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Reward and emotion: an affective neuroscience approach

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Pleasure and reward are central for motivation, learning, feeling and allostasis. Although *reward* is without any doubt an affective phenomenon, there is no consensus concerning its relationship with emotion. In this mini-review we discuss this conceptual issue both from the perspective of theories of reward and emotion as well as human systems neuroimaging. We first describe how the reward process can be understood and dissected as intertwined with the emotion process, in particular in light of the appraisal theories, and then discuss how different facets of the reward process can be studied using neuroimaging and neurostimulation techniques. We conclude that future work needs to focus on mapping the similarities and differences across stimuli and mechanisms that are involved in reward processing and in emotional processing, and propose that an integrative affective sciences approach would provide means for studying the emotional nature of reward.

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Introduction

Our lives are characterised by a strong need for feeling good in the short and the long term. Human neuroscience has made significant advances in mapping the neurobiological and psychological pathways of pleasure and reward, but the conceptual distinctions between the closely related concepts of *emotion*, *reward* and *motivation* remain hotly debated. Reward is without any doubt an affective phenomenon, but is it also an emotion? Certainly not if one considers typical taxonomies of emotions that do not include reward as an emotion. However, when considering emotions such as interest, curiosity, joy, or pride, it is clear that the reward process is interlinked with the emotion process at many levels. In this mini-review we address this conceptual issue both from the perspective of theories of reward and emotion as well as human systems neuroimaging.

Is the reward process an emotion process?

Many approaches consider reward and emotion to be related, and sometimes emotions are even defined as states elicited by rewards and punishments: rewards may elicit emotions such as elation or extasy, and the absence of expected rewards may elicit frustration or rage [1]. Rewards are sometimes considered as a category of stimuli such that properties of emotion categories are ascribed to properties of stimulus categories. Stimuli that elicit pleasure are typically categorized as rewards, and such a systematic link between dimensions of stimuli and dimensions of emotions is observed broadly. For instance, the valence, arousal, or dominance dimensions are often used to describe *both* sets of stimuli and kinds of emotions. Such reverse mapping between stimuli and resultant emotion is useful both conceptually and experimentally, but it is not universal. For example, consider a satiated person who neither wants nor likes chocolate: for them, chocolate does not hold rewarding value. Similarly, feeding following an overnight fasting may satiate the person but it does not necessarily lead to experience of reward if the meal is considered unpalatable [2••].

Given this situational and subjective variation in value, reward process cannot be ascribed simply in terms of stimulus categories. Instead, reward processing depends on the homeostatic and psychological needs and goals. Reward devaluation procedures highlight that reward value depends on the needs and goals of the individual, underlining the importance of individual differences in reward processing and learning [3]. But if reward is not a property of stimuli, is it then an *evaluation* of stimuli? To circumvent the inconsistent link between 'emotional stimuli' and 'emotional responses', most theoretical approaches accept a relational account of emotion elicitation, where one stimulus may not always elicit the same emotional response in different individuals or even in the same individual. Should it concern food, music, perfume, caresses, money, or even knowledge, this opens the question regarding the neural and psychological evaluative mechanisms that transform a sensory stimulus into a reward.

Mechanisms involved in the evaluation of pleasantness or goal-conduciveness allow a rapid appraisal of valence [4] and may underlie the reward evaluation. Constructs such as goal-relevance, primary appraisal, or motivational relevance that are often used in theories of emotion can be related to key constructs in theories of reward. Accordingly, a conceptual link between the incentive salience hypothesis [5] and appraisal theories of emotion [6] has been suggested [7,8]. As reward can be dissociated into *wanting*, *liking*, and *learning* components, the incentive salience hypothesis highlights that a stimulus has to be motivationally salient to be rewarding. In this approach, *wanting* allows one to mobilize effort in order to obtain a stimulus that is typically pleasurable. Electrophysiological studies using pattern classification approach have found that wanting and relevance coding both take place automatically and rapidly (between 100 and 150 ms), that their ratings are correlated, and that they share similar feature weight maps [9]. Although emotion theories disagree on the mechanism that transforms sensory inputs into emotions, most theories agree that a stimulus needs to be relevant or significant for the organism's homeostatic or psychological needs to elicit an emotion [10]. A parallel has been suggested between motivational saliency and the appraisal notion of appraised relevance [7,8]. A suggested shared brain system for appraised relevance and reward processing is the amygdala, a region typically found to be involved in both appraised relevance and reward processing [11].

