

Information Processing Biases in the Brain: Implications for Decision-Making and Self-Governance

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Abstract To make behavioral choices that are in line with our goals and our moral beliefs, we need to gather and consider information about our current situation. Most information present in our environment is not relevant to the choices we need or would want to make and thus could interfere with our ability to behave in ways that reflect our underlying values. Certain sources of information could even lead us to make choices we later regret, and thus it would be beneficial to be able to ignore that information. Our ability to exert successful self-governance depends on our ability to attend to sources of information that we deem important to our decision-making processes. We generally assume that, at any moment, we have the ability to choose what we pay attention to. However, recent research indicates that what we pay attention to is influenced by our prior experiences, including reward history and past successes and failures, even when we are not aware of this

history. Even momentary distractions can cause us to miss or discount information that should have a greater influence on our decisions given our values. Such biases in attention thus raise questions about the degree to which the choices that we make may be poorly informed and not truly reflect our ability to otherwise exert self-governance.

Keywords Attention · Cognitive control · Working memory · Learning · Self-governance

We continuously gather information to guide and inform our behavior. Given the abundance of information in the environment and the limited processing capacity of the brain, we must regularly select which sources of information to focus on and which, by extension, to ignore. Control over the deployment of attention, the process by which we select some sources of information over others, is therefore intimately associated with our behavioral choices. As a consequence of the tight coupling between attentional selection and the information available to support decision-making, the study of attentional control has strong implications for understanding how we make choices that are consistent with our goals and moral beliefs, referred to here as self-governance.

As we will discuss, behavioral goals do not always prevail in determining which sources of information are attended. We begin by describing how behavioral goals generally do guide attentional selection. We then go on to examine recent work suggesting that implicitly learned reward associations powerfully and automatically shape attentional selection, providing evidence

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that we are sometimes unable to prevent attending to certain stimuli even when the selection of these stimuli is in conflict with our goals. On multiple other levels, we present evidence from psychological research suggesting that we do not always have control over how we allocate our attention. We conclude by exploring the implications of these findings for the issue of self-governance.

By way of example, imagine that you are on a ship that begins to sink. You are a strong swimmer and are able to carry one person to shore with you. Your goals and morals would lead you to help the person in greatest need, perhaps the least capable swimmer. In order to make a decision that reflects these goals and values, you must pay attention to each individual person, evaluate their need, and then use this information to compare across individuals. Accordingly, your desire and intent is to pay equal attention to each person in order to ensure that this decision process is not arbitrarily biased towards one individual or another. The challenge is that you can only pay attention to a small number of people at a particular moment in time, perhaps one or two, and there are pressures to make a decision quickly.

What if a certain individual was more attention-grabbing than the others in this example? Perhaps this person yells the loudest, making it difficult for you to shift your focus to someone else. You would certainly come to learn more about that attention-grabbing person, and you would have greater confidence in the accuracy of that information. The needs of this person would also be more likely to be considered than those of others when evaluating the consequences of potential helping behaviors. You might even be completely oblivious to the needs of certain other people in the process. In short, your decisions would be biased towards this attention-grabbing person, potentially leading you to make a decision that does not objectively reflect your goals and values, even though this was never your intent. The question for successful self-governance then becomes: can you choose or otherwise control what you pay attention to? We argue here that the answer to this question is “not necessarily,” depending on the individual and situation, and we explore the implications that this answer has for the concept of self-governance.

It is important to note that the attention-grabbing individual in the above example does not actually change the observer’s goal of saving the least competent swimmer and the impact of this goal on the decision-making process. Instead, the observer is faced with

needing to make a decision that is most in line with his or her goals given only limited information about the true state of the world. Attentional selection sculpts our perception of the world around us, limiting what information reaches conscious awareness [1, 2]. Throughout, we argue that it is this acquisition of information that is sometimes biased in ways that lead us to make decisions that oppose our behavioral goals, decisions that we would not have made were our representation of the world unbiased. Accordingly, we focus on a particular and important aspect of self-governance in our consideration of attentional biases: the capacity to minimize the difference between the actions our explicitly held goals and aspirations would lead us to perform and the decisions we actually make based on incomplete and noisy information. This is by no means a complete definition of self-governance, and there are several other aspects of goal-oriented control that are relevant to this issue but are outside the scope of this paper. In particular, as we will explain, our abilities to self-govern are tempered by the degree to which the information we rely on to plan our behaviors is biased as the result of attentional selection. That is not to say that all of the goals and values that shape our behavior are explicitly represented, and one may question the role of implicitly held values in determining our behavior and whether that behavior ultimately reflects effective self-governance. But if our ability to act in accordance with explicit goal representations were to be biased by information that is irrelevant to the decision at hand, that would speak in important ways to our ability to self-govern in general. Also, in our consideration of goal-directed behavior, we do not draw a distinction between whether these goals are or are not beneficial to the individual. Again, it is important to the issue of self-governance to understand the circumstances under which explicitly held goal representations are and are not effective in guiding behavior, and it is a separate and interesting issue whether goal-directed yet ultimately self-destructive behavior reflects effective self-governance or a failure to self-govern.

In contrast to our example of the sinking ship in which the observer has the singular goal of selecting the least competent swimmer, in everyday life, our goals are frequently multidimensional such that sub-goals may sometimes conflict. For example, an individual may have the long-term goal of being healthy and happy. Although there are certainly many behavioral choices that successfully fulfill both dimensions of this

goal, what happens when an individual is faced with a choice between prioritizing health or happiness, such as when deciding whether to eat a donut or choose a healthy (but less tasty) snack? In this case, eating the donut fulfills the goal of happiness, but directly opposes the goal of living a healthy lifestyle. When deciding whether to eat the donut, the individual must preferentially weight one goal dimension over the other. Determining the current prioritization of goals gives rise to a conceptually similar challenge as when we must decide between multiple options in the face of a singular goal: there is an optimal decision to be made that reflects an unbiased weighting of the importance of pursuing each of these priorities in light of the circumstances in which we find ourselves, but our access to the current state of our circumstances is limited and influenced by attention. Attending to a particular aspect of the environment, (e.g., the look and smell of the delicious, but unhealthful, food) may give greater weight to the corresponding decision outcome (e.g., consuming the donut) when considering alternatives. If we are acutely aware of the donut and its enticing qualities at the moment we experience it, this may cause us to fail to adequately consider certain aspects of its health consequences before arriving at a decision. Conversely, if the donut were not present, we may more easily prioritize the goal of health when deciding our actions. Although the overall goal of health and happiness does not change, attention biases moment-by-moment behavioral outcomes.

