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Neural circuitry of information seeking

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Abstract

Humans and animals navigate uncertain environments by seeking information about the future. Remarkably, we often seek information even when it has no instrumental value for aiding our decisions – as if the information is a source of value in its own right. In recent years, there has been a flourishing of research into these non-instrumental information preferences and their implementation in the brain. Individuals value information about uncertain future rewards, and do so for multiple reasons, including valuing resolution of uncertainty and overweighting desirable information. The brain motivates this information seeking by tapping into some of the same circuitry as primary rewards like food and water. However, it also employs cortex and basal ganglia circuitry that predicts and values information as distinct from primary reward. Uncovering how these circuits cooperate will be fundamental to understanding information seeking and motivated behavior as a whole, in our increasingly complex and information-rich world.

Keywords

uncertainty; information; information seeking; temporal resolution of uncertainty; observing response; cingulate; striatum; pallidum; orbitofrontal; habenula; Dopamine

Humans and animals navigate uncertain environments by seeking information about the future. Of course, this is partly due to the *instrumental* value of information to help us choose better actions [1–5]. Remarkably, however, we can be strongly motivated to seek information even when we know there is no way to use it to influence our future actions and outcomes – as if knowledge is a source of value in its own right. Many of us have the experience of voting in an election, knowing there is nothing more we can do to influence the outcome, and telling ourselves we should get a good night’s sleep and find out in the morning...and instead, staying up late into the night with our eyes glued to the TV screen, in order to get the information the first moment it becomes available.

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More than ten years ago, neuroscientists began to study how these preferences for *non-instrumental* information are encoded by single neurons in the brain, focusing on information about uncertain rewards [6]. In its simplest form, this preference can be measured by giving a choice between two offers, one of which provides informative cues that indicate the reward outcome in advance, while the other provides non-informative cues that do not indicate the outcome (Figure 1A). Importantly, both offers provide exactly the same reward distribution, and there is no way to use the information to influence the outcome. Yet both humans and animals can strongly prefer information (Figure 1B) and willingly pay a price for it [7–10], assigning it considerable value in their decisions (Figure 1C).

At the time non-instrumental information seeking had a long history in several fields. In psychology it was called a form of “observing behavior” [11] and was primarily studied in rats and pigeons [10,12–14]. In economics it was called “temporal resolution of uncertainty” [15] or informational attitude, and was primarily studied in theoretical models and surveys [16–18], with studies beginning to examine choices with real consequences [7]. Developmental psychology and machine learning also studied the importance of intrinsic motivation for learning about the world [19,20]. However, these literatures were largely independent, approaching the phenomenon and interpreting their findings in very different frameworks, with surprisingly little communication between them. This made it difficult to pool their knowledge to understand how informational preferences are created by neural circuits in the brain.

In the last few years this picture has changed dramatically. There has been an explosion of research on information seeking in neuroscience, bringing together researchers from different backgrounds to bridge the gap between these diverse fields, and a flourishing of new discoveries. This has been especially true for information seeking about a specific type of future event – uncertain rewards – which has become the target of systematic and comparative neuroscientific studies in both humans and animals. Here we highlight advances in understanding the mechanisms that motivate this form of information seeking, and their neural implementations in the brain.

Neural networks integrating information and primary reward

Early neuroscience studies of information seeking in monkeys focused on the “reward prediction error” (RPE) system. The RPE system has a key role in motivating actions to seek primary rewards like food and water, by signaling the difference between a situation’s predicted and actual reward value [21]. The RPE system was shown to have similar signals for information – effectively treating information about uncertain outcomes as a reward in itself [6,22]. For example, just as many midbrain dopamine neurons are excited when a monkey learns that it will get a large water reward (‘more water than predicted’), many are also excited when the monkey learns that it will see an informative cue (‘more information than predicted’; Figure 2B). This suggested that information seeking is motivated by the same RPE circuitry that motivates primary reward seeking.

Recent studies have replicated and greatly extended this finding in humans, uncovering principles by which this network evaluates information. Midbrain regions that contain dopamine neurons have a blood oxygen level dependent (BOLD) signal responding to informational prediction errors [**9]. This signal is sensitive to the subjective value of the information – scaling up for desirable information about likely monetary gains, and scaling down for less desirable information about likely losses. Indeed, the signal strength in a major target of dopamine projections, the ventral striatum, predicts information preferences. This suggests that dopamine projections to basal ganglia may transform prediction errors into motivation to seek information.

