



Systems neuroscience of curiosity

Roberto Lopez Cervera, Maya Zhe Wang and Benjamin Y Hayden

Curiosity refers to a demand for information that has no instrumental benefit. Because of its critical role in development and in the regulation of learning, curiosity has long fascinated psychologists. However, it has been difficult to study curiosity from the perspective of the single neuron or the circuit – that is, at the *systems* level. Recent advances; however, have made doing so more feasible. These include theoretical advances in defining curiosity in animal models, the development of tasks that manipulate curiosity, and the preliminary identification of circuits responsible for curiosity-motivated learning. Taken together, resulting scholarship demonstrates the key roles of executive control, reward, and learning circuits in driving curiosity and has helped us to understand how curiosity relates to information-seeking more broadly. This work has implications for mechanisms of reward-based decisions. Here we summarize these results and highlight important remaining questions for the future of curiosity studies.

Address

Department of Neuroscience, Center for Magnetic Resonance Research, and Center for Neuroengineering, University of Minnesota, Minneapolis MN 55455, United States

Corresponding author: Cervera, Roberto Lopez (lopez927@umn.edu)

Current Opinion in Behavioral Sciences 2020, 35:48–55

This review comes from a themed issue on **Curiosity (Exolore versus Exoloit)**

Edited by **Daphna Shohamy** and **Ran Hassin**

<https://doi.org/10.1016/j.cobeha.2020.06.011>

2352-1546/© 2020 Elsevier Ltd. All rights reserved.

Introduction

Pitfall is a classic Atari game in which a player must navigate an avatar around a virtual screen to explore and score points [1]. Although a typical seven-year old can do quite well at the game with minimal practice, well-trained deep learning agents that can master many Atari games were unable to score even a single point until 2019 [2]. The reason is that Pitfall is a ‘hard-exploration’ problem – it has several factors that punish learning styles of typical deep learning agents [3]. Importantly, survival for animals in the real world has many of the same features, meaning that life, in general, is likely also a hard-exploration

problem. AI agents can now beat the best humans at Pitfall and the key innovation was endowing them with features that mimic curiosity, especially an internal reward for simply gaining information [2,4]. Curiosity, it seems, may be an indispensable element in our cognitive repertoires [5–8].

That is not to say we now know all we need to about curiosity. There are many ways in which AI curiosity is inferior to the evolved, biological kind (discussed, for example, in Ref. [2]). Moreover, we have yet to learn how to harness curiosity to improve our educational systems, with corresponding benefits for human welfare [9[•],10,11]. And we have yet to harness the study of curiosity for diseases associated with aberrant patterns of curiosity and information-seeking [12]. Nor do we know much about how different taxa differ in how their curiosity is deployed. Clearly, a greater understanding of curiosity is called for.

For these reasons, understanding the neural basis of curiosity has become an important issue in cognitive neuroscience. Indeed, in recent years, there has been a growing number of curiosity-related studies in psychology and cognitive neuroscience [6,8,13–17,18^{••}]. The study of curiosity has lagged, however, in branches of neuroscience concerned with how neurons perform task-relevant computations (i.e. systems neuroscience). However, because neural activity is the ultimate driver of behavior, such understanding is critical for a full accounting of the mechanisms of curiosity in the field.

Defining curiosity

One major barrier to understanding curiosity has long been the difficulty of defining it. Most definitions have tended to be heuristic. We have argued that this is a good thing – that definitions need to wait for sufficient empirical advances because we need to know what it is before we can precisely define it [8]. Nonetheless, there is still value in makeshift definitions. They allow us to do the types of experiments that will allow further work. This is especially important in animal models, which currently provide the best tools for systems neuroscience, but cannot provide reports about internal states and motivations (i.e. how curious they feel). We therefore have developed a rough-and-ready definition [19,20^{••}] that is inspired by an integrative reading of the recent literature and especially by the foundational work of Loewenstein, who described curiosity as a drive to fill perceived gaps in knowledge (i.e. uncertainty) [6,14,15,21].

Our proposal is that a research subject demonstrates curiosity if it (i) is willing to pay a real price solely for information, (ii) that information is demonstrably non-strategic, and (iii) the subject's demand scales with the amount of information (over some range) [19,20^{**}]. This definition has limitations; in particular, it is overly conservative (i.e. it rejects many likely cases of curiosity), and it assumes that subjects have acquired and are using the correct model of the task/environment in directing their information-seeking behaviors (i.e. behaviors that reduce uncertainty about the world), such that they understood that the information was non-strategic. However, we believe this definition is valuable for the time being.