Converging evidence from studies of non-human primate and human cognition has revealed the importance of attentional selection for behavioral choice outcomes [3]. Human fixation patterns bias behavioral choices such that items that are fixated longer are more likely to ultimately be chosen as having greater value [4–6]. For example, when deciding which of two apples to select at the supermarket, an individual may repeatedly make eye movements between both fruits, accumulating evidence about the quality of each. Using a variant of a drift diffusion model, a popular computational approach for modeling the accumulation of evidence for each of two options for a binary choice, Krajbich and colleagues found that behavioral decisions were biased in favor of targets that participants spent more time fixating while making a decision [4]. If one apple is particularly salient, and thus more likely to be attended, the observer's goal of selecting the best apple does not change, but the observer's information on which to base his or her decision will be biased toward

the preferentially attended apple. Whether an observer is selecting an apple at the supermarket or the least capable swimmer on a sinking ship, they must make a behavioral decision based on the incomplete, and potentially biased, information that they have gathered about the current state of their environment.

Until recently, researchers have attributed the likelihood that a particular source of information will be attended, referred to as the stimulus's attentional priority, purely to the physical properties of the stimulus and to the moment-by-moment goals of the observer. For example, the abrupt onset of a stimulus involuntarily captures the focus of attention [7–9] and stimuli that differ in physical characteristics compared to surrounding stimuli receive elevated priority [10–13]. However, behavioral goals shape the degree to which physically salient stimuli involuntarily capture attention [14–17]. For example, although a physically salient, but task-irrelevant, stimulus (referred to as a distractor) captures participants' attention when they search for a physically salient target, they are able to ignore this same distractor when the target itself is not physically salient. Although participants use physical salience to guide visual search in the first case, they readily ignore salient stimuli in the latter because salience itself does not provide goal-relevant information [18, 19]. Relatedly, when searching for a target that is identifiable on the basis of a known physical feature, such as the color red, stimuli that share this feature capture attention while those that lack this goal-relevant feature do not [14–16]. Our moment-by-moment behavioral goals, therefore, powerfully influence the likelihood that a particular item in the world will be attended, thereby promoting self-governance in accordance with the principles that we hold to be important.

A large body of research supports biased competition as the mechanism through which goal-relevant stimuli are given greater representation in the brain and irrelevant information is suppressed [20, 21]. It is thought that the connections among neurons within a particular brain area, which represents a particular kind of information, are mutually inhibitory. This organization leads to winner-take-all competition between the set of neurons that represent one object (for example) and the set of neurons that represent a different object. The outcome of the competition can be influenced by excitatory inputs from other brain areas. These inputs are called "bias signals." Bias signals are thought to increase the activity of the cells representing the information that has high

attentional priority, making it more likely that the activity of these cells will win the competition. These bias signals come from prefrontal and parietal regions of the cerebral cortex.

The prefrontal and parietal cortices have been implicated in the maintenance of behavioral goals and task rules [22–29]. The ability to consistently keep our current goals and the individual pieces of information that are necessary to achieve those goals actively in mind, and the ability to use that information to direct thought and behavior, has been called “working memory.” Working memory depends critically on the prefrontal cortex (PFC), where reverberating neural circuits appear to enable patterns of activity representing currently relevant information to be sustained for several seconds [30]. Unlike long-term memory, working memory has a very limited capacity because its purpose is to only remember what is most important right now, so that our behavior is guided only by what is most important. The PFC integrates information from multiple senses, and across time [31, 32]. It also may participate in predicting possible future outcomes based on models of the state of the environment [33]. Furthermore, there appears to exist a gradient of representation within the PFC such that more anterior regions represent more abstract information, or information that is further extended in time, that then feeds back and influences lower levels of the hierarchy [34]. Thus, if one’s long-term goal is to graduate from school, and the more immediate goal is to pass today’s exam, then attention needs to first be focused on when and where the exam will be given, and then on the content necessary to perform well during the exam. A question arises, however, as to how we arrive at those initial goal representations that then influence attentional selection and ultimately allow for successful self-governance. Furthermore, how do we maintain and use those goal representations in the face of distractions that could capture attention despite our best intentions?

The PFC receives inputs from all of the sensory areas, including somatosensory and parietal cortex, which provide feedback about what actions we are currently engaged in and are intending for the future [35]. The PFC also receives inputs from brain areas involved in representing information recalled from long-term memory. These inputs are thought to be integrated and compared in the PFC [36]. This accumulation and integration of evidence about the current environment and how it compares to past experience leads to

the representation in PFC of expected rewards for controlling our attention or other behaviors in a particular way [37]. The representation of behavioral goals and their relationship to the current sensory environment may proactively bias attention in accordance with context-based expectations. For example you may bias your attention toward red things when searching for a friend whom you know to be wearing a red shirt. We may also reactively refresh or refine our representation of the information that we need to affectively bias our attention to reach our goals when certain stimuli inform us that our current biases are not effective. For example, you may add hair color to shirt color in your representation of things that should draw your attention after being distracted during your search for your friend by other individuals who happen to be wearing red [38].

In summary, the determination of relevance arises from the accumulation of evidence from all of the brain areas representing sensory inputs, memories, and expected rewards. Our understanding of the current situation and predicted future outcomes then biases the competition among sensory representations in areas such as visual cortex. We argue that it is this accumulation of evidence that forms the basis of our goals and beliefs. In other words, we learn from this evidence what the nature of the world is and what behaviors tend to result in good or bad outcomes in different situations. As defined above, comparing an individual’s actual actions in a particular situation to these goals and beliefs about what behavior should have resulted in a good outcome serves as a metric of self-governance. When we attend to sources of information that we expect to be important for achieving our goals, our behavior may closely match the aspirations and beliefs we have acquired through previous experiences, an indicator of effective self-governance. However, what happens when attention instead selects information that is not relevant to our current goals? Moreover, as discussed above, we may have multiple goals that can at times come into conflict, such as when deciding between a tasty but unhealthy food option (goal of enjoying food) and a healthful but not very tasty food option (goal of becoming more healthy). In such cases for which there exists competition between conflicting goals, the biases introduced by involuntary attentional control processes may hold even greater significance in the determination of behavioral outcomes. The greater input from the involuntarily attended information may tip the balance of the competing representations in favor of that with the most prior

experience and potentially in the direction opposite what we would have chosen had our representation of the world been unbiased by this experience-driven attention.

Up until this point, we have reviewed a number of studies that provide evidence that goal representations, arising from the accumulation of sensory evidence, guide the deployment of attention. Such an account is readily applied to the question of self-governance. Behavioral goals bias competing sensory representations of information in the brain, allowing those sources that are most relevant at any particular moment to receive preferential processing and guide our future behavior.

