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Neuroscience of affect: brain mechanisms of pleasure and displeasure

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Affective neuroscience aims to understand how *affect* (pleasure or displeasure) is created by brains. Progress is aided by recognizing that affect has both objective and subjective features. Those dual aspects reflect that affective reactions are generated by neural mechanisms, selected in evolution based on their real (objective) consequences for genetic fitness. We review evidence for neural representation of pleasure in the brain (gained largely from neuroimaging studies), and evidence for the causal generation of pleasure (gained largely from brain manipulation studies). We suggest that representation and causation may actually reflect somewhat separable neuropsychological functions. Representation reaches an apex in limbic regions of prefrontal cortex, especially orbitofrontal cortex, influencing decisions and affective regulation. Causation of core pleasure or 'liking' reactions is much more subcortically weighted, and sometimes surprisingly localized. Pleasure 'liking' is especially generated by restricted hedonic hotspot circuits in nucleus accumbens (NAc) and ventral pallidum. Another example of localized valence generation, beyond hedonic hotspots, is an affective keyboard mechanism in NAc for releasing intense motivations such as either positively valenced desire and/or negatively valenced dread.

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Introduction

Affect, the hedonic quality of pleasure or displeasure, is what distinguishes emotion from other psychological processes. Affect therefore distinguishes affective neuroscience from other branches of neuroscience, and in a sense, all affective neuroscience could be viewed as a search for affect in the brain. Yet to search for affect itself, as a core process of pleasure or displeasure, has rarely been the explicit goal of affective neuroscience studies. Consequently, the degree of understanding of how affect *per se* is created by brain mechanisms has remained relatively undeveloped even as brain studies of emotion have multiplied [1•]. Yet fortunately, substantial progress has begun to be made in the past few years in understanding brain mechanisms of pleasure and displeasure [2••,3,4,5].

We will focus here on the prototypical affect of pleasure as sensory reward. Pleasure and reward are important, both today and in evolutionary history. Healthy well-being requires capacity for normal pleasure reactions. Dysfunction in reward circuitry can produce affective psychopathologies ranging from depression to addiction. Evolutionarily, selected pleasure reactions shape behavior toward adaptive goals.

Reward involves multiple neuropsychological components together: first, the hedonic affect of pleasure itself ('liking'); second, motivation to obtain the reward ('wanting' or incentive salience); and third, reward-related learning. Each component likely played key roles in optimizing the allocation of brain resources necessary for evolutionary survival, by helping to initiate, sustain and switch behavior adaptively among different available options [5–7]. Here, we concentrate on describing the progress made in uncovering brain mechanisms involved in 'liking' or core pleasure reactions, but note that 'wanting' and learning components involve overlapping neural systems.

Pleasure arises from hedonic brain systems: subjective and objective features

What is pleasure or core 'liking'? First, pleasure is never merely a sensation. Even a sensory pleasure such as a sweet taste requires the co-recruitment of additional specialized pleasure-generating neural circuitry to add the positive hedonic impact to the sweetness that elicits 'liking' reactions (described in details below) [4,5,8]. Without that pleasure gloss, even a sweet sensation can remain neutral or actually become unpleasant.

Second, pleasure has not only subjective, but also objective features. Although the conscious experience of pleasure is its most striking feature, brain systems naturally evolved as objective mechanisms to produce behavior. Pleasure mechanisms were selected and conserved by the same natural evolutionary pressures that shape any

psychological function. Hedonic mechanisms require millions of neurons arranged into patterns of mesocorticolimbic circuitry, a combination constituting substantial biological investment that was unlikely to have evolved if affective reactions did not convey significant objective benefits [3,9•,10,11].

Our focus on objective affective reactions to identify core hedonic processes takes its lead from Darwin's original book on emotion over a century ago [12]. Darwin noted distinctive affective expressions (facial, bodily, and autonomic) in humans and animals in various emotional situations. Darwin's approach is also echoed by Joseph LeDoux's recent proposal: ''By focusing on survival functions instantiated in conserved circuits, key phenomena relevant to emotions and feelings are discussed with the natural direction of brain evolution in mind (by asking to what extent are functions and circuits that are present in other mammals are also present in humans)...'' (p. 654) [9•]. We similarly suggest that considering animal and human studies together allows the best progress to be made in understanding how affective reactions are mediated by brain systems.