This convergence of information and monetary reward processing extends to cortex. Both monetary and informational prediction errors induce electroencephalographic (EEG) signals with strikingly similar spatial and temporal profiles [*23]. This feedback-related negativity originates from medial prefrontal cortex (mPFC), including anterior cingulate cortex (ACC) and supplementary eye field [24,25]. Many mPFC neurons respond to unpredicted outcomes that motivate changes in behavior [25–31] and may regulate evaluation of uncertain rewards [32]. Thus, mPFC may also motivate adjustments in information seeking behavior.

In these cases people sought information with no instrumental value. Could the same network handle information that *does* have instrumental value? This was recently addressed by allowing humans to pay for partial information about a lottery's outcome before deciding whether to accept the lottery [*33]. People valued information for both instrumental and non-instrumental reasons. This combined subjective value of information correlated with BOLD signals in many of the same regions as the value of money. This included the ventral striatum region discussed above and the ventromedial prefrontal cortex. Thus, these areas may represent the total value of information and primary reward to guide decisions.

Neural networks for information seeking

The networks discussed so far may combine information and primary reward into a common currency of total value. However, we can also treat information and primary reward as distinct, separate entities (Fig 1C). After all, when we sit down in a restaurant we are pleased to get the menu or to get the meal itself – but we know exactly which we are expecting, and something is wrong if one comes in place of the other!

Early support for this hypothesis came from evidence that the monkey orbitofrontal cortex (OFC) can encode the distinct values of both *information about primary reward* and *primary reward* itself [8]. This is consistent with evidence that OFC associates cues with the distinct values of different rewards [34–36], and separately encodes the confidence of a decision and its primary reward value [37]. Human OFC regions respond to the availability [**9] and receipt [*38] of information about uncertain rewards. Thus OFC may separately adjust the values of information and primary reward cues – so that hunger leads us to seek signs of food, while curiosity and uncertainty lead us to seek signs of information.

How, then, could the brain create a specific motivation to seek information? It would need to (1) detect when rewards are uncertain, (2) predict when information will become available to resolve the uncertainty, and (3) use this prediction to promote information seeking actions.

A recent study showed evidence for a neural system that carries out these steps, in an anatomically interconnected cortex-basal ganglia network including regions of ACC, dorsal striatum (DS), and pallidum (Pal) [**39]. A subset of neurons there have *information predictive activity*. They activate when monkeys are uncertain about future rewards and ramp up to the time information will arrive to resolve the uncertainty (Figure 2A, red). They have much less activity when rewards are certain or no information is predicted (Figure 2A, gray and blue).

Crucially, this network's activity causally influences information seeking. Monkeys rapidly shift their gaze to view informative cues [6] in a manner sensitive to reward uncertainty [40]. These information seeking gaze shifts are predictive, ramping up to the time of getting information [**39]. The neural information prediction signal is linked to this behavior. Strong neural signals are followed by gaze shifts toward information-related cues, while weak signals are followed by gaze shifts away from them. The signal has no comparable relationship to primary reward seeking. Furthermore, inactivating basal ganglia regions that contain the information signal impairs information seeking gaze shifts. This suggests that the network's information prediction signal specifically motivates and sustains information seeking.

The ACC may have a supervisory role in sustaining information seeking. In the ACC-DS-Pal network its information predictions have early tuning to graded levels of uncertainty, and are the earliest predictor of information-seeking gaze shifts [**39]. ACC activity has been linked to anticipation of multiple pieces of information to resolve reward uncertainty [41], and integrating gathered information to change actions or strategies [42–44].

Furthermore, a recent study implicated ACC in sustained information sampling [**45]. Humans and monkeys were allowed to collect information about choice options before making a final decision. Both species showed evidence of non-instrumental information seeking. After they collected strong evidence favoring a specific option, they did not simply choose it immediately, and instead spent additional time gathering information about its future outcome [**45,46]. In parallel, a subset of monkey ACC neurons tracked how each piece of information influenced the certainty of choosing that favored option, and hence the certainty of receiving that outcome. This activity was prevalent in ACC and rare in OFC and dorsolateral prefrontal cortex, supporting a key role of ACC in information sampling.