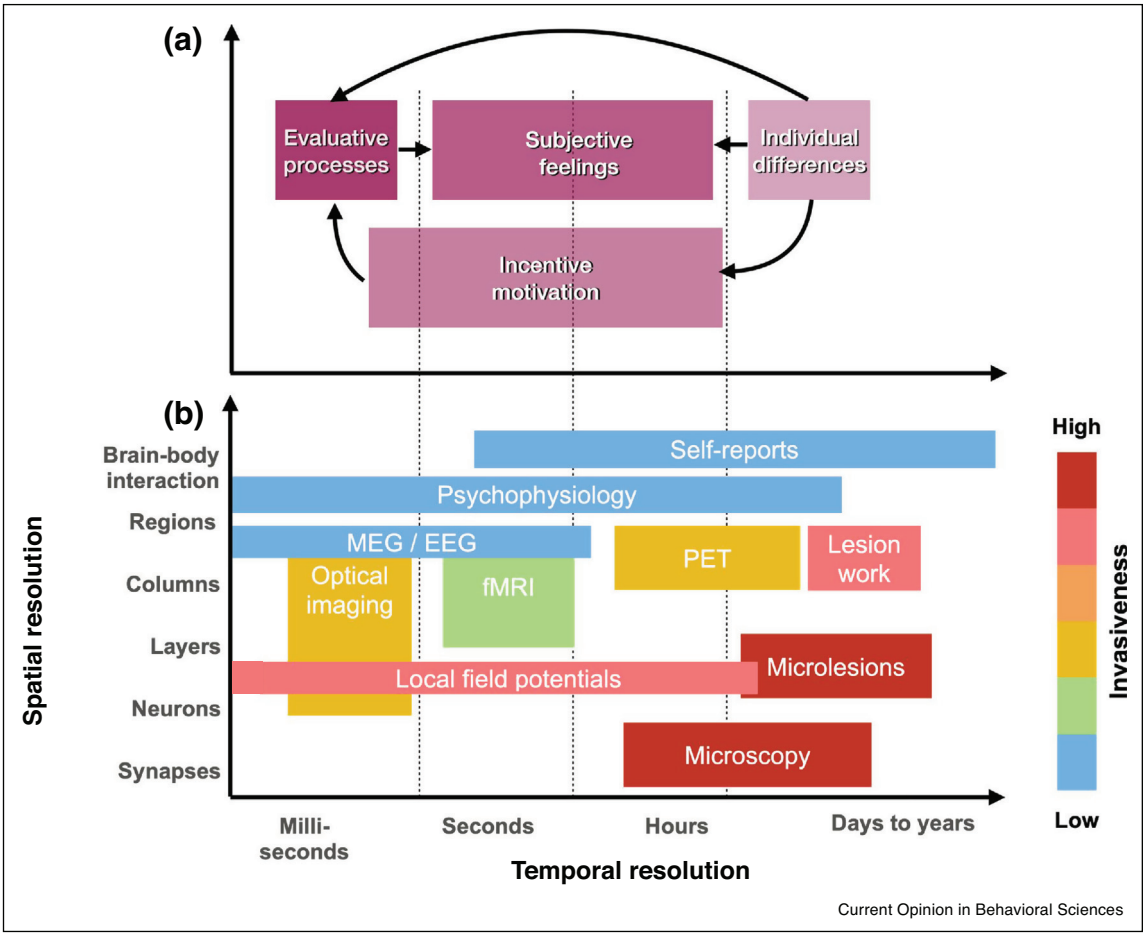
The idea that reward processing includes affective relevance evaluation accords with perspectives suggesting that mechanisms that allows predicting the expected value of the reward precede reward consumption. For an individual, any cue that is predictive of the probability that she may feel a given affective experience is particularly relevant. The valuation of a stimulus may allow an anticipatory affect relying on activity of the nucleus accumbens [12], and recent evidence suggests that curiosity elicitation relies on the ventral striatum [13]. Most models of emotion consider that several components of an emotional response follow a series of specific mechanisms involved in the elicitation of the emotion [11]. Similarly, models of rewards consider that after a process of wanting/expected value/reward prediction/anticipatory affect, an affective response occurs that can be related to prediction error or to the consumption of the reward such as liking [5] or positive arousal with an approach action tendency [12]. Such a distinction also warrants asking whether reward is also part of the *emotional response*. Measures of the reward-related response can be conceptualized for typical components of the emotional response: In autonomic nervous system, reward is associated with an increased psychophysiological arousal (e.g. electrodermal activity, heart rate . . .); with respect to the action tendency response, reward is associated with an increased approach tendency; with respect to the motor response, reward would be particularly associated with 'liking' orofacial expressions (e.g. tongue protrusions, smiles . . .); and, with respect to the feeling response, reward is associated with phenomenological hedonic experience of conscious liking, or as it is often conceptualized in human studies, *pleasure*.