Concerning human affect, not only can subjective pleasure ratings (liking in the ordinary sense) be assessed in adults, but also objective 'liking'-related reactions exist that can be measured in adults and even infants. In adults, objective affective reactions alone, without any subjective feelings, can occur as unconscious pleasures under limited circumstances (e.g. as unfelt but behaviorally biasing affective reactions to subliminally brief stimuli) [13–15]. The translation of objective 'liking' reaction into subjective pleasure feeling probably requires recruitment of additional brain mechanisms specialized for cognitive appraisal and conscious experience. An implication of the objective-subjective distinction is that subjective ratings of felt pleasure, while crucial signatures of human affective experience, are interpretive readouts of underlying affective processes, not always infallible windows into core pleasure reactions themselves. Indeed, 'liking' can sometimes occur unconsciously, and at other times even conscious pleasure ratings sometimes detach substantially from core affective reactions (as people concoct explanations to themselves for how they think they should feel) [16–19]. Therefore objective measures can be equally as useful as subjective measures for probing pleasure and displeasure mechanisms.

Comparing limbic systems: affect circuitry in humans and animals

The brain's circuitry for affective reactions spans from front to back of nearly the entire brain (Figure 1). Much of this circuitry is remarkably similar between humans and other mammals [20–22]. Even some apparent differences between humans and other species in limbic circuits may be more exaggerated in name than in fact. For example, essentially the same homologous region of deep ventral anterior cingulate cortex exists in both, but is called the subgenual anterior cingulate cortex (Area 25) in humans, and called infralimbic cortex in rodents.

Still, some real differences do exist between limbic brains of humans and other animals. The most obvious difference is the massive expansion of prefrontal cortex in humans, reflecting greater encephalization. Anatomically, encephalization also creates greater differentiation among prefrontal subregions. This may produce a few human cortex subregions that lack any clear homologue in nonprimates, such as dorsal anterior insula [23•]. This may also produce some neuronal differences, such as the granular layer in anterior orbitofrontal cortex of humans, that is, missing in rats.

Encephalization may also foster greater invasion by descending projections from prefrontal cortex into subcortical structures and functions. A possible human feature is greater 'freeway' connectivity, or direct projections between cortex and deep subcortical structures. By comparison, other animals might rely a bit more on 'local' road connections, which make more frequent intermediate stops. For example, descending projections from orbitofrontal cortex make more clearly defined connections to hypothalamus and brainstem structures in primates than in rats [24]. Conversely, ascending sensory pain and taste signals toward cortex from the brainstem primary visceral/sensory relay, the nucleus of the solitary tract in the medulla, may leap directly to the thalamus in primates, but make an obligatory stop at the pontine parabrachial nucleus in rats [23•,25]. Psychologically, human encephalization may consequently result in a greater cortical involvement of affect and emotion, expressed as top-down regulation of affective reactions. Still, mesocorticolimbic circuits for mediating core affective reactions are largely similar across all mammals.

Many pleasures: one hedonic brain system to mediate them all?

The sensory pleasure of a delicious-tasting food feels different from pleasures of sex or drugs. Even more different seem social or cognitive pleasures of seeing a loved one or listening to music. But does each psychological pleasure have its own neural circuit? Perhaps not. Instead there appears heavy overlap, with a shared mesocorticolimbic circuit or single common neural currency, involved in all those diverse pleasures [6,7,26–35]. Neuroimaging studies often implicate the same list of usual culprits as activated by various pleasures. The list includes cortical regions (e.g. orbitofrontal, anterior cingulate, and insula cortices) and subcortical structures (nucleus accumbens (NAc), ventral pallidum, amygdala, and mesolimbic tegmentum). This overlapping pattern opens the possibility that the same hedonic generating circuit, embedded in larger mesocorticolimbic systems,