However, recent research demonstrates that there are multiple factors that influence our attention and our behavior. Explicit goals maintained in working memory or recalled reactively are not always effective in guiding the deployment of attention. For example, it is known that the goal-directed orienting of attention is imprecise, such that we often mistakenly direct our attention to stimuli that only look somewhat like what we actually want to pay attention to [39, 40]. Furthermore, there are limits in the degree to which these deliberately remembered goals can allow us to ignore certain stimuli. Automatic control of attention according to learned reward associations is generally useful for guiding behavior with less effort and more reliability than constantly maintaining goals and the means to achieve them in working memory. Thus, reward learning can improve self-governance. However, the effects of reward learning can also lead to failures of self-governance if one's situation or goals have changed. Next, we examine the evidence that reward learning plays a crucial role in future, automatic attentional selection and discuss its implications for self-governance.

Extrinsic Reward and Attentional Control

Learned reward associations modulate representations of stimuli throughout early visual cortex [41]. Moreover, these reward-based changes in representation are independent of the participant's value ratings of stimuli, suggesting that neural representations of value are at least partially divorced from our subjective valuations. In particular, the actual experienced rewards were a better predictor of visual cortical activity than were explicit value perceptions derived from these

experiences, and these explicit value perceptions were only weakly associated with the actual differential value of the stimuli. In addition to increasing the amplitude of early visual responses, reward history has also been associated with a change in the tuning of neurons in early visual areas, presumably allowing for better discrimination between high and low reward stimuli [42]. The visual system may therefore regularly adjust tuning according to reward expectations, thereby influencing the sensory information that is available to guide behavioral decision making.

In addition to altering early sensory representations, associations with reward have been linked to changes in attentional priority. In particular, when behavioral goals and learned reward associations are in agreement, attentional selection is facilitated [43, 44]. Using the N2pc, an event-related potential component in electroencephalography recordings consisting of enhanced contralateral negativity over posterior electrode sites following the deployment of spatial attention [45], Kiss and colleagues measured whether reward associations modulated the time course and strength of attentional selection. Participants completed a visual search task in which color-defined targets were associated with either high or low magnitude monetary rewards. High-value targets were associated with earlier and stronger N2pc components than were low-value targets, suggesting that participants deployed attention earlier and more robustly to the high-value targets than to the low-value targets [43]. Moreover, priming of pop-out, a phenomenon in which repeated presentations of a salient target leads to more efficient selection [46], is enhanced for targets associated with comparatively high monetary value [47], providing further evidence that is consistent with more robust processing of stimuli that are currently associated with reward. One way to interpret these findings is that extrinsic reward provides an incentive that enhances the pertinence of current goals, priorities, and moral considerations, thereby facilitating attention in a way that promotes self-governance when goals are consistent with reward associations.

Other research suggests that attending and ignoring biases can become habitual when reinforced by a reward structure. Della Libera and Chelazzi trained participants to associate target and distractor stimuli with monetary rewards. In a follow-up test phase in which participants no longer received rewards, stimuli that were previously rewarded as targets were more interfering when later presented as distractors than stimuli that were not

associated with reward. However, those stimuli that were previously associated with high reward when ignored during training were more easily ignored during the test phase [48]. Thus, reward history can influence attentional priorities, either biasing selection or facilitating ignoring, even when the reward structure is no longer in place to explicitly incentivize performance. Similarly persistent attentional biases were reported by Raymond and O'Brien when examining the selection of stimuli over time [49].

Relatedly, response conflict resolution is also sensitive to reward learning. Krebs, Boehler, and Woldorff showed participants Stroop color word stimuli for which the semantic meaning of the word (e.g. "GREEN") was printed in either a congruent (green) or incongruent (red) ink color [50]. Participants reported the color of the ink, therefore requiring suppression of the irrelevant semantic meaning. Critically, a subset of the ink colors used in the study was associated with monetary rewards. Participants demonstrated increased behavioral interference of the incongruent to-be-ignored semantic meaning when this meaning matched a rewarded ink color, relative to when the incongruent meaning lacked a reward association [50]. Conversely, interference was reduced when the ink color was a more highly reward-associated color. These results provide further evidence that reward associations influence information processing, facilitating self-governance when these associations are consistent with behavioral goals, but critically, impairing performance when they oppose current behavioral goals. In a follow-up study employing functional neuroimaging, researchers found dissociable neural mechanisms for the relevant and irrelevant reward associations, suggesting that dissociable neural systems may play a role in reward-facilitated and reward-impaired cognitive control [51].

Beyond Behavioral Goals: Implicit Reward Associations Involuntarily Guide Attention

In the studies reviewed above, the value-associated stimuli were not explicitly task-irrelevant. That is, participants did not have the explicit goal of ignoring the previously reward-associated stimuli. It is therefore impossible based on these data alone to determine whether learned reward associations can compete with, and even override, behavioral goals. To investigate whether stimulus-reward associations can indeed compete and

win against representations of goals when setting attentional priority, other researchers have used paradigms in which selection of reward-associated targets is in contradiction to current behavioral goals [52–54].

In a typical study, participants first complete a training phase in which they search for color-defined targets in an array of multi-colored distractor items and accumulate monetary rewards for correct target identification (see Fig. 1). Critically, participants receive a high magnitude reward when they select targets of a particular color and a low magnitude reward when they select targets of the other color. Following training, participants complete a test phase in which stimulus color is now irrelevant and they search for a shape-defined target. For one-half of test phase trials, one of the non-targets is rendered in a previously rewarded target color from the training phase, making this item a task-irrelevant distractor. Using this design, Anderson and colleagues found that response times (RT) for trials in which a previously rewarded distractor item was present were slower than were RTs for trials in which the previously rewarded distractor items were absent, reflecting involuntary attentional processing of the distractor [53]. Importantly, since the formerly rewarded color never served as the target in the test phase, the findings cannot be attributed to behavioral goals. Other studies have revealed that value-based attentional priority transfers across experimental tasks [55], involves the spatially-specific processing of the distractor [56], extends to involuntary eye movements [57, 58], and can persist over long periods of time without intervening training [59]. In all cases, learned value associations influenced attentional priority in opposition to the observer's behavioral goals—participants could not resist paying attention to previously rewarded stimuli that they wanted to ignore.

