

Intrinsic reward: potential cognitive and neural mechanisms

Bastien Blain, Tali Sharot

▶ To cite this version:

Bastien Blain, Tali Sharot. Intrinsic reward: potential cognitive and neural mechanisms. Current Opinion in Behavioral Sciences, 2021, 39, pp.113 - 118. 10.1016/j.cobeha.2021.03.008 . hal-04358392

HAL Id: hal-04358392 https://hal.science/hal-04358392

Submitted on 21 Dec 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



ScienceDirect



Intrinsic reward: potential cognitive and neural mechanisms Bastien Blain^{1,2} and Tali Sharot^{1,2}



From child play to scientific discovery, many activities human engage in are rewarding in and of themselves. Here, we ask what makes such activities intrinsically rewarding. Based on the existing literature we propose the answer is an increased sense of self-efficacy. That is, an activity that is intrinsically rewarding is one that strengthens a person's belief that they can execute actions required to successfully deal with prospective situations. We show this notion can explain the rewarding nature of many activities and situations from solving cross word puzzles to helping others, consuming arts and playing sports. We suggest that processes that lead to increased self-efficacy, such as executing agency and learning, activate the neural reward system. This in turn is experienced as pleasure and reinforces the activity that generated the response. Intrinsic rewards would lead biological organism to improve their knowledge and skills which could help them adapt to changing environments.

Addresses

¹ Affective Brain Lab, Department of Experimental Psychology, University College London, London WC1H 0AP, UK

² Max Planck University College London Centre for Computational Psychiatry and Ageing Research, London WC1B 5EH, UK

Corresponding authors: Blain, Bastien (b.blain@ucl.ac.uk), Sharot, Tali (t.sharot@ucl.ac.uk)

Current Opinion in Behavioral Sciences 2021, 39:113-118

This review comes from a themed issue on Positive Affect

Edited by Henk van Steenbergen, Disa Sauter, Blair Saunders and Gilles Pourtois

For a complete overview see the <u>Issue</u> and the <u>Editorial</u>

Available online 7th April 2021

https://doi.org/10.1016/j.cobeha.2021.03.008

2352-1546/© 2021 The Author(s). Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (http://creative-commons.org/licenses/by-nc-nd/4.0/).

Many activities are pleasurable in their own right. They are undertaken even when they do not lead to an external outcome: they are intrinsically rewarding. Playing, problem solving, cross word puzzles, exploring nature, reading, observing works of art, are a few such examples. Engagement in such activities is strongly associated with feelings of happiness, increased well-being, improved mental health [1^{••},2], and even professional achievement [3]. It is thus important to understand what makes certain activities intrinsically rewarding. Psychologists and philosophers have debated the characteristics and function of intrinsically rewarding activities for almost a century [4]. More recently, neuroscientist have been studying the neural responses such activities elicit [5••,6••] and computer scientists, who develop intelligent machines, have turned their attention to this issue as well [7]. Here, we highlight some of this recent research to address the question of what makes the so called 'intrinsically rewarding activities' rewarding.

Primary, secondary and intrinsic rewards: differences and similarities

Primary rewarding stimuli (e.g. food, water) and activities (e.g. fornicating) are shaped by evolution, guiding the organism to select actions that increase survival and reproduction. Second order rewards (e.g. money) correspond to stimuli that are associated with primary reward. Via such association they take on the rewarding properties of the primary reward, becoming rewarding themselves. When second order rewards are no longer associated with a primary reward they stop being rewarding [8].

Actions that lead to primary or secondary rewards (like labour in exchange for food or money) are not necessarily rewarding in and of themselves. In contrast, intrinsically rewarding activities are rewarding in and of themselves and they do not require an association with a primary or secondary reward to be reinforced. While they may be associated with such rewards, they will not cease to be rewarding when such association is broken [4]. As such they are clearly distinct from secondary rewards. In contrast to primary reward, these activities (such as making art, playing, solving puzzles) do not have clear and *immediate* survival benefit.