Measuring rewards and pleasures in the brain

Above we proposed that the reward process is intertwined with the emotion process and 'dissected' it into phasic subcomponents. These subcomponents start from the sensory and evaluative processes to those that are involved in the phenomenological experience of the pleasant emotional or appetitive-motivational stage, the actual motivational processes guiding the long-term allostasis and finally even longer-term differences in affective dispositions such as personality, preferences, and well-being. When the timescale of these processes is contrasted against the temporal resolution of common research methods used in affective neuroscience, it becomes clear that a complete picture of reward cannot be painted using any single technique in human. Figure 1 illustrates this by summarizing the approximate temporal and spatial resolution of some of the most common techniques used for measuring the phasic components of the reward process including evaluative processes, subjective feelings and incentive motivation, as well as individual differences in these processes and their elicitation. While, for example, PET excels in distinguishing alterations in slow phasic processes such as sustained motivation and mood [14], it does not allow characterising the fast-acting evaluative processes, which in turn can be reliably quantified with MEG and EEG [15]. Haemodynamic imaging, in turn, falls somewhere between these two time-points and whereas cortical transcranial magnetic stimulation can be used to indirectly influence the subcortical components of the reward circuit [16], most techniques allowing any sort of causal inference are limited to slower timescales.

The bulk of human neuroimaging on rewards and pleasures has been carried with BOLD contrast imaging (see Figure 2 and below). These studies have indicated dorsal and ventral striatum, amygdala, insula, thalamus, various brainstem nuclei and anterior cingulate and orbitofrontal and lateral frontal cortices in reward processing. This technique also allows temporally separating, for instance, the reward anticipation and consumption processes [17]. Although BOLD contrast lacks molecular specificity, neuroreceptor imaging with PET has confirmed that rewards ranging from feeding to social contact and physical exercise lead to release of both of the two key neurotransmitters involved in rewards: dopamine [18–20] and opioids [2,21,22]. Studies using systemic administration of dopamine and opioid antagonists have also found that these systems have distinct roles in modulating anticipation and hedonic feelings triggered by different rewards [23]. PET measurements are however complicated and subject to radiation exposure, currently PET studies only allow measurement of slow phasic

Figure 1



A framework for different subcomponents linking emotion and reward, and techniques for investigating them. **(a)** Putative timescale of some of the phasic components of the reward process. **(b)** Temporal and spatial resolution of common neuroscientific and behavioural measurement techniques used for investigating reward and pleasure.