How do these networks cooperate to motivate behavior?

We have discussed networks that (1) specifically signal information, and (2) integrate information and primary reward. How do they cooperate to motivate behavior? We propose the following hypothesis (Figure 3).

Cortex-basal ganglia pathways have primary reward predictive neurons that promote primary reward seeking [47–49], and the work reviewed here suggests they contain a parallel process

for information seeking (Figure 3, top). These processes are intermixed, with information and primary reward signals in nearby neurons [**39] and potentially mixed in single neurons. However, there is some clustering. For example, information-related neurons are enriched in a DS region that receives strong ACC projections [**39] and can activate in humans during risky decisions [50].

As a result, these pathways could combine information and primary reward predictions to compute the total predicted reward value that guides decisions. These total reward predictions could also be used to compute RPEs, by sending them directly to the classic RPE system that regulates dopamine, including the lateral habenula, rostromedial tegmental nucleus, and dopamine neurons themselves [51] (Figure 3, bottom; LHb, RMTg, DA). RPE computations could also occur in the cortex-basal ganglia pathway itself, where subsets of neurons have RPE-related signals [52–55]. Indeed, these areas have all been implicated in predicting values, controlling the RPE system, or both [48,55–66].

Neural systems for information prediction and RPEs are well positioned to support each other. Information seeking provides the raw material for predictions, while erroneous predictions indicate the need for new information. In particular, information predictive activity anticipates the moment of gaining information about uncertain future rewards (Figure 2A), and this information immediately triggers a phasic RPE signal based on whether it is better or worse than predicted (Figure 2B). Therefore, information prediction signals may have a special role in preparing the brain to compute and learn from RPEs (Figure 3).

Conversely, RPEs are ideally suited to instruct information predictions (Figure 3). An RPE indicates the receipt of new information about rewards. In classic theories, RPEs instruct learning of *reward* predictions: positive RPEs increase reward predictions, while negative RPEs decrease reward predictions [67]. In principle, however, RPEs could also instruct learning of *information* predictions: large positive and negative RPEs both indicate the receipt of a large amount of information about future reward value, while small RPEs typically indicate the receipt of little information. If so, RPEs could instruct both total reward value predictions and information predictions.

In addition, many dopamine neurons are activated by alerting events, which are important for motivated behavior but do not increase the situation's reward value [68–70] (such as memoranda in a memory task [71], unexpected stop signals [72], and rewards changing flavor [73,74]). Some dopamine neurons are also activated by certain aversive events [70,75–77]. This could motivate information prediction and seeking about these important events as well.

What algorithm does the brain use to calculate the value of information?

We have discussed networks that translate the value of information into motivated behavior. How, then, does the brain decide information's value? Shortly after the discovery of “observing behavior” in 1952 [11], two general theories emerged about the underlying mechanism [78,79] (Figure 1C). These theories have been remarkably durable, emerging in

similar forms in multiple fields. They share the common basis that, since non-instrumental information cannot be used to change the objective rate of gaining primary rewards from the environment, the brain must value information based on how it changes subjective, internal states.

The first theory, proposed by the curiosity research pioneer Daniel Berlyne, is that we value information because it reduces uncertainty [78] (Figure 1C). His original paper suggested computing uncertainty with Shannon's newly invented information theory [80]. Later work proposed alternate computations for uncertainty, often considering its experience and resolution over time [81]. For instance, uncertainty about potential gains and losses may produce anticipatory emotions like hope and anxiety [16–18]. This theory is supported by evidence that uncertainty and its resolution activate cortex-basal ganglia networks in monkeys [**39] (Figure 2A) and multiple cortical areas in humans [*38], and in those settings uncertainty strongly influences information seeking [*38,**39].

The second theory, proposed by the “observing behavior” discoverer L. Benjamin Wyckoff, is that we value information because we overweight desirable information [79] (Figure 1C). In a nutshell, objectively neutral information sources may become subjectively valuable if we overweight their desirable information (‘good news’), or underweight their undesirable information (‘bad news’). The first proposal by economists was a similar mechanism, even suggesting the same equation for overweighting (a squaring nonlinearity) [15]. Later work proposed many mechanisms for overweighting, including selective observing [13], engagement [82], savoring desirable outcomes, and dreading undesirable outcomes [83,84].