Despite these differences, such activities, which do not have clear and immediate instrumental utility, seem to elicit similar behavioural responses as primary rewards. In particular, rewarding stimuli have the following characteristics: (i) they generate approach/consummatory behaviours, (ii) they are reinforcing in the sense that they increase the likelihood of the action that lead to them, (iii) they elicit positive emotions [4].

Indeed, people approach activities, such as reading novels, listening to music, going for walks, playing, exploring [2]. In fact, the term intrinsic reward was initially coined to describe the persistence of certain behaviours observed in non-human primate, such as playing with mechanical puzzles, in the absence of extrinsic rewards [9]. As for reinforcement, performing these activities increase the likelihood of performing it again. For example, it has been observed that when animals engage in an exploratory behaviour this results in an increase of such behaviour in the absence of expectations of extrinsic rewards [10]. Intuitively, once we try a new pleasurable activity or hobby, we are likely to repeat it. Finally, with regards to positive emotions, studies examining momentary affect using real time sampling methods show that people often feel happy when engaging in activities such as playing sports, reading, being in nature, learning [2,11]. A recent study [1^{••}] showed that when both extrinsic rewards (e.g. money) and intrinsic rewards (e.g. learning) can be achieved in the same task, happiness variations are driven by the latter more so than the former. What is it then exactly about an activity that causes it to elicit approach, reinforcement and positive feelings, without an association with a primary reward?

What makes an 'intrinsically rewarding activity' rewarding?

Here, we speculate that the characteristic which makes an activity 'intrinsically rewarding' is its tendency to increase self-efficacy. Self-efficacy is a person's belief of how well they can execute actions required to successfully deal with prospective situations [12]. We suggest that activities that are associated with cognitive changes that increase the sense of self-efficacy will be intrinsically rewarding. These processes often include variations of learning such as knowledge acquisition, skill development, pattern recognition, problem solving, motor learning, exploration, consolidation etc. (see Figure 1).

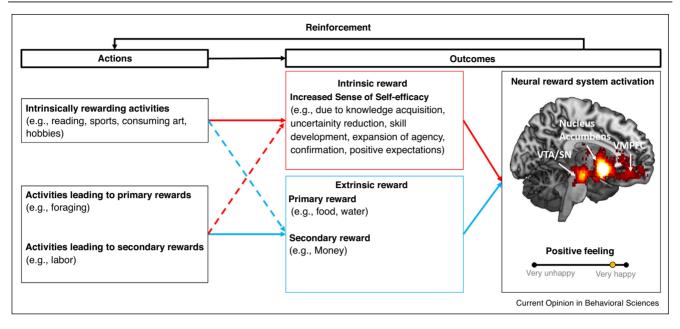
Many intrinsically rewarding activities, which on the surface do not seem to offer much in the way of increased self-efficacy do exactly that at closer look. Staring at the ocean, for example, allows a relaxed state for consolidating thoughts [13]. Helping others, which improves wellbeing [14] increases self-esteem, the feeling of autonomy and of mastery [15]. Let's take musical pleasure as another example. A recent study suggests that musical pleasure improved memory via activation of reward mechanisms [16]. Music offers an opportunity to learn sequences of notes, which listeners automatically do. Interestingly, people prefer musical pieces with an intermediate level of complexity [17], which are able to manipulate the listener's expectations to produce both surprise and confirmation [18,19°].

Indeed, intrinsically rewarding activities are those which are not completely familiar, but not completely new [11,20]. Very familiar tasks offer little in terms of learning opportunities while tasks involving uncontrollable random process are simply unlearnable [21^{••}]. Activities with intermediate-level of difficulty trigger a sense of 'flow' an experiential state of total absorption, optimal challenge, and non-self-conscious enjoyment [11]. Such levels are optimal for learning [21^{••}]. Biological organisms have limited amount of resources and time at their disposal and thus need to select between the infinite number of activities the natural environment offers. A good choice would be one that allows an optimal rate of learning progress [21^{••}]. Interestingly, activities that are most pleasant are often activities with intermediate levels of difficulty [11]. This suggests that a function of intrinsic reward is to nudge the agent towards activities that allow learning progress. These, in turn, would allow agents to better adapt to changing environment, and even combat existential threats such as climate change or pandemics [22,23]. This is because the scientific and technological advances (such as a vaccine development) are needed to address such threats. Such advances would not be possible if humans were not driven to learn and explore.