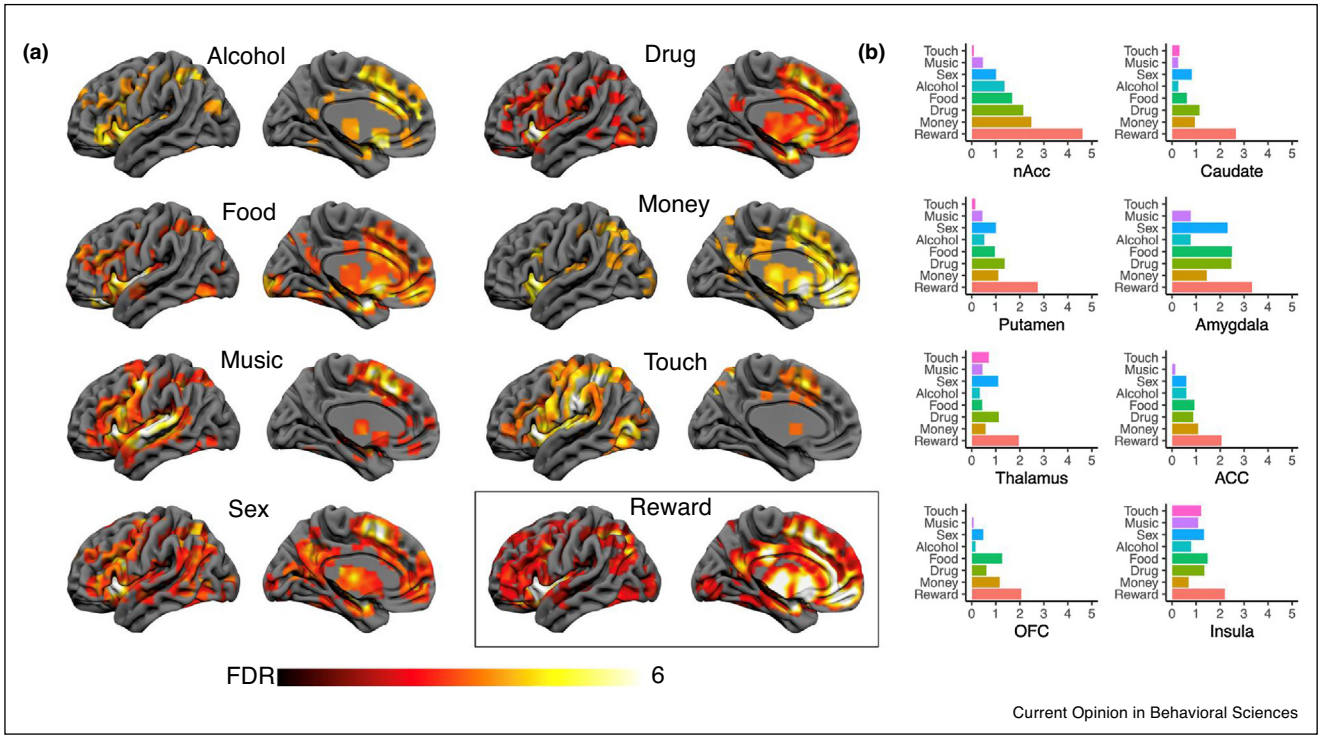
changes in neurotransmitter release, thus precluding dissociations of the different temporal aspects of reward processing.

Causality and correlation in reward and brain activation

BOLD-fMRI and PET studies cannot however confirm that the activated regions would be *necessary* for reward processing. Animal microstimulation studies have characterised the causal hedonic and incentive encoding properties of nucleus accumbens regions [24]. Such pharmacological studies cannot be done in humans and the few direct human electrical stimulation studies have yielded inconclusive results regarding the causal role of striatal activation and pleasure [5]. Outside striatum, meta-analyses however show that deep brain stimulation (DBS) in subgenual ACC and medial forebrain bundle is effective in alleviating depressive symptoms, but due to limited number of studies and variable stimulation sites it is difficult to translate these findings to reward function in healthy subjects [25]. And while r-TMS on dorsolateral prefrontal cortex is effective in alleviating depression [26,27], direct stimulation of the subcortical components of the reward system is currently not feasible in humans, although transcranial focused ultrasound stimulation of deep brain structures such as amygdala is already applicable in non-human primate studies [28].