The observing task

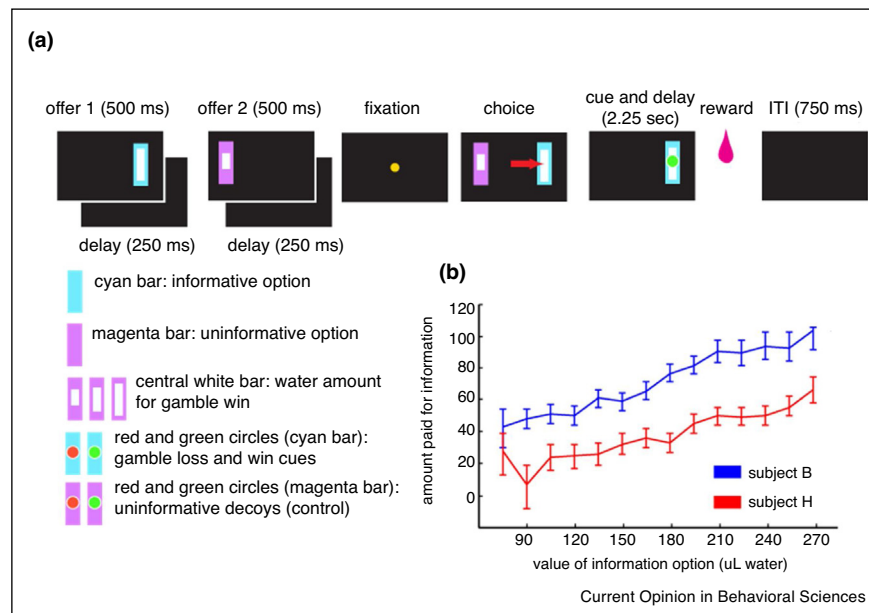
Among non-human animal tasks that generally satisfy criteria for curiosity, and thus is important for systems neuroscience, the *observing task* has proven to be especially useful (Figure 1) [22–28,29^{**}]. In this task, the decision-maker is faced with risky options, where resolution (that is, the information about the gamble's outcome) takes place after some delay relative to the choice. The decision-maker then has the opportunity to choose an option that provides earlier resolution but does not affect the reward's probability, size, or timing. Preference for this observing option can be taken as an indicator of curiosity. This task neatly

excludes strategic information-seeking because the reward itself is dispensed at the same time regardless of choice.

It is important to note that this task is no magic bullet. Indeed, there is residual debate about whether information-seeking behavior in the task reflects curiosity [30,31,32^{**}]. Specifically, the apparent preference for advance information could be accounted for by greater levels of attentional engagement on informative trials, leading to increased associative learning for informative cues, and thus promoting their choice even in the absence of curiosity [30]. The general argument is plausible, and differential attention may explain some of the effect; however, it appears insufficient to explain several results [20^{**},33^{**},34^{**}]. To give one example, lateral habenula neurons reliably signal information prediction errors for informative as well as uninformative cues, indicating that animals do not forget their reward predictions due to task disengagement even in uninformative trials [35].

In a different RL-inspired critique, Iigaya *et al.* [31] propose that viewing information provides a boost to the value of anticipating primary reward, which can be thought of as a time-dependent savoring effect that increases the overall value of a primary reward, and does not require curiosity. This proposal is supported by both behavior [31] and neuroimaging data [32^{**}] This model,

Figure 1



Observing task used in rhesus macaques [41]. **(a)** Schematic of the computerized version of the observing task. Macaque subjects choose on each trial between 50/50 gambles with differing and randomly chosen stakes (indicated by size of inscribed white bar). Informative offers (cyan color) promise gamble resolution immediately after choice; uninformative ones (magenta color) promise task-irrelevant decoy information. Stochastic reward occurs after 2.25 s regardless of choice. **(b)** Behavior of two example subjects on the task. Y-axis indicates indifference point (equivalence point) for informative and uninformative options. Both subjects placed value on advance information (as did a third subject, data not shown) and the value of that information increased roughly linearly with the stakes of the gamble.

while likely valid, seems unlikely to fully explain observing behavior; for example, it cannot explain willingness to pay for counterfactual information, a hallmark of human curiosity that is also demonstrated in monkeys [20**,36**].

Functional neuroanatomy of curiosity

Functional neuroanatomical studies have generally demonstrated the critical importance of regions involved in (1) reward, (2) learning/memory, and (3) control – a finding that is reassuring if not surprising given that curiosity can roughly be defined as the control of self-motivated learning.

Reward areas

Neuroimaging literature supports the involvement of the three ‘usual suspects’ reward regions — dopaminergic midbrain, striatum, and the ventral orbital surface — in curiosity. In perhaps the first neuroscientific study of human curiosity, Kang *et al.* reported activation in the striatum when subjects were anticipating the answer to a trivia question that they were curious about [37]. Since then, several studies have reported activation in the midbrain and striatum in anticipation of information through a variety of tasks including trivia, lottery, and observing tasks [33**,38,39**]. These results, along with others, support the idea that curiosity works by commandeering the brain’s usual reward regions to drive information-seeking (i.e. behavior that reduces uncertainty about the world). In other words, curiosity works just like any other motivated process [40–44].

Electrophysiological results support the involvement of reward areas in curiosity and provide insight into computational processes. Bromberg-Martin *et al.* used the observing task to understand the role of midbrain dopamine (DA) neurons in curiosity [28]. In that study, rhesus macaques had to choose between two risky options that were equivalent except that one option resolved outcome uncertainty early (2.25 s). The critical finding of the study was that dopaminergic midbrain neurons that responded to the expectation of primary reward also responded to the expectation of receiving information. This suggested that reward-seeking and information-seeking share a ‘common currency’ or neural code – or, perhaps, that curiosity and non-curiosity motivation converge at the level before the DA system.