Additional evidence that reward associations influence the deployment of attention in a fashion that is independent of goal-directed control comes from studies of reward priming [48, 60, 61]. In one study, participants searched for the uniquely-shaped item in a search array while receiving rewards for accurate performance [60]. On the majority of trials, one of the non-target items served as a salient color singleton. Critically, the majority and singleton colors sometimes swapped between trials such that the previously ignored color of trial n would become the goal-relevant color of trial $n + 1$. In line with the research described above, participants were slower for color swap trials relative to no color swap

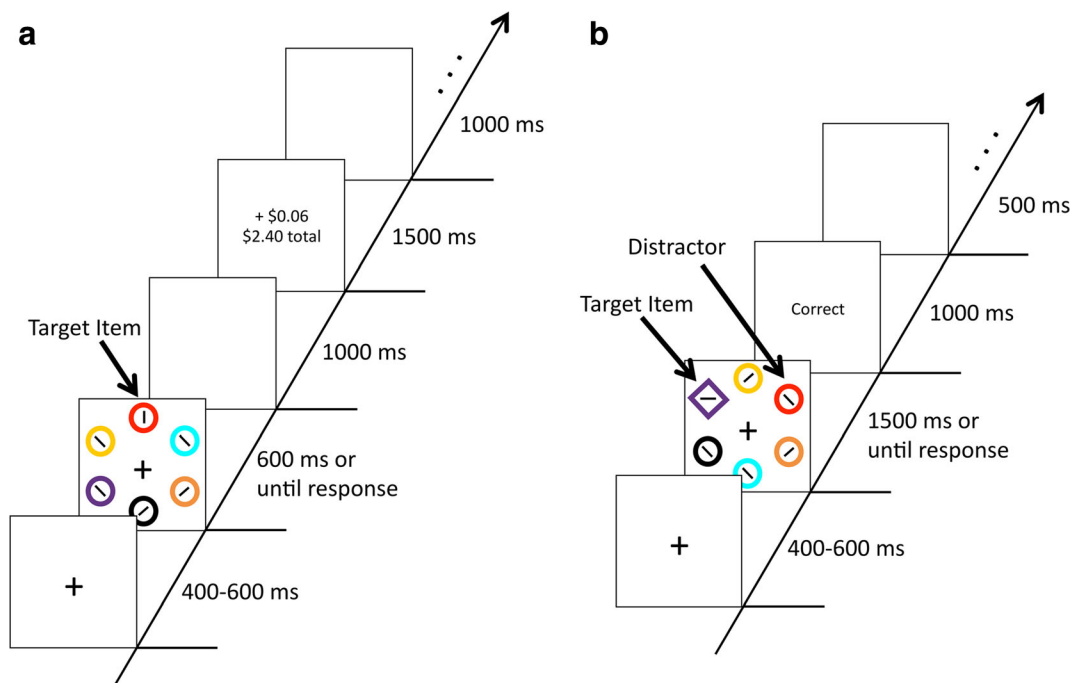


Fig. 1 The value-driven attentional capture paradigm. **(a)** During the training phase, participants searched for a red or green circle target and reported the orientation of the line segment falling within the target. For half of the participants, successfully finding the red target was associated with a high magnitude monetary reward, while successfully finding the green target was associated with a low magnitude monetary reward. The reward-color

relationship was reversed for the remainder of the participants. **(b)** During a subsequent test phase, participants searched for the unique shape in each array. On half of the trials, a non-target item appeared in one of the previously reward-associated colors (distractor present trials), while on the remainder of trials none of the colors had been associated with reward during training (distractor absent trials) [Figure adapted from 53]

trials following a trial in which they received a high magnitude reward. Conversely, the pattern was reversed following low reward trials. The receipt of a high value reward on one trial thus primes greater distraction on the next, even when this priming contradicts behavioral goals [60, 61].

One possible account of value-driven attentional capture is that reward serves as a motivator that speeds up the development of automatic selection habits. This explanation would suggest that the degree to which previously rewarded items capture attention is to some degree dependent on, and a reflection of, the goals of the observer during training. Even in the absence of explicit reward, individuals develop over time the tendency to automatically select items that have repeatedly been behaviorally relevant in the past, reflecting something akin to a perseverating goal. This phenomenon, referred to as perceptual learning, has been observed across a wide range of paradigms and usually occurs following thousands of trials of exposure to a particular stimulus set [62–65]. Although value-driven attentional capture

has been observed following far fewer than the number of trials necessary for traditional perceptual learning, reward serves as a motivator of accurate behavioral performance [66] and reward speeds the rate at which individuals are able to locate targets that are consistent with behavioral goals [43, 47, 67]. Therefore, it is possible that goal-oriented processes, seeking to maximize reward, generally speed the rate at which automatic selection unfolds for simple visual search tasks.

To address this possibility, Sali and colleagues tested participants on a variant of the paradigm developed by Anderson et al. [53, 68]. Critically, across multiple tasks, participants received monetary rewards for visual search that were not uniquely predicted by the target stimulus color. Instead, reward magnitude was either selected randomly from a predetermined distribution, was consistent for all trials, or was based on trial-by-trial performance. One final group of participants completed a version of the task in which target color predicted trial-by-trial reward magnitude as in the earlier work by Anderson and colleagues. Participants demonstrated

significant slowing for distractor present trials relative to distractor absent trials in the test phase only following training in which trial-by-trial target stimulus color predicted reward magnitude, even though they were strongly motivated by reward to select the target during learning in each case [68]. This finding is consistent with animal models of associative reward learning, which state that stimulus-reward associations form only for those stimuli that provide information regarding the receipt of reward that is not redundant with other stimuli in the environment [69, 70]. Thus, attentional biases for reward-related stimuli are learned only when this specific association with a particular stimulus is important for optimizing behavior. The motivational aspects of being in a rewarding context while performing a task with that stimulus are not sufficient to modulate attentional priority in an enduring way.

Although motivation alone does not serve as the mechanism for value-based attentional priority, value-driven attentional capture may still require that participants are motivated to select the reward-associated stimuli during training. To test whether stimuli must be goal relevant to acquire value-based priority, Le Pelley and colleagues employed a clever design in which the color of a salient distractor predicted the size of the reward that would be given for correctly performing a task in which the color of stimuli was explicitly irrelevant [71]. Participants were slower to report a shape-defined target when the high value distractor was present relative to the low value distractor. This effect was true even when selection of the distractor actually resulted in omission of the reward [71–74]. These findings suggest that stimuli do not need to be goal relevant in order for associated rewards to powerfully influence the deployment of attention—reward associations may influence how we process and experience our environment without ever being relevant to our behavioral goals.

The above findings have strong implications for the role value-driven attention plays in self-governance. The rapid value-based instantiation of attentional priority described above suggests that implicitly learned reward associations can counteract explicit goal-oriented attentional control processes. We may attend to a source of information if it was associated with reward in the past even if that information actually conflicts with our current behavioral goals. For example, although we may pay attention to specific food items when it is our goal to eat them, the rewarding experience of consuming particular foods can cause those foods to later capture our

attention even if they conflict with a diet we are currently on. Furthermore, we may not always be consciously aware of these involuntary attentional selections [75–77]. In this way, reward history likely plays an important role in determining which information about the environment receives attentional selection. These attentional biases play a particularly important role when goal representations conflict, tipping the balance in competition between potential behavioral outcomes according to an incomplete and often skewed representation of the current state of the world. It is important to note that not all decisions require evaluation of information about the current state of the world and may instead place greater weight on previous experiences, but such prior experiences must also be selectively recalled from memory from amongst competing alternatives, and this selection process is similarly subject to bias [78], including biases driven by reward history [79–82]. Even the decisions we make with our goals in mind are susceptible to the influence of biased attentional selections. With information from sources that may directly oppose our current goals, our behavior may deviate from the decisions our aspirations and moral responsibilities would lead us to make given a complete and unbiased representation of the environment.