According to Self-Determination Theory [24], intrinsic rewarding activities often generate feelings of autonomy and competence (i.e. self-efficacy). Autonomy refers to an experience of volition and of self-organisation. Indeed, studies show that people are more likely to find activities they initiate themselves intrinsically rewarding compared to activities they are forced to do, even if the activity is the same [25,26]. A metaanalysis of 41 studies revealed that agency increases both motivation and performance [27]. In fact, making a choice in and of itself is intrinsically rewarding. When given a choice, people prefer options that allow further choice over those that do not; they are also willing to pay to control their own payoffs, rather than delegate [28]. This is true even when maximizing monetary rewards and minimizing monetary losses are known to require delegation [29]. This is because choosing increases the subjective value of what is chosen: people value items they had selected themselves more than identical items that were selected for them [30]. A sense of agency in its own right is tightly related to a sense of efficacy, but it can also increase learning [32]. For example, exercising agency in the form of creating an object or solving a problem, provides the agent with a blueprint of how to create similar objects and solve similar problems in the future. If an object or a solution is simply provided by another person, the agent would lack such blueprint. Agency also helps inform an agent regarding their own preference [33[•]]. We therefore suggest that agency is intrinsically rewarding in that it corresponds to a condition that favour an increase in self-efficacy.

If indeed intrinsic rewards are shaped by evolution they would likely be shared with other biological organisms. This notion is supported by the literature. Non-human animals perform activities which seem to be rewarding (that is they are approached, reinforced and seem to elicit pleasure), but do not lead to extrinsic rewards. For example, when wild mice first encounter wheels they run on them continually [34]. Such running can increase motor





Intrinsic rewarding activities elicit an increased sense of self-efficacy (solid red line). They may also at times lead to primary or secondary reward (dotted blue line), but this association is not necessary for them to be rewarding. Similarly, actions that lead to primary or secondary reward may also be intrinsically rewarding (dotted red line). Both intrinsic and extrinsic rewards activate the neural reward system. This neural reward signal is often experienced as a positive feeling and reinforces the action it elicited. The brain map was derived from neurosynth.org — an automated meta-analysis of 922 studies. It shows voxels that were preferentially related to the term 'reward'. As observed these voxels are mostly in the ventral tegmental area/substantia nigra (VTA/SN), the nucleus accumbens and the ventro-medial prefrontal cortex (VMPFC). FDR threshold, p = 0.01. Most of the studies in this meta-analysis by neurosynth are of those examining responses to primary and secondary rewards, as studies examining responses to intrinsically rewarding activities are very few at present time. For example, entering the term 'intrinsic reward' or other associated terms does not generate a map in neurosynth.

skill learning [35] and metabolic efficiency, which can be beneficial in the long run by enhancing the ability to escape from predator and to forage [36]. Pigeons, starlings, rats, monkeys and humans (as quoted in [37]) all display behaviours that suggest uncertainty reduction is intrinsically rewarding. For example, all these species prefer to know in advance about future outcomes even when such knowledge is not instrumental. Humans $[6^{\bullet\bullet}, 38^{\bullet\bullet}]$ and non-humans primates [39] will even pay for such knowledge, suggesting that they perceive the opportunity to gain knowledge as rewarding. It is thought that the rewarding nature of non-instrumental knowledge acquisition is nonetheless adaptive, because while such knowledge may not be useful at the moment it may end up being useful down the line.