In a follow-up study, Bromberg-Martin *et al.* used a similar task, but included an option that only revealed outcome information 50% of the time [35]. This allowed them to calculate information prediction errors (IPEs) when monkeys chose the semi-informative option and were unexpectedly delivered or denied information (this is analogous to how the brain calculates reward prediction errors, RPEs, from the delivery or denial of primary reward). The critical finding of this study was that a subpopulation of neurons in the lateral habenula (LHb), a subcortical reward structure, signaled IPEs in addition to conventional RPEs. This result further supported the subcortical

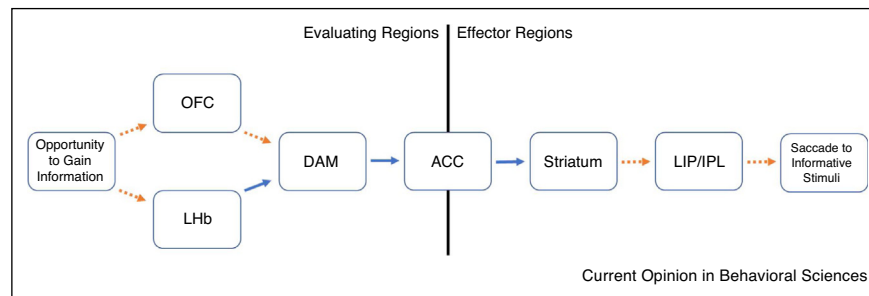
‘common currency’ hypothesis. Moreover, because of projections from LHb to the midbrain DA system, these results presented the start of a possible hierarchical anatomical pathway along which curiosity representations are transformed into choices.

In a related study performed in our lab, we examined responses in the orbitofrontal cortex (OFC, area 13) while monkeys performed a version of the observing task with titrated rewards [45]. This is a brain region associated with valuation processes, but also, to some extent, with executive ones [46–48]. This task allowed us to assess the specific value of information for each subject. We found that subjects were willing to pay up to 20–30% of their regular reward intake for advance information. We found that instantaneous firing rates of neurons in this region encode both the value of information (on a continuous scale) and the value of the primary (liquid) rewards, but use orthogonal ensemble coding formats to do so. This fact indicates that OFC tracks multiple influences on choice, but does not integrate them into a coherent abstract value variable, and suggests that such integration into an abstract value variable, if it occurs, takes place in a downstream structure. (Note that a good deal of evidence supports the idea that the midbrain DA system is downstream of OFC [49–51]. More broadly, these results fit into theories about hierarchies in reward processing [52–56].

Our data also bear on the debate about the causes of information-seeking. On one hand, subjects may value information because it allows them to physically or mentally prepare for reward delivery [21,31,32**,57]. If this were the case, informative offers would increase primary reward-related signals in OFC. Alternately, the brain could give reward a distinct value assignment – if so, then OFC primary reward signals should have no net enhancement by information. Our data supported the second inherent value tagging view. Specifically, signals coding water reward were not affected by the promise of information about those rewards. Indeed, OFC neurons appeared to use distinct (orthogonal) codes for information about upcoming rewards and unsignaled rewards (which also provided information), suggesting that they encode the value of the information and not the information itself [58].

Though not mutually exclusive, White *et al.* [34**] proposed a cortico-basal ganglia circuit to also explain information-seeking using an observing task that was adapted from Bromberg-Martin and Hikosaka [35]. Their model showed that ACC and striatum both track uncertainty. Activity in both of these regions ramps up in anticipation of information becoming available to resolve that uncertainty (even before reward delivery). In addition, striatum was found to causally direct gaze towards informative targets while anterior pallidum was found to inhibit gaze

Figure 2



A putative circuit diagram based on the evidence referenced in this review. Blue arrows indicate direct functional connectivity relating to information-seeking as suggested by literature referenced here. Orange arrows indicate indirect functional connectivity or functional connectivity with no clear evidence to disambiguate direct versus indirect connectivity. OFC, LHb, and DAM are involved in different processes that collectively evaluate and feed the value of information and opportunity to gain information to ACC, which then activates effector regions (e.g. striatum, LIP/IPL) to acquire information. OFC = orbital frontal cortex, LHb = lateral habenula, DAM = dopaminergic midbrain, ACC = anterior cingulate cortex, LIP = lateral intraparietal cortex (non-human primate), IPL = inferior parietal lobule (human).

to uninformative targets. These results further delineate the circuitry of curiosity.

Involvement of learning areas in curiosity

Information-seeking implies learning, which implies memory. Indeed, curiosity enhances memory formation for acquired information. It is not surprising, then, that it naturally involves learning [9^{••},37,59–61,62^{••}]. Most importantly, curiosity activates the hippocampus and the associated parahippocampal gyrus [36^{••},59,38]. It was also found that variation in hippocampal involvement predicted subsequent information recall accuracy. Moreover, increased activity while waiting for the answer to a high-curiosity question and after incorrectly answering a high-curiosity question lead to more accurate recall.

There are currently no electrophysiological studies on the role of memory regions in curiosity-motivated learning. Clearly, this is an important job for future research. In particular, it remains critical to record in hippocampal regions and in regions that are likely to anatomically mediate between the hippocampus and the reward/punishment systems, such as OFC and posterior cingulate cortex [63], vmPFC [32^{••}], and amygdala [64].

Involvement of control areas in curiosity

Perhaps less obvious than motivation and learning, curiosity involves executive control. That is, it involves carefully managing the tradeoff between competing interests, including the ability to de-emphasize the demand for immediate reward in favor of the most indirect benefits of information. This fact may explain the involvement of classic control areas, the most important of which is the dorsal anterior cingulate cortex (dACC). Several theories suggest that dACC serves to monitor the demand for control or the need to adjust foraging

strategy, and send this information to downstream structures that regulate behavior, such as guiding gaze to salient stimuli [65–73]. Curiosity about lottery outcomes was shown to disinhibit the ACC in humans via the increased amplitude of a ‘feedback-related negativity’ EEG signal that is believed to be related to dopaminergic projections to the ACC [74]. ACC was also shown to be responsive to anticipation of information during an observing task in monkeys [34^{••}].