Reward Biases Attention Unequally Across Individuals

Also relevant to the control of attention, as it applies to the concept of self-governance, is the issue of individual responsibility. Perhaps we are biased by reward history to process certain sources of information more readily than other sources, but if we are all similarly subject to the same sort of biases, maybe we are all equally accountable for our failures to uphold principles we believe to be important. Recent findings suggest that this assumption is also not without serious challenges. One prominent challenge can be found in the case of drug addiction. It is well known that chronically drug-dependent individuals have great difficulty ignoring stimuli associated with their drug of abuse [83], and the magnitude of such attentional biases in an individual predicts whether that individual will relapse during treatment [84, 85]. In particular, addicted individuals may simultaneously have the goal of being healthy as well as the goal of relieving craving and withdrawal symptoms. In such cases, involuntary attentional

selections may tip the balance of competition between conflicting goal representations, such that paying attention to drug-associated stimuli in turn draws attention to craving and withdrawal symptoms, thus increasing the likelihood that the individual will use the drug [86]. This example is very contextually specific, however, and an important question that arises is whether some people are more susceptible to reward-related attention biases in general, and thus a greater tendency towards chronic maladaptive behavior, than others.

It turns out that drug-dependent patients also exhibit a reduced ability to ignore stimuli previously associated with non-drug (monetary) reward compared to individuals who are not struggling with drug dependence [76], suggesting a broader bias to attend to irrelevant information that was previously associated with reward. The same is true for individuals who are not currently drug dependent but have a history of drug dependence [77], suggesting that such attentional biases reflect a stable individual trait that does not come and go as a consequence of active drug use. The magnitude of reward-related attentional biases also predicts impulsive non-planning behaviors (e.g., acting without considering the consequences) [77], providing further evidence that these biases are relevant to failures to exert self-control. Susceptibility to attentional capture by previously rewarded stimuli also changes over the lifespan, being greater in adolescents than in young adults [87], reflecting age-related changes in risky decision-making. When it comes to our ability to exert control over the information that we pay attention to, it would appear that the playing field is unequal—some people may be more capable of self-governance than others.

Environmental Influences on Attentional Control

A final area of research on reward-related attentional capture with implications regarding the regulation of behavior is the role of the environment in shaping the deployment of attention. If an individual learns to associate a particular stimulus feature in one environmental context with reward, does that mean that this bias will color perception in all contexts? Recent evidence suggests that value-driven attentional priority is context specific [75]. Participants learned to associate stimulus color with monetary rewards, as in earlier studies. However, a background scene (either a city or forest image) predicted which of two potential target colors

could be rewarded if present. In a subsequent unrewarded test phase, reward-associated distractors only captured attention if they appeared in the context for which they were rewarded in the past. Contextual cues therefore play a role in determining the degree to which reward associations guide our behavior. This finding is important for self-governance because it suggests that reward associations are called upon to guide behavior only for contexts in which these associations were previously experienced. It also implies that the prior reward associations that guide attention are activated by the experience of a physical environment, rather than the kind of reward expectations that are under voluntary control, suggesting that unbiased self-governance may be more feasible in certain situations compared to others.

Other recent evidence has suggested that environmental structure may also influence how effectively our goals influence attentional selection. Across a series of studies, researchers manipulated the statistical structure of a goal-directed attentional orienting paradigm such that participants were more likely to be cued to perform a spatial shift of attention either at particular moments in time or in particular contexts [88]. In support of an environmental influence on preparatory goal-directed control, participants were more efficient at shifting attention in contexts that had previously been associated with the need to frequently shift attention than in contexts previously associated with maintaining a stable focus of attention. The statistical regularities of an environment, and their associated demands on selection, may therefore influence the degree to which an individual is able to quickly shift the current focus of attention. Once we learn that shifting or maintaining the focus of attention is advantageous in a particular situation, we have a strong tendency to bias future attention allocation accordingly.

Of course, as discussed earlier, these automatic and unconscious influences on attention can be (at least eventually) overridden by voluntary control. The better one is able to keep in mind one's goals and explicit reward expectations for the current situation, the better one will be able to refocus attention away from irrelevant information. As discussed earlier, this ability is referred to as working memory, and it depends on neural activity patterns in the PFC that represent information that we are consciously aware is important to the current task. The strength and specificity of these patterns of activity influences the degree to which working memory representations are able to guide attention and behavior.

The ability to guide attention according to the contents of working memory is also variable across individuals and variable within an individual at different ages [89] and in different circumstances. For example, stress is known to modulate the degree to which PFC-mediated working memory representations guide behavior relative to basal ganglia-dependent habitual responses [90], which includes value-driven attentional orienting [91–93]. Researchers have proposed that our ability to maintain information in working memory (such as behavioral goals) follows an inverted U-shaped curve of D1 receptor activity in both non-human primates and humans [94]. Under conditions of high stress, elevated levels of noradrenaline and dopamine impair executive functioning that is carried out in the PFC, but strengthen fear conditioning that is mediated by subcortical structures such as the amygdala [90]. The overall availability of dopamine and other neuromodulators, and their receptors, also varies genetically, and the combinations of several different genetic variations influence both PFC function and decision-making [95]. Our ability to control behavior in accordance with our goals and concept of morality therefore diminishes in periods of stress, and may overall be stronger in some individuals than others.

Conclusions

In order to consistently make decisions that reflect our goals and values, we need to gather the information necessary to guide these decisions, and ignore information that is irrelevant. Although the momentary acquisition of irrelevant information will not likely change our goals, biases in attentional selection may still profoundly influence behavioral outcomes, tipping the balance between competing options when faced with a single goal (e.g., save the least competent swimmer) or between simultaneously competing goals (e.g., relieve drug craving and withdrawal symptoms vs. maintain abstinence). An important component of self-governance might, therefore, be the ability to exert control over how we represent our world as we consider different potential courses of action. Our experiences throughout our lives shape our goals and values, and this can explicitly bias how we choose to interpret the world. One who is successful at self-governance will still be influenced, for good or ill, by these experiences. As we have argued here, however, our history also biases the information that we have access to in ways

that are beyond control and awareness. The information that influences our decisions about which course of action to take is subject not only to the influence of our explicitly held goals and values. At times unconscious biases in information processing can be in direct opposition to what we think we are paying attention to. Furthermore, some individuals seem more prone to failures to ignore task-irrelevant stimuli than others. This individual variability can be driven both by differences in the degree of capture by previously rewarded stimuli and by differences in the degree to which we can maintain our explicit, current goals in working memory in order to override such distraction.