If intrinsically rewarding activities and primary rewards both have evolutionary utility and elicit similar behavioural responses, is there in fact a distinction to be made between them? Indeed, there is. Primary rewards are *necessary* for survival, while intrinsic rewards can increase survival but are not necessary. For example, if a person has no food or water they will for certain die within days. However, if a person does not find intrinsically rewarding activities rewarding, this may reduce their likelihood of survival in the long run, but they could in principle live a long life. Second, as we mentioned in the introduction the survival benefit of primary rewards manifests itself *immediately*, while for intrinsic rewards the adaptive benefit manifests over longer periods of time.

We note, however, that an improved sense of efficacy will be intrinsically rewarding even if it is false and thus not always adaptive. For example, having our views confirmed by others or receiving information which create positive expectations will lead to an increased sense of self-efficacy (thus be intrinsically rewarding) even if such confirmations or positive expectations are based on false information. This is analogues to artificial sweeteners that taste like sugar, eliciting the same behavioural and neural response as the real thing, but are calorie free, providing no energy to the organism.

Neural mechanisms of intrinsically rewarding activities

While both lay people and experts use the word 'reward' to refer to primary, secondary and intrinsic rewards, whether the brain generates the response to all three using the same neural architecture and computational rules is not fully understood. Neural response to an intrinsically rewarding activity may well involve neural architecture that is more evolutionary recent, than the neural architecture required to process primary rewards. While some mammals do seem to get pleasure from activities in their own right, it is unclear whether animals lower on the evolutionary ladder do. Moreover, it seems that humans engage with such activities to a larger extent than other mammals. Thus, one hypothesis is that the rewarding response to such activities is neurally distinct from that to primary rewards. It may involve the neocortex and not rely on the dopaminergic midbrain system already in place. Another hypothesis is that the response involves a combination of the evolutionary old system as well as more high-level processing. A third hypothesis is that intrinsic rewards simply 'hijack' the exact same system that evolved in order to guide agents towards food/water and reproduction.

The extent to which the response to primary and intrinsic rewards is overlapping, and the details of divergence, can provide new insight into intrinsic rewards. For example, such knowledge can enable us to make predictions regarding how intrinsic rewarding activities earn their reinforcing nature and when this happens over the life span. It will give us clue to when and how intrinsic rewards lose their rewarding properties, such as in certain mental disorders.

There has only been a small number of studies explicitly examining the neural representation of, and response to, intrinsic rewards. This is surprising given the importance of intrinsic reward to productivity and well-being [3]. We can, however, make inferences from studies investigating agency, acquisition of knowledge and learning, play, altruistic behaviour and musical pleasure, even if these studies did not intend to directly study the rewarding nature of these processes. These studies point towards a neural system that partially overlaps but is also partially distinct from that involved in processing primary rewards.

Giving to a charity, controlling the environment, acquiring knowledge, playing, listening to music are activities that seem to have little in common. Yet, recent studies suggest that they are all linked to the activation of the same brain areas as for primary and secondary rewards that is the VMPFC/OFC and ventral striatum. For example, a recent meta-analysis of 36 studies show that altruistic decisions activate the brain reward system (including the VMPFC and the ventral striatum) more than selfishdecisions [40]. Similarly, a recent meta-analysis comparing hedonic responses to food (21 studies) and music (17 studies) revealed a significant conjunction notably in the VMPFC is also involved in both playing games and getting an extrinsic reward [42^{••}]. Interestingly, individuals for which the VMPFC tracks intrinsic outcomes more so than extrinsic outcomes are also those whose explicit happiness ratings are influenced more by the former [35], suggesting that the VMPFC may reflect the relative preference for intrinsic and extrinsic rewards.

Studies show that the perception of agency is often associated with the brain reward system (e.g. Ref. $[5^{\bullet\bullet}]$), at different decision stages. At stimulus presentation, when a subject is given an option to make a choice, activity in the ventral striatum is enhanced [26]. Postchoice, BOLD signals in the caudate nucleus and VMPFC are greater in response to outcomes participants selected after making a choice relative to before, suggesting that choice boosted the rewarding nature of the outcome [43], and activity in the VMPFC representing the subjective value of selected option was increased by 30% [5^{••}].