In addition to regions that monitor the demand for control, downstream effector structures are also necessary to carry out the command. Gottlieb *et al.* have shown that neurons in the monkey lateral intraparietal cortex (LIP) produce stronger responses to informative task cues (after they appear in the monkey’s peripheral vision, but before a saccade is executed) compared to noninformative cues in active sampling tasks [13,75–77,78^{••}]. A recent study provides human support for these findings, where the authors found that the inferior parietal lobule (IPL, which is believed to be the human homolog of monkey LIP) encoded uncertainty in a lottery task. This finding was based on an increased BOLD response during the presentation of lottery probabilities, which was highest when outcome uncertainty was also highest [79]. These results are important because they demonstrate that gaze can be controlled by a drive to resolve uncertainty independent of reward value and suggest that different circuits may govern different types of executive control [78^{••}]. Figure 2 shows a putative circuit diagram summarizing the results on reward and control regions.

Conclusion

Our brains did not evolve to perform laboratory tasks; they evolved to solve complex foraging problems embedded in a rich natural world [80–84]. In the natural world,

information is almost always missing; natural foragers therefore have a constant pressing hunger for information [19]. A clever forager ought to devote a good deal of its resources simply to learning about the world in an effort to reduce uncertainty because even a small amount of information gain can provide a strong competitive advantage [85,86]. The value of information (or resolving uncertainty) has likely endowed our cognitive repertoires with an intrinsic information-seeking drive, which we call curiosity [8]. This drive is likely reflected in the organization of specific brain circuits and the underlying computations they implement.

So far research implicates three types of systems in curiosity – reward, learning, and control. This work is, naturally, prey to standard problems of reverse inference. Therefore, future studies will be needed to work out the specific processes associated with curiosity. In particular, we need to fully delineate the circuits. Second, we have to understand how curiosity both resembles and differs from other basic drives. Third, we will have to understand the role of valence – how curiosity relates to the price people are willing to pay to avoid information [33**,60,87,88]. Fourth, we need to integrate study of curiosity into our understanding of the systems neuroscience decision-making under uncertainty more generally [89–92]. Finally, we need to integrate the study of curiosity into the systems neuroscience of learning and motivation more broadly, especially as how it can teach us about intrinsic motivational variables. This information will ultimately help us harness curiosity to improve education, theories of learning, psychiatry, and our understanding of ourselves and our animal friends.

Conflict of interest statement

Nothing declared.

Acknowledgements

This work was supported by the National Institutes of Health grant T32 NS105604 (R.L.C.) and by the National Institutes of Health Medical Scientist Training Program grant T32 GM008244 (R.L.C.).