In light of these findings, the concept of self-governance needs to be understood within a framework in which the individual may be operating with incomplete information and with certain sources of information more strongly represented than others. Two people with the same goals and values but with different learning histories may experience the same situation differently, leading them to different conclusions or actions. And the control each individual has over this process is not without limits, nor is it necessarily equal across individuals. Neither case necessarily reflects a failure of self-governance, even if the individual would have decided differently if they had complete and unbiased access to all information relevant to a particular situation. Rather, such a reality demands that the congruence between actions and a person's ethical and moral principles, which we often use as a standard for successful self-governance, be tempered with the understanding that how a situation is experienced is not entirely a matter over which self-control is possible.

Compliance with Ethical Standards

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Conflict of Interest The authors declare that they have no conflict of interest.

References

1. Mack, A., and Irvin Rock. 1998. *Inattention blindness*. Cambridge: MIT Press.
2. Rensink, R.A., J. Kevin O'Regan, and James J. Clark. 1997. To see or not to see: the need for attention to perceive changes in scenes. *Psychological Science* 8: 368–373.

3. Gottlieb, J., Mary Hayhoe, Okihide Hikosaka, and Antonio Rangel. 2014. Attention, reward, and information seeking. *Journal of Neuroscience* 34: 15497–15504.
4. Krajbich, I., Carrie Armel, and Antonio Rangel. 2010. Visual fixations and the computation and comparison of value in simple choice. *Nature Neuroscience* 13: 1292–1298.
5. Krajbich, I., and Antonio Rangel. 2011. Multialternative drift-diffusion model predicts the relationship between visual fixations and choice in value-based decisions. *Proceedings of the National Academy of Sciences* 108: 13852–13857.
6. Krajbich, I., Dingchao Lu, Colin Camerer, and Antonio Rangel. 2012. The attentional drift diffusion model extends to simple purchasing decisions. *Frontiers in Cognitive Science* 3: 193.
7. Yantis, Steven, and John Jonides. 1984. Abrupt visual onsets and selective attention: evidence from visual search. *Journal of Experimental Psychology: Human Perception and Performance* 10: 601–621.
8. Yantis, Steven, and John Jonides. 1990. Abrupt visual onsets and selective attention: voluntary versus automatic allocation. *Journal of Experimental Psychology: Human Perception and Performance* 16: 121–134.
9. Egeth, Howard E., and Steven Yantis. 1997. Visual attention: control, representation, and time course. *Annual Review of Psychology* 48: 269–297.
10. Duncan, John, and Glyn W. Humphreys. 1989. Visual-search and stimulus similarity. *Psychological Review* 96: 433–458.
11. Itti, Laurent, and Christof Koch. 2001. Computational modeling of visual attention. *Nature Reviews Neuroscience* 2: 194–203.
12. Theeuwes, Jan. 1992. Perceptual selectivity for color and form. *Perception & Psychophysics* 51: 599–606.
13. Theeuwes, Jan. 1994. Stimulus-driven capture and attentional set - selective search for color and visual abrupt onsets. *Journal of Experimental Psychology: Human Perception and Performance* 20: 799–806.
14. Folk, Charles L., Rodger W. Remington, and James C. Johnston. 1992. Involuntary covert orienting is contingent on attentional control settings. *Journal of Experimental Psychology: Human Perception and Performance* 18: 1030–1044.
15. Folk, Charles L., Andrew B. Leber, and Howard E. Egeth. 2002. Made you blink! contingent attentional capture produces a spatial blink. *Perception & Psychophysics* 64: 741–753.
16. Serences, John T., Sarah Shomstein, Andrew B. Leber, Xavier Golay, Howard E. Egeth, and Steven Yantis. 2005. Coordination of voluntary and stimulus-driven attentional control in human cortex. *Psychological Science* 16: 114–122.
17. Wolfe, Jeremy M., Kyle R. Cave, and Susan L. Franzel. 1989. Guided search: An alternative to the feature integration model for visual search. *Journal of Experimental Psychology: Human Perception and Performance* 15: 419–433.
18. Bacon, William F., and Howard E. Egeth. 1994. Overriding stimulus-driven attentional capture. *Perception & Psychophysics* 55: 485–496.
19. Leber, Andrew B., and Howard E. Egeth. 2006. It's undercontrol: top-down search strategies can override attentional capture. *Psychonomic Bulletin & Review* 13: 132–138.
20. Desimone, Robert, and John Duncan. 1995. Neural mechanisms of selective visual attention. *Annual Review of Neuroscience* 18: 193–222.
21. Reynolds, John H., Leonardo Chelazzi, and Robert Desimone. 1999. Competitive mechanisms subserve attention in macaque areas V2 and V4. *Journal of Neuroscience* 19: 1736–1753.
22. Cohen, Jonathan D., William M. Pearstein, Todd S. Braver, Leigh E. Nystrom, Douglas C. Noll, John Jonides, and Edward E. Smith. 1997. Temporal dynamics of brain activation during a working memory task. *Nature* 386: 604–608.
23. Courtney, Susan M., Laurent Petit, José M. Maisog, Leslie G. Ungerleider, and James V. Haxby. 1998. An area specialized for spatial working memory in human frontal cortex. *Science* 279: 1347–1351.
24. Courtney, Susan M., Leslie G. Ungerleider, Katrina Keil, and James V. Haxby. 1997. Transient and sustained activity in a distributed neural system for human working memory. *Nature* 386: 608–611.
25. D'Esposito, Mark, Brad R. Postle, Dana Ballard, and Jessica Lease. 1999. Maintenance versus manipulation of information held in working memory: An event-related fMRI study. *Brain and Cognition* 41: 66–86.
26. Miller, Earl K., Cynthia A. Erickson, and Robert Desimone. 1996. Neural mechanisms of visual working memory in prefrontal cortex of the macaque. *Journal of Neuroscience* 16: 5154–5167.
27. Montojo, Caroline A., and Susan M. Courtney. 2008. Differential neural activation for updating rule versus stimulus information in working memory. *Neuron* 59: 173–182.
28. Rainer, Gregor, Wael F. Asaad, and Earl K. Miller. 1998. Selective representation of relevant information by neurons in the primate prefrontal cortex. *Nature* 393: 577–579.
29. Wallis, Jonathan D., Kathleen C. Anderson, and Earl K. Miller. 2001. Single neurons in prefrontal cortex encode abstract rules. *Nature* 411: 953–956.
30. Goldman-Rakic, Patricia S. 1995. Cellular basis of working memory. *Neuron* 14: 477–485.
31. Sala, Joseph B., and Susan M. Courtney. 2007. Binding of what and where during working memory maintenance. *Cortex* 43: 5–21.
32. Fuster, Joaquin M. 2001. The prefrontal cortex – An update: time is of the essence. *Neuron* 30: 319–333.
33. Jan, Gläscher, Nathaniel Daw, Peter Dayan, and John P. O'Doherty. 2010. States versus rewards: dissociable neural prediction error signals underlying model-based and model-free reinforcement learning. *Neuron* 66: 585–595.
34. Badre, David, and Mark D'Esposito. 2009. Is the rostro-caudal axis of the frontal lobe hierarchical? *Nature Reviews Neuroscience* 10: 659–669.
35. Michael, Desmurget, and Angela Sirigu. 2009. A parietal-premotor network for movement intention and motor awareness. *Trends in Cognitive Science* 13: 411–419.
36. Miller, Earl K., and Jonathan D. Cohen. 2001. An integrative theory of prefrontal cortex function. *Annual Review in Neuroscience* 24: 167–202.
37. Dixon, Matthew L., and Kalina Christoff. 2012. The decision to engage cognitive control is driven by expected reward-value: neural and behavioral evidence. *PloS one* 7: e51637.
38. Braver, Todd S., Jeremy R. Gray, and C. Burgess Gregory. 2007. Explaining the many varieties of working memory variation: Dual mechanisms of cognitive control. In