An important message of recent work is that individuals may value information about uncertain rewards through *both* mechanisms – in a way that may vary across individuals, species, and situations. For example, information seeking can be tuned to both reward uncertainty and expected reward value, but to different degrees in different studies [**9,*38,40,**85,86]. Even work reporting predominance of uncertainty often finds some effect of expected value [*38,86], while work reporting predominance of ‘good news’ often finds that this requires variance between good news and other possible outcomes [84,87]. Most strikingly, even in a single study, humans have a remarkable diversity of information attitudes: some are guided by uncertainty, some by expected value, and some by both [**85]. Taken together, this work suggests the need for hybrid theories [18,88,89] with flexible mechanisms to value information.

Looking forward

A key goal of future research will be to uncover the neural basis of a broader spectrum of information attitudes. We have discussed information seeking *about uncertain rewards*, but similar neural mechanisms may apply to other events. Humans have similar information seeking about trivia, and even remember trivia better when it evokes a more positive informational prediction error – when it satisfies their curiosity better than predicted [90]. Humans and animals can also seek information about aversive events [91], and humans can have ‘morbid fascination’ with observing the aversive experiences of others [92] that may activate regions of mPFC and OFC [93]. A recent study reported evidence that monkeys

even seek information about counterfactual outcomes – outcomes they *would have* received if they had chosen a different option [*94]. Lastly, we have discussed information *seeking*, but humans and animals sometimes *avoid* information [9,12,95,96], such as avoiding medical screening for disease [95] or refusing to check their stock portfolio during a bear market [**9].

Finally, an important long-term goal will be to discover the evolutionary and developmental origin of information seeking. That is, why do brains develop a motivational system that treats non-instrumental information as valuable? In natural environments, organisms can rarely estimate the instrumental value of a specific piece of information with high precision. This is especially true for unfamiliar environments and important life events, such as moving to a new home, finding a mate, or voting in a national election.

We hypothesize that the brain solves this problem by nudging its estimate of information value toward the value that similar types of information typically have in natural environments. This could be based on the environments the organism encountered during its development, and an evolved prior about the environments its species typically encounters. This would explain why organisms can be well adapted to natural environments, yet persistently seek information in controlled lab experiments where it has no instrumental value.

There is precedent for this phenomenon in neuroscience. ‘Visual illusions’ are often viewed as simple errors in perception, perhaps due to the brain using flawed algorithms for visual processing. Why should we perceive certain objects to be closer than they really are, and others to move slower than they really are? However, when vision scientists measured the natural statistics of visual scenes, they realized that many illusions may actually result from the brain making rational inferences about the world based on its evolved and learned knowledge about the structure of natural environments [97,98]. ‘Most objects move slowly, so err on the side of slowness.’ In a similar manner, non-instrumental information seeking may arise from a ‘value illusion’ as the brain attempts to infer the value of information based on the natural statistics of cues, rewards, and actions. ‘Information about rewards is usually valuable, so err on the side of value.’ If so, then measuring the natural statistics of motivational events would revolutionize our understanding of why we value information, and what rules we use to calculate its value.

Our increasingly interconnected world puts a vast ocean of information at our fingertips. Learning to navigate it is vital for our own happiness and the health of our society. Thus, understanding our informational preferences is becoming increasingly important not only for the sake of scientific discovery, but also society as a whole.

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HIGHLIGHTS

- Humans and animals seek information about uncertain future rewards
- Information is valued for resolving uncertainty and signaling desirable outcomes
- The reward prediction error system integrates information with primary reward
- A cortex-basal ganglia network specifically predicts and drives information seeking