References and recommended reading

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

•• of outstanding interest

- Montfort N, Bogost I: *Racing the Beam: the Atari Video Computer System*. MIT Press; 2009.
- Ecoffet A, Huizinga J, Lehman J, Stanley KO, Clune J: *Go-explore: a new approach for hard-exploration problems*. arXiv preprint arXiv:1901.10995 2019.
- Mnih V, Kavukcuoglu K, Silver D, Rusu AA, Veness J, Bellemare MG et al.: **Human-level control through deep reinforcement learning**. *Nature* 2015, **518**:529-533 <http://dx.doi.org/10.1038/nature14236>.
- Murayama K, FitzGibbon L, Sakaki M: **Process account of curiosity and interest: a reward-learning perspective**. *Educ Psychol Rev* 2019:1-21.
- Urgen Schmidhuber JJ: *A Possibility for Implementing Curiosity and Boredom in Model-Building Neural Controllers*. Bradford Books: MIT Press; 1991.
- Loewenstein G: **The psychology of curiosity: a review and reinterpretation**. *Psychol Bull* 1994, **116**:75-98 <http://dx.doi.org/10.1037/0033-2909.116.1.75>.
- Oudeyer PY, Kaplan F: **What is intrinsic motivation? A typology of computational approaches**. *Front Neurobot* 2009, **1**:6.
- Kidd C, Hayden BY: **The psychology and neuroscience of curiosity**. *Neuron* 2015, **88**:449-460 <http://dx.doi.org/10.1016/j.neuron.2015.09.010>.
- Wade S, Kidd C: **The role of prior knowledge and curiosity in learning**. *Psychon Bull Rev* 2019:1377-1387 <http://dx.doi.org/10.3758/s13423-019-01598-6>.
This study used trivia questions to link human research participant's own perceived knowledge with their curiosity about a question, where the closer a subject thought they were to a correct answer, the more curious they were. The authors also showed that increased curiosity was increased with improved learning outcomes. This study provides important implications for maximizing student learning outcomes.
- Engel S: **Children's need to know: curiosity in schools**. *Harv Educ Rev* 2011, **81**:625-645.
- Gordon G, Breazeal C, Engel S: **Can children catch curiosity from a social robot?** 2015 10th ACM/IEEE International Conference on Human-Robot Interaction (HRI); IEEE. March: 2015:91-98.
- Jovanovic V, Brdaric D: **Did curiosity kill the cat? Evidence from subjective well-being in adolescents**. *Pers Individual Differences* 2012, **52**:380-384 <http://dx.doi.org/10.1016/j.paid.2011.10.043>.
- Gottlieb J, Oudeyer PY, Lopes M, Baranes A: **Information-seeking, curiosity, and attention: computational and neural mechanisms**. *Trends Cogn Sci* 2013, **17**:585-593 <http://dx.doi.org/10.1016/j.tics.2013.09.001>.
- Golman R, Loewenstein G: **Curiosity, information gaps, and the utility of knowledge**. *Information Gaps, and the Utility of Knowledge*. 2015. (April 16, 2015).
- Golman R, Loewenstein G: **Information gaps: a theory of preferences regarding the presence and absence of information**. *Decision* 2018, **5**:143.
- Gottlieb J, Oudeyer PY: **Towards a neuroscience of active sampling and curiosity**. *Nat Rev Neurosci* 2018, **19**:758-770 <http://dx.doi.org/10.1038/s41583-018-0078-0>.
- Gruber MJ, Ranganath C: **How curiosity enhances hippocampus-dependent memory: the prediction, appraisal, curiosity, and exploration (PACE) framework**. *Trends Cogn Sci* 2019:1-12 <http://dx.doi.org/10.1016/j.tics.2019.10.003>.
- van Lieshout L, de Lange F, Cools R: **Curiosity: An Appetitive or an Aversive Drive?** 2020.
The authors used a lottery task and self-reported measures of curiosity and happiness to show that curiosity increased with increasing uncertainty and happiness decreased with increasing uncertainty, regardless of whether the outcome was positive or negative. This suggests that uncertainty-based curiosity reflects an aversive drive rather than an appetitive drive.
- Wang MZ, Hayden BY: **Latent learning, cognitive maps, and curiosity**. *Curr Opin Behav Sci* 2020, **38**:1-7.
- Wang MZ, Hayden BY: **Monkeys are curious about counterfactual outcomes**. *Cognition* 2019, **189**:1-10 <http://dx.doi.org/10.1016/j.cognition.2019.03.009>.
Previous studies showed that monkeys can learn from counterfactual outcomes - outcomes that could have occurred but did not. This study showed that monkeys will pay a measurable positive price to choose options that provide counterfactual information about counterfactual outcomes. These results greatly enrich the set of information that motivates information-seeking in monkeys.
- Loewenstein G: **Anticipation and the valuation of delayed consumption**. *Econ J* 1987, **97**:666 <http://dx.doi.org/10.2307/2232929>.