- Variation in working memory*, eds. A. Conway, C. Jarrold, M. Kane, A. Miyake, and J. Towse, 76–106. New York: Oxford University Press.
39. Anderson, Brian A. 2014. On the precision of goal-directed attentional selection. *Journal of Experimental Psychology: Human Perception and Performance* 40: 1755–1762.
 40. Anderson, Brian A., and Charles L. Folk. 2010. Variations in the magnitude of attentional capture: testing a two-process model. *Attention, Perception, & Psychophysics* 72: 342–352.
 41. Serences, John T. 2008. Value-based modulations in human visual cortex. *Neuron* 60: 1169–1181.
 42. Serences, John T., and Sameer Sapru. 2010. Population response profile in early visual cortex are biased in favor of more valuable stimuli. *Journal of Neurophysiology* 104: 76–87.
 43. Kiss, Monica, Jon Driver, and Martin Eimer. 2009. Reward priority of visual target singletons modulates event-related potential signatures of attentional selection. *Psychological Science* 20: 245–251.
 44. Navalpakkam, Vidhya, Christof Koch, Antonio Rangel, and Pietro Perona. 2010. Optimal reward harvesting in complex perceptual environments. *Proceedings of the National Academy of Sciences of the United States of America* 107: 5232–5237.
 45. Woodman, Geoffrey F., and Steven J. Luck. 1999. Electrophysiological measurement of rapid shifts of attention during visual search. *Nature* 400: 867–869.
 46. Maljkovic, Vera, and Ken Nakayama. 1994. Priming of pop-out: I. role of features. *Memory and Cognition* 22: 657–672.
 47. Kristjansson, Árni, Ólafía Sigurjonsdóttir, and Jon Driver. 2010. Fortune and reversals of fortune in visual search: reward contingencies for pop-out targets affect search efficiency and target repetition effects. *Attention, Perception, & Psychophysics* 72: 1229–1236.
 48. C., Della Libera, and Leonardo Chelazzi. 2009. Learning to attend and to ignore is a matter of gains and losses. *Psychological Science* 20: 778–784.
 49. Raymond, Jane E., and Jennifer L. O'Brien. 2009. Selective visual attention and motivation: the consequences of value learning in an attentional blink task. *Psychological Science* 20: 981–988.
 50. Krebs, Ruth M., Carsten N. Boehler, and Marty G. Woldorff. 2010. The influence of reward associations on conflict processing in the stroop task. *Cognition* 117: 341–347.
 51. Krebs, Ruth M., Carsten N. Boehler, Tobias Egner, and Marty G. Woldorff. 2011. The neural underpinnings of how reward associations can both guide and misguide attention. *Journal of Neuroscience* 31: 9752–9759.
 52. Anderson, Brian A., Patryk A. Laurent, and Steven Yantis. 2011a. Learned value magnifies salience-based attentional capture. *PloS One* 6: e27926.
 53. Anderson, Brian A., Patryk A. Laurent, and Steven Yantis. 2011b. Value-driven attentional capture. *Proceedings of the National Academy of Sciences of the United States of America* 108: 10367–10371.
 54. Anderson, Brian A. 2013. A value-driven mechanism of attentional selection. *Journal of Vision* 13: 1–16.
 55. Anderson, Brian A., Patryk A. Laurent, and Steven Yantis. 2012. Generalization of value-based attentional priority. *Visual Cognition* 20: 647–658.
 56. Failing, Michael F., and Jan Theeuwes. 2014. Exogenous visual orienting by reward. *Journal of Vision* 14: 1–9.
 57. Anderson, Brian A., and Steven Yantis. 2012. Value-driven attentional and oculomotor capture during goal-directed, unconstrained viewing. *Attention, Perception, & Psychophysics* 74: 1644–1653.
 58. Theeuwes, Jan, and Artem V. Belopolsky. 2012. Reward grabs the eye: oculomotor capture by rewarding stimuli. *Vision Research* 74: 80–85.
 59. Anderson, Brian A., and Steven Yantis. 2013. Persistence of value-driven attentional capture. *Journal of Experimental Psychology: Human Perception and Performance* 39: 6–9.
 60. Hickey, Clayton, Leonardo Chelazzi, and Jan Theeuwes. 2010a. Reward changes salience in human vision via the anterior cingulate. *Journal of Neuroscience* 30: 11096–11103.
 61. Hickey, Clayton, Leonardo Chelazzi, and Jan Theeuwes. 2010b. Reward guides vision when it's your thing: trait reward-seeking in reward-mediated visual priming. *PloS One* 5: e14087.
 62. Kyllingsbaek, Søren, Werner X. Schneider, and Claus Bundesen. 2001. Automatic attraction of attention to former targets in visual displays of letters. *Perception & Psychophysics* 12: 763–764.
 63. Roelfsema, Pieter R., Arjen van Ooyen, and Takeo Watanabe. 2010. Perceptual learning rules based on reinforcers and attention. *Trends in Cognitive Sciences* 14: 64–71.
 64. Shiffrin, Richard M., and Walter Schneider. 1977. Controlled and automatic human information processing: II. perceptual learning, automatic attending, and a general theory. *Psychological Review* 84: 127–190.
 65. Watanabe, Takeo, José E. Náñez, and Yuka Sasaki. 2001. Perceptual learning without perception. *Nature* 413: 844–848.
 66. Jimura, Koji, Hannah S. Locke, and Todd S. Braver. 2010. Prefrontal cortex mediation of cognitive enhancement in rewarding motivational contexts. *Proceedings of the National Academy of Sciences of the United States of America* 107: 8871–8876.
 67. Pessoa, Luiz, and Jan B. Engelmann. 2010. Embedding reward signals into perception and cognition. *Frontiers in Neuroscience* 4: 1–8.
 68. Sali, Anthony W., Brian A. Anderson, and Steven Yantis. 2014. The role of reward prediction in the control of attention. *Journal of Experimental Psychology: Human Perception and Performance* 40: 1654–1664.
 69. Kamin, Leon J. (1969). Punishment and aversive behavior. B. A. Campbell, R. M. Church Appleton-Century-Crofts, New York. 279–296.
 70. Pearce, John M., and Geoffrey Hall. 1980. A model for pavlovian learning: variations in the effectiveness of conditioned but not of unconditioned stimuli. *Psychological Review* 87: 532–552.
 71. Pelley, Le, E. Mike, Daniel Pearson, Oren Griffiths, and Tom Beesley. 2015. When goals conflict with values: counterproductive attentional and oculomotor capture by reward-related stimuli. *Journal of Experimental Psychology: General* 144: 158–171.
 72. Buckner, Berno, Artem V. Belopolsky, and Jan Theeuwes. 2014. Distractors that signal reward attract the eyes. *Visual Cognition* 23: 1–24.