Striatal and other subcortical components of the reward circuit are rarely directly influenced by traumatic brain injury (TBI) or infarctions, and the corresponding literature is sparse. One study [29] found that general and specific (musical) anhedonia following TBI occurs rarely, and does not clearly localize to any region based on 3D lesion mapping. Reward circuit is also surprisingly robust against neurodegeneration despite being affected by Parkinson's disease (PD). Although depression and impulse control disorders are common in PD [30], people with numerous neurodegenerative diseases such as

Figure 2



(a) Distinct and overlapping reward responses in the brain. Meta-analytic NeuroSynth uniformity test maps for specific rewards as well as different rewards combined (bottom right). The maps were obtained in August 27th 2020 using the keywords shown above each map. The uniformity maps test whether the proportion of studies reporting activations for voxel differs from what would be expected if activations were distributed uniformly throughout the grey matter. The data are thresholded at $p < .05$, FDR corrected. **(b)** Regional meta-analytic effects (z scores) for specific rewards. The bar charts show reward-specific mean effects in different anatomical components of the reward circuit. The averaged z-scores are square root transformed to aid in visualizing the skewed distribution of means.

Alzheimer's disease (AD) [31], PD [32] and fronto-temporal dementia (FTD) may still enjoy pleasures such as music [33]. Sexual dysfunctions such as hypersexuality are sometimes associated with PD, but these effects are typically linked with the dopamine agonist therapy [34]. Also, alterations to sexual drive and pleasure are uncommon following TBI [35], although some studies report lowered sex drive and motivation following TBI [36].

Finally, while anhedonia is commonly linked with depression and schizophrenia, even in these patient groups conscious liking responses may remain surprisingly intact [37]. The most consistent causal evidence between brain damage and reward processing comes from a lesion mapping study with smokers, that found that damage to anterior insula leads to causal and consistent disruption of smoking addiction [38]. Although interpreted as disruption of incentive motivation, it is possible that the insula damage also leads to disrupted experience of pleasure. Indeed, one recent study found that damage to right insula also disrupts perception of affective touch [39•]. All in all, the main conclusion from the studies allowing causal inference on brain and reward is that reward processing is remarkably robust against brain damage, and the causal roles of specific components of the striato-amygdalar and frontal circuits are still poorly understood in humans.

Could self-report be the common-currency measure for pleasures?

Given the diverse conceptualizations of reward and stimuli that may evoke it, what about the resulting phenomenological experience? Even the most carnal pleasures — enjoying a good meal or having sex involve different behaviours and sensory experiences, yet they share some underlying qualia that we describe as *pleasure*. But how should such subjective pleasure be defined and measured from the scientific point of view? Some aspects of the reward response are easier to study in human than in animal (e.g. the feeling component), and others can be studied both in animals and humans. While orofacial expressions are observed in animals during reward consumption [5] the two muscles that are typically involved in facial expressions of emotions in human are modulated during reward processing: rewards led to a relaxation of the corrugator, and an activation of the zygomaticus [40•].

Behavioural and physiological measurements such as licking [41] or ultrasonic vocalizations [42] are also commonly used to index pleasure in animal studies. Although objective, these measures are complicated by the diversity of behavioural indicators of pleasure and their complex linkage with actual reward anticipation or consumption in humans. For example, laughter is often equated with amusement, but is in reality a poor indicator of pleasure in humans [43] and copulatory vocalizations may not be linked with the actual reward peak (orgasm), but rather with partners' orgasm, suggesting a communicative rather than hedonia-dependent mechanism [44]. Salivation is reliably linked with appetitive motivation related to feeding [45,46], but not to social or sexual pleasures, and indicators of genital blood flow track sexual pleasure and arousal but not enjoyment of a good meal [47]. Accordingly, there is on-going debate whether such individual low-dimensional autonomic responses differentiate even between negative and positive emotional states [48,49].

One solution has been to focus on the self-reported emotional and motivational states [50]. Humans can provide complex evaluations of both sensory affective qualities as well as the resultant emotional states. However, humans have only limited access to their current mental, neural and somatic states, thus validity of emotional self-reports has been questioned on conceptual [51] and empirical grounds with data showing poor correlation between physiological and self-reported indices of emotion [52]. On the contrary, activity in the reward circuit can be used for forecasting reward engagement while viewing videos even better than self-reports [53••]. Thus, it is clear that the self-reports cannot constitute the ground truth in measuring reward and pleasure. However, subjective feelings correlate well with multivariate neural activation patterns associated with specific emotions [54,55•] as well as their bodily signatures [50]. Self-report also has the advantage that it can be made comparable across pleasures in human. Even though different in nature, pleasure elicited by sex, feeding, sociability and monetary rewards can be evaluated in human using the 'common currency' of a simple question: '*how pleasant does that feel?*'. This provides convenient and comparable metric to the hedonic value of different pleasures, even though they might be noisy at best and unreliable at worst.