Single cell recording in monkeys [44] as well as neuroimaging $[6^{\bullet\bullet},40]$ and pharmacological $[38^{\bullet\bullet}]$ studies in humans, show that the opportunity to acquire knowledge is also represented by the same neural system, algorithms and neuromodulators as primary rewards. In particular, it has been shown that information prediction errors (IPEs), that is errors in predicting the opportunity to gain knowledge, are encoded by the same neural system as primary reward prediction errors (including the ventral striatum) $[6^{\bullet\bullet},39]$.

Overall, these results strongly suggest that intrinsically rewarding activity are associated with the same brain areas as primary rewards. Yet, studies also suggest different activations in response to primary/secondary and intrinsic rewards. For example, it has been shown that distinct neurons in the monkey orbitofrontal cortex encode either the values of knowledge acquisition or of primary reward, but not both [44]. Thus, the representation of intrinsic rewards may be partially separable from primary rewards at the cell level. At a system-level, different regions may be necessary for domain specific pleasure. For example, musical pleasure is correlated with activity in the auditory cortex [41[•]]. This suggests that intrinsic rewards may involve both activation of the system involved in processing primary rewards as well as additional regions within the neocortex. Further studies are needed to support these conclusions.

Concluding remark

Intrinsically rewarding activities include a large variety of human behaviours, ranging from play to scientific discovery and art. We hypothesize that the rewarding nature of these activities lies in their ability to trigger a sense of increased self-efficacy. Often this is the result of learning (e.g. knowledge acquisition, skill development, motor learning, consolidation etc.), but situations that increase one's sense of confidence and positive expectations (and thus sense of self efficacy) will also be rewarding, even if this sense is in fact false. Intrinsically rewarding activities seem to elicit a neural response similar to that elicited by primary and secondary rewards, despite not been directly associated with such rewards. These signals in turn generate positive emotions and reinforce the activity that triggered them.

While a large body of literature has been dedicated to the empirical study of primary and secondary rewards the empirical study of intrinsic rewards is still in its infancy and many open questions remain. Studies are scarce and replicability has not yet been tested. We hope this opinion piece will generate research that examines the key hypothesis described. In particular, are rewarding activities rewarding because they increase self-efficacy? Is an increased sense of self efficacy necessary for an intrinsically rewarding activity to be rewarding? Do all processes that increase self-efficacy activate the neural reward system? Do they share a common neural response with primary rewards?

A starting point for investigation could be to systematically establish that different tasks which are not linked to any extrinsic rewards are indeed rewarding. This could be done for example by quantifying approach behaviour, positive feeling, reinforcing power and neural response in the brain reward system to these activities. These metrics could also be used along with experimental manipulation of the sense of self-efficacy. Participants could be exposed to the same task under different conditions generating different levels of self-efficacy. Interestingly, the use of false feedbacks could further dissociate between the actual improvement and the subjective belief regarding improvement. This line of research is challenging as intrinsic rewards are difficult to quantify, yet critical for a full and deep understanding of the human experience.

Conflict of interest statement

Nothing declared.

Acknowledgement

TS is funded by a Wellcome Trust Senior Research Fellowship.

References and recommended reading

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

- of special interest
- . of outstanding interest
- 1. Blain B, Rutledge RB: Momentary subjective well-being

• depends on learning and not reward. *eLife* 2020, **9** e57977 This paper disentangles a neural secondary-reward signal from a learning signal in a reinforcement learning task and shows that happiness ratings depends more on the latter.

2. Taquet M, Quoidbach J, Gross JJ, Saunders KEA, Goodwin GM: Mood homeostasis, low mood, and history of depression in **2 large population samples.** *JAMA Psychiatry* 2020, **77**:944-951 http://dx.doi.org/10.1001/jamapsychiatry.2020.0588.