22. Wyckoff LB: **The role of observing responses in discrimination learning. Part I.** *Psychol Rev* 1952, **59**:431-442 <http://dx.doi.org/10.1037/h0053932>.
23. Prokasy WF: **The acquisition of observing responses in the absence of differential external reinforcement.** *J Comp Physiol Psychol* 1956, **49**:131-134 <http://dx.doi.org/10.1037/h0046740>.
24. Ward EF: **Acquisition and extinction of the observing response as a function of stimulus predictive validity.** *Psychon Sci* 1971, **24**:139-141 <http://dx.doi.org/10.3758/BF03331790>.
25. Dinsmoor JA: **Observing and conditioned reinforcement.** *Behav Brain Sci* 1983, **6**:693-704 <http://dx.doi.org/10.1017/S0140525X00017969>.
26. Spetch ML, Belke TW, Barnet RC, Dunn R, Pierce WD: **Suboptimal choice in a percentage-reinforcement procedure: effects of signal condition and terminal-link length.** *J Exp Anal Behav* 1990, **53**:219-234 <http://dx.doi.org/10.1901/jeab.1990.53-219>.
27. Lieberman DA, Cathro JS, Nichol K, Watson E: **The role of S-in human observing behavior: bad news is sometimes better than no news.** *Learn Motiv* 1997, **28**:20-42 <http://dx.doi.org/10.1006/lmot.1997.0951>.
28. Bromberg-Martin ES, Hikosaka O: **Midbrain dopamine neurons signal preference for advance information about upcoming rewards.** *Neuron* 2009, **63**:119-126 <http://dx.doi.org/10.1016/j.neuron.2009.06.009>.
29. Cabrero JMR, Zhu JQ, Ludvig EA: **Costly curiosity: people pay a price to resolve an uncertain gamble early.** *Behav Process* 2019, **160**:20-25.
- This study used a card-flipping task to show that, like non-human animals, people were willing to pay a cost to receive information early even when that information did not affect the probability of receiving reward. Interestingly, reward magnitude did not significantly affect information-seeking behavior.
30. Beierholm UR, Dayan P: **Pavlovian-instrumental interaction in "observing behavior".** *PLoS Comput Biol* 2010, **6** <http://dx.doi.org/10.1371/journal.pcbi.1000903>.
31. Iigaya K, Story GW, Kurth-Nelson Z, Dolan RJ, Dayan P: **The modulation of savouring by prediction error and its effects on choice.** *eLife* 2016, **5**:1-24 <http://dx.doi.org/10.7554/eLife.13747>.
32. Iigaya K, Hauser TU, Kurth-Nelson Z, O'Doherty JP, Dayan P, Dolan RJ: **The value of what's to come: neural mechanisms coupling prediction error and reward anticipation.** *BioRxiv* 2019:588699 <http://dx.doi.org/10.1101/588699>.
- In contrast to the idea that human brains assign intrinsic value to information, the authors provide evidence that behavior during an observing task can be accounted for by the anticipatory boost model. Based on fMRI data, they suggest that vmPFC encodes a base value of anticipation and that hippocampus boosts the value of anticipation proportionally to the magnitude of an anticipatory reward prediction error, as opposed to an information prediction error, signaled by VTA/SN.
33. Charpentier CJ, Bromberg-Martin ES, Sharot T: **Valuation of knowledge and ignorance in mesolimbic reward circuitry.** *Proc Natl Acad Sci U S A* 2018, **115**:E7255-E7264 <http://dx.doi.org/10.1073/pnas.1800547115>.
- Using an observing task adapted from Bromberg-Martin and Hikosaka [32] and a stock market simulation, the authors found that activations in OFC, nucleus accumbens, and midbrain were associated with the value of the opportunity to gain knowledge about favorable outcomes. They also found that people are willing to pay a cost to avoid undesirable information. This is the only study to our knowledge that reveals a neurological mechanism for the differential treatment of knowledge and ignorance.
34. White JK, Bromberg-Martin ES, Heilbronner SR, Zhang K, Pai J, Haber SN, Monosov IE: **A neural network for information seeking.** *Nat Commun* 2019, **10**:1-19.
- The authors used an observing task with rhesus macaques to uncover a cortico-basal ganglia circuit that causally drives visual information-seeking. To our knowledge, this is the first study to identify an information-seeking brain circuit.
35. Bromberg-Martin ES, Hikosaka O: **Lateral habenula neurons signal errors in the prediction of reward information.** *Nat Neurosci* 2011, **14**:1209-1218 <http://dx.doi.org/10.1038/nn.2902>.
36. FitzGibbon L, Moll H, Carboni J, Lee R, Dehghani M: **Counterfactual curiosity in preschool children.** *J Exp Child Psychol* 2019, **183**:146-157.
- This was the first study on counterfactual curiosity in children using a card-matching game. The data showed that children preferentially sought information about unchosen outcomes they had control over, especially when their chosen outcome was negative. The authors conjectured that counterfactual curiosity may developmentally precede counterfactual reasoning.
37. Kang MJ, Hsu M, Krajbich IM, Loewenstein G, McClure SM, Wang JT, Camerer CF: **The wick in the candle of learning.** *Psychol Sci* 2009, **20**:963-973 <http://dx.doi.org/10.1111/j.1467-9280.2009.02402.x>.
38. Gruber MJ, Gelman BD, Ranganath C: **States of curiosity modulate hippocampus-dependent learning via the dopaminergic circuit.** *Neuron* 2014, **84**:486-496 <http://dx.doi.org/10.1016/j.neuron.2014.08.060>.
39. Kobayashi K, Hsu M: **Common neural code for reward and information value.** *Proc Natl Acad Sci U S A* 2019, **116**:13061-13066 <http://dx.doi.org/10.1073/pnas.1820145116>.
- The authors developed a model for information-seeking that assigned value to information that helps to maximize reward (VOI, an instrumental motive) and the value of anticipation (a non-instrumental motive) to describe subjective value of information (SVOI, a measure of the value of instrumental and non-instrumental information). They showed that their model could best explain human curiosity during a lottery task that allowed participants to reject unfavorable gambles. They also used BOLD signals to identify SVOI representations in vmPFC and striatum. This study was unique in that it allowed subjects to make decisions based on both instrumental and non-instrumental information.
40. Adcock RA, Thangavel A, Whitfield-Gabrieli S, Knutson B, Gabrieli JDE: **Reward-motivated learning: mesolimbic activation precedes memory formation.** *Neuron* 2006, **50**:507-517 <http://dx.doi.org/10.1016/j.neuron.2006.03.036>.
41. Fehr E, Camerer CF: **Social neuroeconomics: the neural circuitry of social preferences.** *Trends Cogn Sci* 2007, **11**:419-427.
42. D'Ardenne K, McClure SM, Nystrom LE, Cohen JD: **BOLD responses reflecting dopaminergic signals in the human ventral tegmental area.** *Science* 2008, **319**:1264-1267 <http://dx.doi.org/10.1126/science.1150605>.
43. Hikosaka O, Bromberg-Martin E, Hong S, Matsumoto M: **New insights on the subcortical representation of reward.** *Curr Opin Neurobiol* 2008, **18**:203-208 <http://dx.doi.org/10.1016/j.conb.2008.07.002>.
44. Shohamy D, Adcock RA: **Dopamine and adaptive memory.** *Trends Cogn Sci* 2010, **14**:464-472 <http://dx.doi.org/10.1016/j.tics.2010.08.002>.
45. Blanchard TC, Hayden BY, Bromberg-Martin ES: **Orbitofrontal cortex uses distinct codes for different choice attributes in decisions motivated by curiosity.** *Neuron* 2015, **85**:602-614 <http://dx.doi.org/10.1016/j.neuron.2014.12.050>.
46. Wallis JD: **Orbitofrontal cortex and its contribution to decision-making.** *Annu Rev Neurosci* 2007, **30**:31-56.
47. Izquierdo A: **Functional heterogeneity within rat orbitofrontal cortex in reward learning and decision making.** *J Neurosci* 2017, **37**:10529-10540.
48. Sleezer BJ, Castagno MD, Hayden BY: **Rule encoding in orbitofrontal cortex and striatum guides selection.** *J Neurosci* 2016, **36**:11223-11237.
49. Takahashi YK, Stalnaker TA, Roesch MR, Schoenbaum G: **Effects of inference on dopaminergic prediction errors depend on orbitofrontal processing.** *Behav Neurosci* 2017, **131** <http://dx.doi.org/10.1037/bne0000192>.
50. Stalnaker TA, Liu TL, Takahashi YK, Schoenbaum G: **Orbitofrontal neurons signal reward predictions, not reward prediction errors.** *Neurobiol Learn Mem* 2018, **153**:137-143 <http://dx.doi.org/10.1016/j.nlm.2018.01.013>.
51. Nambodiri VMK, Otis JM, van Heeswijk K, Voets ES, Alghorazi RA, Rodriguez-Romaguera J et al.: **Single-cell activity tracking reveals that orbitofrontal neurons acquire and**