73. Mine, Chisato, and Jun Saiki. 2015. Task-irrelevant stimulus-reward association induces value-driven attentional capture. *Attention, Perception, & Psychophysics* 77: 1896–1907.
74. Pearson, Daniel, Chris Donkin, Sophia C. Tran, Steven B. Most, and Michael E. Le Pelley. 2015. Cognitive control and counterproductive oculomotor capture by reward-related stimuli. *Visual Cognition* 23: 41–66.
75. Anderson, Brian A. 2015. Value-driven attentional priority is context specific. *Psychonomic Bulletin and Review* 22: 750–756.
76. Anderson, Brian A., Monica L. Faulkner, Jessica J. Rilee, Steven Yantis, and Cherie L. Marvel. 2013. Attentional bias for non-drug reward is magnified in addiction. *Experimental and Clinical Psychopharmacology* 21: 499–506.
77. Anderson, Brian A., Sharif I. Kronemer, Jessica J. Rilee, Ned Sacktor, and Cherie L. Marvel. In press. Reward, attention, and HIV-related risk in HIV+ individuals. *Neurobiology of Disease* doi:10.1016/j.nbd.2015.10.018.
78. Gluth, Sebastian, Tobias Sommer, Jörg Rieskamp, and Christian Büchel. 2015. Effective connectivity between hippocampus and ventromedial prefrontal cortex control preferential choices from memory. *Neuron* 86: 1078–1090.
79. Gong, M., and Sheng Li. 2014. Learned reward association improves visual working memory. *Journal of Experimental Psychology: Human Perception and Performance* 40: 841–856.
80. Infanti, E., Clayton Hickey, and Massimo Turatto. 2015. Reward associations impact both iconic and visual working memory. *Vision Research* 107: 22–29.
81. Doallo, S., Eva Z. Patai, and Anna C. Nobre. 2013. Reward associations magnify memory-based biases on perception. *Journal of Cognitive Neuroscience* 25: 245–257.
82. Thomas, P. M. J., Lily FitzGibbon, and Jane E. Raymond. 2016. Value conditioning modulates visual working memory processes. *Journal of Experimental Psychology: Human Perception and Performance* 42:6–10
83. Field, Matt, and W. Miles Cox. 2008. Attentional bias in addictive behaviors: A review of its development, causes, and consequences. *Drug and Alcohol Dependence* 97: 1–20.
84. Carpenter, Kenneth M., Elizabeth Schreiber, Sarah Church, and David McDowell. 2006. Drug Stroop performance: relationships with primary substance of use and treatment outcome in a drug-dependent outpatient sample. *Addictive Behaviors* 31: 174–181.
85. Marissen, Marlies A.E., Ingmar H.A. Franken, Andrew J. Waters, Peter Blanken, Wim van den Brink, and Vincent M. Hendriks. 2006. Attentional bias predicts heroin relapse following treatment. *Addiction* 101: 1306–1312.
86. Robinson, T.E., and Kent C. Berridge. 1993. The neural basis of drug craving: an incentive-sensitization theory of addiction. *Brain Research Reviews* 18: 247–291.
87. Roper, Zachary J.J., Shaun P. Vecera, and Jatin G. Vaidya. 2014. Value-driven attentional capture in adolescence. *Psychological Science* 25: 1987–1993.
88. Sali, Anthony W., Brian A. Anderson, and Steven Yantis. 2015. Learned states of preparatory attentional control. *Journal of Experimental Psychology: Learning, Memory, and Cognition* 41: 1790–1805.
89. McNab Fiona, Peter Zeidman, Robb B. Rutledge, Peter Smittenaar, Harriet R. Brown, Rick A. Adams, and Raymond J. Dolan. 2015. Age-related changes in working memory and the ability to ignore distraction. *Proceedings of the National Academy of Sciences of the United States of America* 112: 6515–6518.
90. Arnsten Amy, F.T. 2009. Stress signalling pathways that impair prefrontal cortex structure and function. *Nature Reviews Neuroscience* 10: 410–422.
91. Anderson, Brian A., Patryk A. Laurent, and Steven Yantis. 2014. Value-driven attentional priority signals in human basal ganglia and visual cortex. *Brain Research* 1587: 88–96.
92. Anderson, Brian A., Hiroto Kuwabara, Dean F. Wong, Emily G. Gean, Rahmim Arman, James R. Brasic, Noble George, Boris Frolov, Susan M. Courtney, and Steven Yantis. 2016. The role of dopamine in value-based attentional orienting. *Current Biology*. 26: 550–555.
93. Hikosaka, Okihide, Shinya Yamamoto, Masaharu Yasuda, and Hyoungh F. Kim. 2013. Why skill matters. *Trends in Cognitive Sciences* 17: 434–441.
94. Vijayraghavan, Susheel, Min Wang, Shari G. Birbaum, Graham V. Williams, and Amy F.T. Arnsten. 2007. Inverted-U dopamine D1 receptor actions on prefrontal neurons engaged in working memory. *Nature Neuroscience* 10: 376–384.
95. Kohno, Milky, Erika L. Nurmi, Christopher P. Laughlin, Angelica M. Morales, Emma H. Gail, Gerhard S. Hellemann, and Edythe D. London. 2016. Functional genetic variation in dopamine signaling moderates prefrontal cortical activity during risky decision making. *Neuropsychopharmacology* 41: 695–703.