- Rozek CS, Svoboda RC, Harackiewicz JM, Hulleman CS, Hyde JS: Utility-value intervention with parents increases students' STEM preparation and career pursuit. Proc Natl Acad Sci US A 2017, 114:909-914.
- 4. Schultz W: Neuronal reward and decision signals: from theories to data. *Physiol Rev* 2015, 95:853-951.
- Wang KS, Delgado MR: Corticostriatal circuits encode the subjective value of perceived control. Cereb Cortex 2019,

29:5049-5060 This study shows that people have an intrinsic preference for controlling outcomes, and that the reward system responds to such an opportunity.

- 6. 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

The article show that information seeking is modulated by the expected valance of the information, as are dopaminergic information prediction errors in VTA.

- Gottlieb J, Oudeyer P-Y: Towards a neuroscience of active sampling and curiosity. Nat Rev Neurosci 2018, 19:758-770.
- Pavlov IP: Conditioned Reflexes. London: Oxford Univ. Press; 1927.
- Harlow HF: Learning and satiation of response in intrinsically motivated complex puzzle performance by monkeys. J Comp Physiol Psychol 1950, 43:289-294.
- Montgomery KC: The role of the exploratory drive in learning. J Comp Physiol Psychol 1954, 47:60-64.
- 11. Csikszentmihalyi M: *Flow: The Psychology of Optimal Experience*. Harper & Row; 1990.
- 12. Bandura A: Self-efficacy: toward a unifying theory of behavioral change. *Psychol Rev* 1977, 84:191.
- Schapiro AC, McDevitt EA, Rogers TT, Mednick SC, Norman KA: Human hippocampal replay during rest prioritizes weakly learned information and predicts memory performance. Nat Commun 2018, 9:3920.
- Curry OS, Rowland LA, Van Lissa CJ, Zlotowitz S, McAlaney J, Whitehouse H: Happy to help? A systematic review and meta-analysis of the effects of performing acts of kindness on the well-being of the actor. J Exp Soc Psychol 2018, 76:320-329.
- Feng L, Guo Q: Beneficial effect of altruism on well-being among Chinese college students: the role of self-esteem and family socioeconomic status. J Soc Serv Res 2017, 43:416-431.
- Cardona G, Rodriguez-Fornells A, Nye H, Rifà-Ros X, Ferreri L: The impact of musical pleasure and musical hedonia on verbal episodic memory. *Sci Rep* 2020, 10:16113.
- Gold BP, Pearce MT, Mas-Herrero E, Dagher A, Zatorre RJ: Predictability and uncertainty in the pleasure of music: a reward for learning? J Neurosci 2019, 39:9397-9409.
- Huron D: Musical aesthetics: uncertainty and surprise enhance our enjoyment of music. Curr Biol 2019, 29:R1238-R1240.
- Cheung VKM, Harrison PMC, Meyer L, Pearce MT, Haynes J-D,
 Koelsch S: Uncertainty and surprise jointly predict musical pleasure and amygdala, hippocampus, and auditory cortex activity. *Curr Biol* 2019, 29:4084-4092.e4

This study shows that uncertainty and surprise are associated with musical pleasure, in relation with amygdala, hippocampus and auditory cortex activity.

- Ly V, Wang KS, Bhanji J, Delgado MR: A reward-based framework of perceived control. Front Neurosci 2019, 13.
- 21. Ten A, Kaushik P, Oudeyer P-Y, Gottlieb J: Humans monitor
 learning progress in curiosity-driven exploration. *PsyArXiv*. 2020 http://dx.doi.org/10.31234/osf.io/7dbr6

The authors show that when people have the choice to perform different tasks, they prioritize tasks that maximise learning progress.