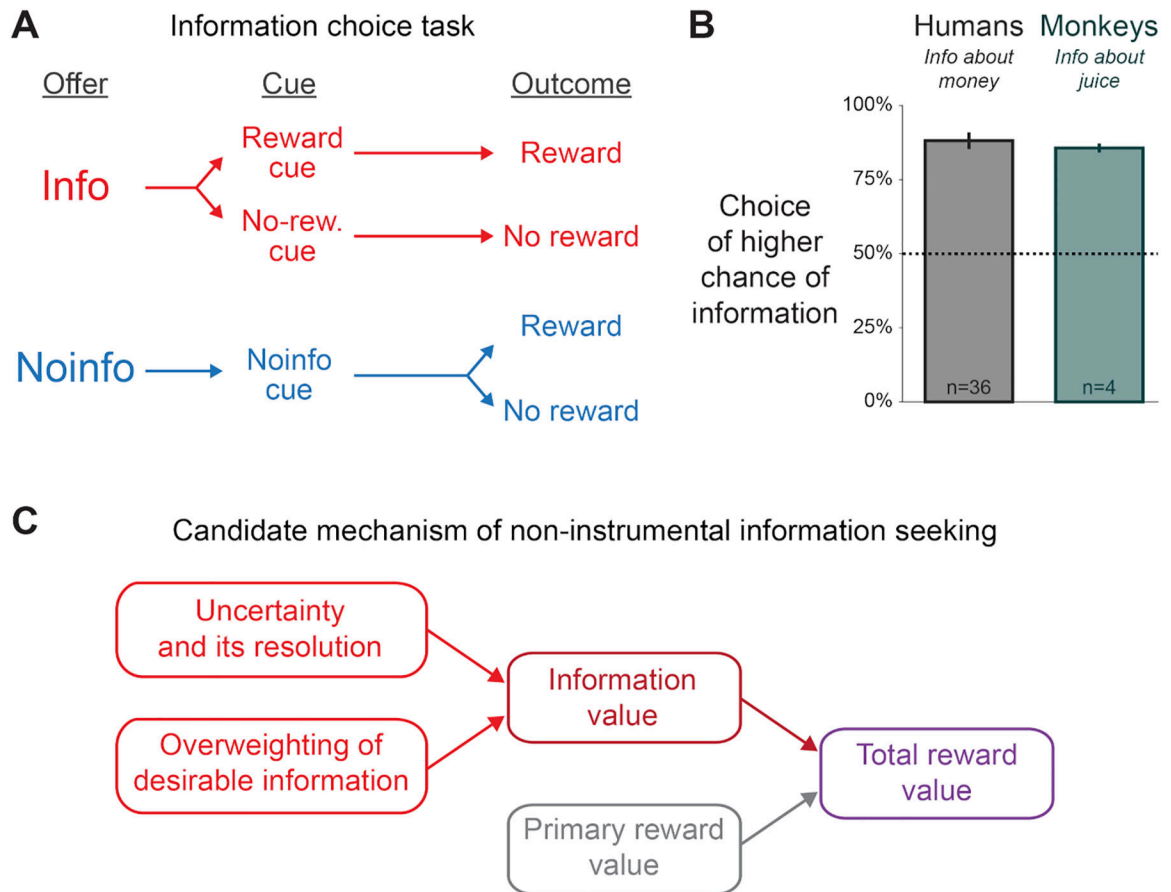
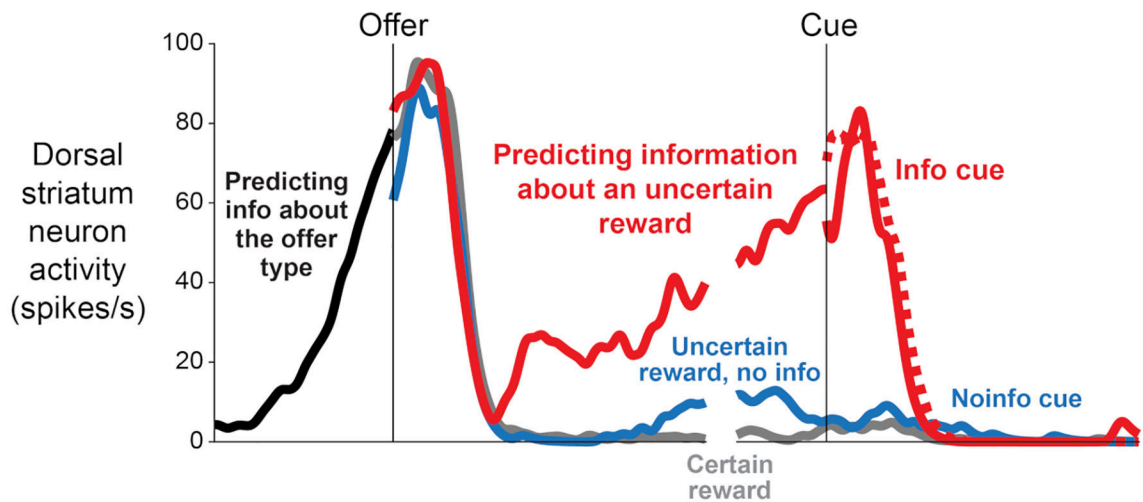


Figure 1. Humans and animals can seek non-instrumental information about uncertain future rewards.