Unknown pleasures

Human neuroscience has been surprisingly selective when mapping the pleasure space. Certainly because of methodological difficulties, there is a paucity of neuroimaging evidence on sexual pleasures (except studies on viewing other people having sex), actual social interaction (except studies on viewing other people being social) and even in the context of feeding related rewards, most studies have focussed on sensory evaluation of foods, rather than actual food consumption. Importantly, a large bulk of studies have established that artificial laboratory stimuli elicit significantly weaker neural responses than the complex and high-dimensional natural events that the brain has evolved to parse [56], necessitating a naturalistic approach for mapping the different pleasure systems in real-life contexts.

Such variability of neural basis of different rewarding behaviours and stimuli is evident in Figure 2, that shows-meta-analytic activation maps for different pleasures derived from the NeuroSynth database. Engagement of the putative reward network varies across pleasures (Figure 2a), both due to the stimulus modality but also likely due to the sensory properties of the stimulus itself, and the intensity of the elicited reward. Yet when asked, the subjects receiving any of these stimuli would (under the right circumstances) consider them as pleasant. This variability in reward-related neural responses is further demonstrated in Figure 2b with regional activation data extracted from Neurorsynth maps in panel A. Whereas there is consistent activity in the nAcc for all pleasures (expect touch), the consistency of these responses varies considerably, with most consistent response for monetary rewards. Other regions yield different patterns, such as strong bias for social pleasures in amygdala and ACC, and food and social rewards peaking in the OFC. These differential response patterns likely reflect both sensory differences between pleasures as well as the subcomponents of the appraisal and reward processes engaged during different rewarding contexts and conditions.

To understand phenomenological as well as neural and physiological aspects of different pleasures, we thus need to go both ways – to understand what is shared across all pleasures, but also simultaneously go beyond such 'g factor' of hedonia, and aim for detailed decomposition of different pleasures [57]. We thus need a better understanding of what is similar and what is different among the situations and events that people experience as subjectively pleasant. One way to approach this question is mapping rewarding properties of sensory signals using data-driven reverse correlation techniques. In this type of studies, response to stimuli drawn from high-dimensional stimulus space are measured to reconstruct the optimal stimulus for a given neural system [58]. With concomitant subjective ratings of the stimuli, this would allow comparison of the organization of the neural and phenomenological pleasure spaces [59].

Conclusions

There is a clear added value in considering rewards not just as a category of emotional stimuli and exploring the links between dynamic reward and emotion processes. Whether one can reduce emotion complexity to more fundamental affective dimensions has been the topic of

intense debates and it may be premature, or even inaccurate, to collapse all emotions into just rewards and punishments [60••,61]. Although the relationship between the reward process and the emotion process is neither a one-to-one matching nor dimensional mapping, the reward process definitely interacts with the emotion process. Although reward responses in the brain centre in the ventral striatum, there is considerable variability in how different rewards are processed in the brain (Figure 2). Further empirical and conceptual research should overcome the different research traditions that focus either on reward or on emotion in order to benefit from integrative affective sciences approach, and investigate the determinant role of reward processes both in the emotion elicitation processes and in the emotional response processes using multiple levels of analyses. In our view, an approach that addresses both the evaluative appraisal processes that determine whether something becomes rewarding, as well as the systems that govern reward-related behaviour and phenomenology would provide an integrative means for studying the emotional nature of reward. This could involve, for example, careful longitudinal measurements of motivational, evaluative and hedonic processes when adapting to new diets, social networks, or physical activity routines [62]. Combined with concomitant physiological, neural and phenomenological measurements, such time-series based analysis would yield critical new insight into the nature of emotion and reward in the brain, body, and mind.

Conflict of interest statement

Nothing declared.

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