- Singh S, Lewis RL, Barto AG: Where do rewards come from. In Proceedings of the Annual Conference of the Cognitive Science Society; Cognitive Science Society: 2009:2601-2606.
- Behrens TEJ, Muller TH, Whittington JCR, Mark S, Baram AB, Stachenfeld KL, Kurth-Nelson Z: What is a cognitive map? Organizing knowledge for flexible behavior. *Neuron* 2018, 100:490-509.
- Ryan RM, Deci EL: Intrinsic and extrinsic motivation from a selfdetermination theory perspective: definitions, theory, practices, and future directions. Contemp Educ Psychol 2020, 60 Article 101860.
- Ruggeri A, Markant DB, Gureckis TM, Bretzke M, Xu F: Memory enhancements from active control of learning emerge across development. Cognition 2019, 186:82-94.
- Murty VP, DuBrow S, Davachi L: The simple act of choosing influences declarative memory. J Neurosci 2015, 35:6255-6264.
- Patall EA, Cooper H, Robinson JC: The effects of choice on intrinsic motivation and related outcomes: a meta-analysis of research findings. *Psychol Bull* 2008, 134:270.
- Owens D, Grossman Z, Fackler R: The control premium: a preference for payoff autonomy. Am Econ J: Microecon 2014, 6:138-161.
- Bobadilla-Suarez S, Sunstein CR, Sharot T: The intrinsic value of choice: the propensity to under-delegate in the face of potential gains and losses. J Risk Uncertain 2017, 54:187-202.
- Sharot T, Velasquez CM, Dolan RJ: Do decisions shape preference?: evidence from blind choice. Psychol Sci 2010, 21:1231-1235.
- 32. Katzman PL, Hartley CA: The value of choice facilitates subsequent memory across development. *Cognition* 2020, 199 104239.
- 33. Lee D, Daunizeau J: Choosing what we like vs liking what we
- choose: how choice-induced preference change might actually be instrumental to decision-making. *PLoS One* 2020, 15 e0231081

The authors show that choice-induced preference change results in a continuous reassessment of the option's value until a satisfactory level of confidence in value is achieved.

34. Meijer JH, Robbers Y: Wheel running in the wild. Proc R Soc B: Biol Sci 2014, 281 20140210.

- Li H, Spitzer NC: Exercise enhances motor skill learning by neurotransmitter switching in the adult midbrain. Nat Commun 2020, 11:2195.
- Novak CM, Burghardt PR, Levine JA: The use of a running wheel to measure activity in rodents: relationship to energy balance, general activity, and reward. Neurosci Biobehav Rev 2012, 36:1001-1014.
- Schwartenbeck P, Passecker J, Hauser TU, FitzGerald TH, Kronbichler M, Friston KJ: Computational mechanisms of curiosity and goal-directed exploration. *eLife* 2019, 8 e41703.
- 38. Vellani V, de Vries LP, Gaule A, Sharot T: A selective effect of

• **dopamine on information-seeking**. *eLife* 2020, **9** e59152 By manipulating dopamine levels pharmacologically, the authors provide causal evidence for the role of dopamine in information seeking.

- Bromberg-Martin ES, Hikosaka O: Midbrain dopamine neurons signal preference for advance information about upcoming rewards. *Neuron* 2009, 63:119-126.
- Cutler J, Campbell-Meiklejohn D: A comparative fMRI metaanalysis of altruistic and strategic decisions to give. NeuroImage 2019, 184:227-241.
- 41. Mas-Herrero E, Maini L, Sescousse G, Zatorre RJ: Common and
- distinct neural correlates of music and food-induced pleasure: a coordinate-based meta-analysis of neuroimaging studies. Neurosci Biobehav Rev 2021, **123**:61-71

This meta-analysis show that both music and food pleasantness correlated with neural activity in the same brain areas, including the ventral striatum and the VMPFC; musical pleasure is also associated with activity in the auditory cortex.

42. Chew B, Blain B, Dolan RJ, Rutledge RB: A neurocomputational • model for intrinsic reward. *bioRxiv* 2019 http://dx.doi.org/

10.1101/2019.12.19.882589 This study shows that a common brain region — the VMPFC — encodes affective responses to both extrinsic and intrinsic rewards (here, playing oames).

- Sharot T, De Martino B, Dolan RJ: How choice reveals and shapes expected hedonic outcome. J Neurosci 2009, 29:3760-3765.
- 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.