(A) A simple task to study information preferences (originally invented by [14]). Individuals are offered a choice between options that provide either informative cues that indicate the outcome in advance (Info, red; reward cue or no-reward cue) or non-informative cues that do not indicate the outcome (Noinfo, blue). Importantly, there is no way to use this information to influence the outcome. (B) Humans and macaque monkeys can both prefer to view informative cues. This data was collected with more sophisticated tasks where offers provided different chances of obtaining information about gaining future rewards – money for humans, and juice or water for monkeys [8, **9,22]. (C) A simple candidate mechanism for non-instrumental information seeking. Individuals can value information for multiple reasons, including valuing the resolution of uncertainty, and overweighting desirable vs. undesirable information. The value of information is then combined with the value of primary rewards to compute the total reward value that guides decisions.

A Information prediction signal



B Reward prediction error signal (information + primary reward)

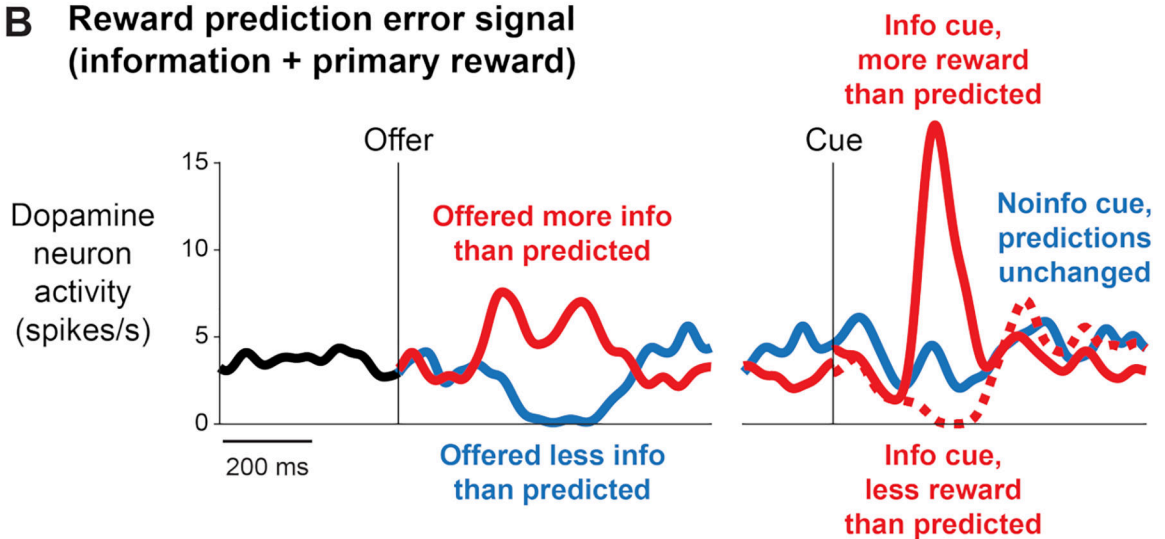


Figure 2. Candidate neural signals to motivate information seeking: information predictions and reward prediction errors.

(A) An example neuron in the dorsal striatum with activity resembling an information prediction (data from [**39]). This neuron activated during reward uncertainty, ramped up to the time the animal expected to receive information, and then returned to baseline after the information was received. Specifically, this neuron had ramping activation in anticipation of the offer, which indicated the availability of information and of juice reward. If the offer indicated that reward was uncertain and information was forthcoming, the neuron activated again and ramped to the predicted time of the informative cue (red). The neuron had much less activity if no information was predicted (blue) or if reward was fully certain to occur (gray). (B) An example midbrain dopamine neuron with an RPE signal treating information as a reward (data from [6]). This neuron was activated by Info offers (red, ‘more information than predicted’) and by informative cues indicating water reward delivery (red solid line, ‘more reward than predicted’); it was inhibited by Noinfo offers (blue, ‘less information than

predicted') and by informative cues indicating reward omission (red dashed line, 'less reward than predicted'); and had little response to non-informative cues (blue, 'predictions unchanged'). As a result, the information prediction signal (A) ramps up to the expected time of detecting an RPE (B).

