J.J. *et al.* (2004) A meta-analysis of smoking cessation interventions with individuals in substance abuse treatment or recovery. *J. Consult. Clin. Psychol.* 72, 1144–1156
103. Hakamata, Y. *et al.* (2010) Attention bias modification treatment: a meta-analysis toward the establishment of novel treatment for anxiety. *Biol. Psychiatry* 68, 982–990
104. Browning, M. *et al.* (2012) Using attentional bias modification as a cognitive vaccine against depression. *BPS* 72, 572–579
105. Lazarov, A. *et al.* (2017) Gaze-contingent music reward therapy for social anxiety disorder: a randomized controlled trial. *Am. J. Psychiatry* 174, 649–656
106. Keshavan, M.S. *et al.* (2014) Cognitive training in mental disorders: update and future directions. *Am. J. Psychiatry* 171, 510–522