- maintain a long-term memory to guide behavioral adaptation. *Nat Neurosci* 2019, **22**:1110-1121 <http://dx.doi.org/10.1038/s41593-019-0408-1>.
52. Hunt LT, Malalasekera WN, de Berker AO, Miranda B, Farmer SF, Behrens TE, Kennerley SW: **Triple dissociation of attention and decision computations across prefrontal cortex.** *Nat Neurosci* 2018, **21**:1471.
53. Murray JD, Bernacchia A, Freedman DJ, Romo R, Wallis JD, Cai X *et al.*: **A hierarchy of intrinsic timescales across primate cortex.** *Nat Neurosci* 2014, **17**:1661.
54. Yoo SBM, Hayden BY: **Economic choice as an untangling of options into actions.** *Neuron* 2018, **99**:434-447.
55. Pezzulo G, Cisek P: **Navigating the affordance landscape: feedback control as a process model of behavior and cognition.** *Trends Cogn Sci* 2016, **20**:414-424 <http://dx.doi.org/10.1016/j.tics.2016.03.013>.
56. Dezza IC, Cleeremans A, Alexander W: **Independent and interacting value systems for reward and information in the human prefrontal cortex.** *bioRxiv* 2020.
57. Perkins CC Jr: **The stimulus conditions which follow learned responses.** *Psychol Rev* 1955, **62**:341.
58. Wang MZ, Hayden BY: **Reactivation of associative structure specific outcome responses during prospective evaluation in reward-based choices.** *Nat Commun* 2017, **8**:15821.
59. Jepma M, Verdonschot RG, van Steenbergen H, Rombouts SARB, Nieuwenhuis S: **Neural mechanisms underlying the induction and relief of perceptual curiosity.** *Front Behav Neurosci* 2012, **6** <http://dx.doi.org/10.3389/fnbeh.2012.00005>.
60. Marvin CB, Shohamy D: **Curiosity and reward: valence predicts choice and information prediction errors enhance learning.** *J Exp Psychol: Gen* 2016, **145**:266-272 <http://dx.doi.org/10.1037/xge0000140>.
61. Stare CJ, Gruber MJ, Nadel L, Ranganath C, Gómez RL: **Curiosity-driven memory enhancement persists over time but does not benefit from post-learning sleep.** *Cogn Neurosci* 2018, **9**:100-115 <http://dx.doi.org/10.1080/17588928.2018.1513399>.
62. Duan H, Fernández G, van Dongen E, Kohn N: **The effect of intrinsic and extrinsic motivation on memory formation: insight from behavioral and imaging study.** *Brain Struct Funct* 2020.
- This study was the first to compare the memory enhancing effects of extrinsic reward (monetary reward) with intrinsic reward (curiosity relief) in a trivia question task. Their results supported previous findings that increasing both extrinsic and intrinsic reward individually enhance memory recall, and together provide an additive effect. More importantly, they found that the neural mechanisms associated with both forms of reward-driven memory enhancement were different. Curiosity activated the fronto-parietal attention network, while monetary reward inactivated task-irrelevant areas in parietal midline regions.
63. Wikenheiser AM, Schoenbaum G: **Over the river, through the woods: cognitive maps in the hippocampus and orbitofrontal cortex.** *Nat Rev Neurosci* 2016, **17**:513-523 <http://dx.doi.org/10.1038/nrn.2016.56>.
64. Alvarez RP, Biggs A, Chen G, Pine DS, Grillon C: **Contextual fear conditioning in humans: cortical-hippocampal and amygdala contributions.** *J Neurosci* 2008, **28**:6211-6219 <http://dx.doi.org/10.1523/JNEUROSCI.1246-08.2008>.
65. Botvinick M, Nystrom LE, Fissell K, Carter CS, Cohen JD: **Conflict monitoring versus selection-for-action in anterior cingulate cortex.** *Nature* 1999, **402**:179.
66. Botvinick MM, Cohen JD: **The computational and neural basis of cognitive control: charted territory and new frontiers.** *Cogn Sci* 2014, **38**:1249-1285 <http://dx.doi.org/10.1111/cogs.12126>.
67. Shenhav A, Botvinick MM, Cohen JD: **The expected value of control: an integrative theory of anterior cingulate cortex function.** *Neuron* 2013 <http://dx.doi.org/10.1016/j.neuron.2013.07.007>.
68. Kolling N, Behrens TEJ, Mars RB, Rushworth MFS: **Neural mechanisms of foraging.** *Science* 2012, **335**:95-98 <http://dx.doi.org/10.1126/science.1216930>.
69. Kolling N, Behrens TEJ, Wittmann MK, Rushworth MFS: **Multiple signals in anterior cingulate cortex.** *Curr Opin Neurobiol* 2016, **37**:36-43.