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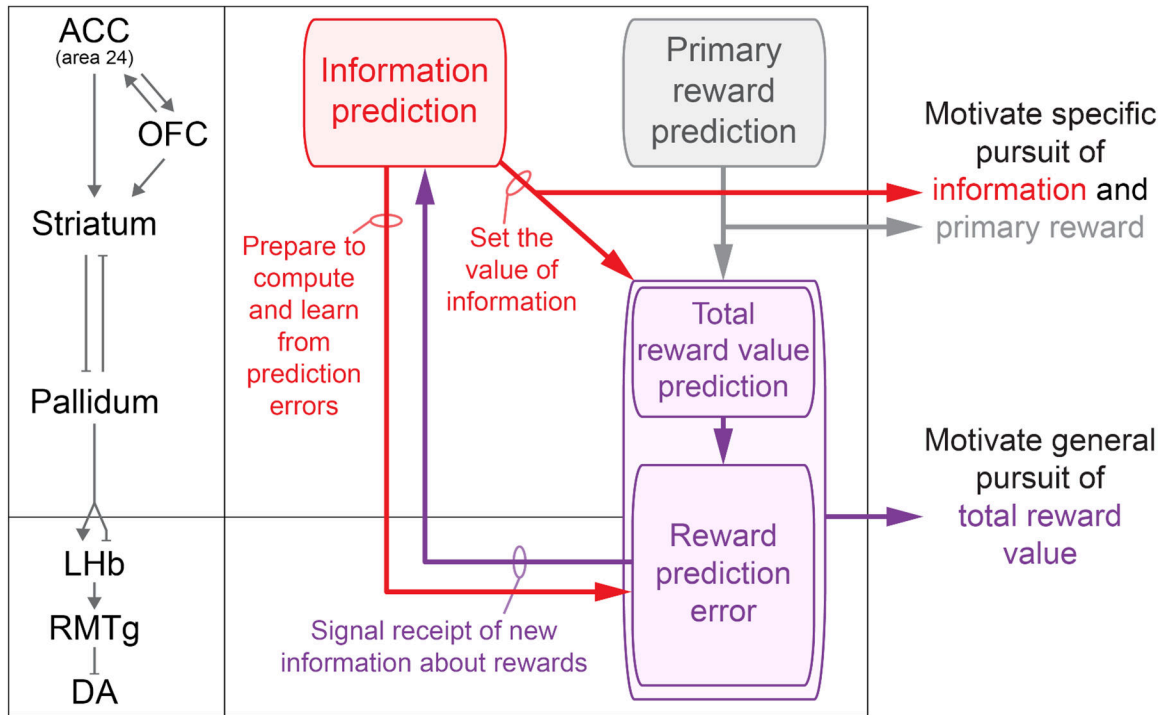


Figure 3. Hypothesized network mechanisms of information seeking.

Left: anatomically connected neural networks for motivated behavior. Left top: cortex-striatum-pallidum network. Left bottom: classic RPE network. Sharp/blunt arrows indicate predominant excitatory/inhibitory projections [**39,51]. Right: neuronal signals demonstrated to exist in each network, and their hypothesized influences on each other (arrows). Note that the RPE signal is depicted to straddle the two networks because RPE-like activity has been reported in subsets of neurons in both. Top: the cortex-striatum-pallidum network contains distinct predictions about the availability of information and primary reward (red, gray). These may directly motivate the specific pursuit of information or of primary reward. They may also be combined (purple) to compute the total predicted reward value, and in turn the total reward prediction error. These signals could then motivate the general pursuit of total reward value. The information prediction signal may also interface with RPEs: information predictions could prepare the brain for impending prediction errors, while RPEs could instruct information predictions by signaling the receipt of new information that changes reward predictions.