70. Heilbronner SR, Hayden BY: **Dorsal anterior cingulate cortex: a bottom-up view.** *Annu Rev Neurosci* 2016, **39**:149-170 <http://dx.doi.org/10.1146/annurev-neuro-070815-013952>.
71. Smith EH, Horga G, Yates MJ, Mikell CB, Banks GP, Pathak YJ, Schevon CA, McKann GA, Hayden BY, Botvinick MM, Sheth SA: **Widespread temporal coding of cognitive control in the human prefrontal cortex.** *Nat Neurosci* 2019:1-9.
72. Azab H, Hayden BY: **Correlates of economic decisions in the dorsal and subgenual anterior cingulate cortices.** *Eur J Neurosci* 2018, **47**:979-993.
73. Rushworth MFS, Noonan MAP, Boorman ED, Walton ME, Behrens TE: **Frontal cortex and reward-guided learning and decision-making.** *Neuron* 2011 <http://dx.doi.org/10.1016/j.neuron.2011.05.014>.
74. Brydevall M, Bennett D, Murawski C, Bode S: **The neural encoding of information prediction errors during non-instrumental information seeking.** *Sci Rep* 2018, **8**(1):1-11 <http://dx.doi.org/10.1038/s41598-018-24566-x>.
75. Gottlieb J, Hayhoe M, Hikosaka O, Rangel A: **Attention, reward, and information seeking.** *J Neurosci* 2014, **34**:15497-15504 <http://dx.doi.org/10.1523/JNEUROSCI.3270-14.2014>.
76. Foley NC, Kelly SP, Mhatre H, Lopes M, Gottlieb J: **Parietal neurons encode expected gains in instrumental information.** *Proc Natl Acad Sci U S A* 2017, **114**:E3315-E3323.
77. Daddaoua N, Lopes M, Gottlieb J: **Intrinsically motivated oculomotor exploration guided by uncertainty reduction and conditioned reinforcement in non-human primates.** *Sci Rep* 2016:6 <http://dx.doi.org/10.1038/srep20202>.
78. Horan M, Daddaoua N, Gottlieb J: **Parietal neurons encode information sampling based on decision uncertainty.** *Nat Neurosci* 2019, **1** <http://dx.doi.org/10.1038/s41593-019-0440-1>.
- The authors used an active sampling task to show that neurons in rhesus macaque LIP encode a saccade's ability to reduce uncertainty, independent of primary reward, and that their activity positively correlates with behavioral efficiency. These results are important because they are inconsistent with the idea that LIP neurons encode economic utility and suggest that oculomotor output in information-seeking may be connected to upstream mechanisms motivated by curiosity.
79. van Lieshout LLF, Vandenbroucke ARE, Müller NCJ, Cools R, de Lange FP: **Induction and relief of curiosity elicit parietal and frontal activity.** *J Neurosci* 2018, **38**:2579-2588 <http://dx.doi.org/10.1523/JNEUROSCI.2816-17.2018>.
80. Pearson JM, Watson KK, Platt ML: **Decision making: the neuroethological turn.** *Neuron* 2014, **82**:950-965.
81. Eisenreich BR, Hayden BY, Zimmermann J: **Macaques are risk-averse in a freely moving foraging task.** *Sci Rep* 2019, **9**:1-12.
82. Krakauer JW, Ghazanfar AA, Gomez-Marín A, MacIver MA, Poeppel D: **Neuroscience needs behavior: correcting a reductionist bias.** *Neuron* 2017, **93**:480-490.
83. Brown AE, De Bivort B: **Ethology as a physical science.** *Nat Phys* 2018, **14**:653-657.
84. Yoo SBM, Tu JC, Piantadosi ST, Hayden BY: **The neural basis of predictive pursuit.** *Nat Neurosci* 2020:1-8.
85. Ebitz RB, Slezzer BJ, Jedema HP, Bradberry CW, Hayden BY: **Tonic exploration governs both flexibility and lapses.** *PLoS Comput Biol* 2019:15.
86. Peterson EJ, Verstynen TD: **A way around the exploration-exploitation dilemma.** *bioRxiv* 2019:671362.
87. Berns GS, Chappelow J, Cekic M, Zink CF, Pagnoni G, Martin-Skurski ME: **Neurobiological substrates of dread.** *Science* 2006, **312**:754-758.
88. Oosterwijk S, Snoek L, Tekoppele J, Engelbert L, Scholte HS: **Choosing to view morbid information involves reward circuitry.** *BioRxiv* 2019:795120.

89. Farashahi S, Azab H, Hayden B, Soltani A: **On the flexibility of basic risk attitudes in monkeys.** *J Neurosci* 2018, **38**:4383-4398.
90. Pirrone A, Azab H, Hayden BY, Stafford T, Marshall JA: **Evidence for the speed-value trade-off: Human and monkey decision making is magnitude sensitive.** *Decision* 2018, **5**:129.
91. Heilbrunner SR, Hayden BY: **The description-experience gap in risky choice in nonhuman primates.** *Psychon Bull Rev* 2016, **23**:593-600.
92. Heilbrunner SR: **Modeling risky decision-making in nonhuman animals: shared core features.** *Curr Opin Behav Sci* 2017, **16**:23-29.