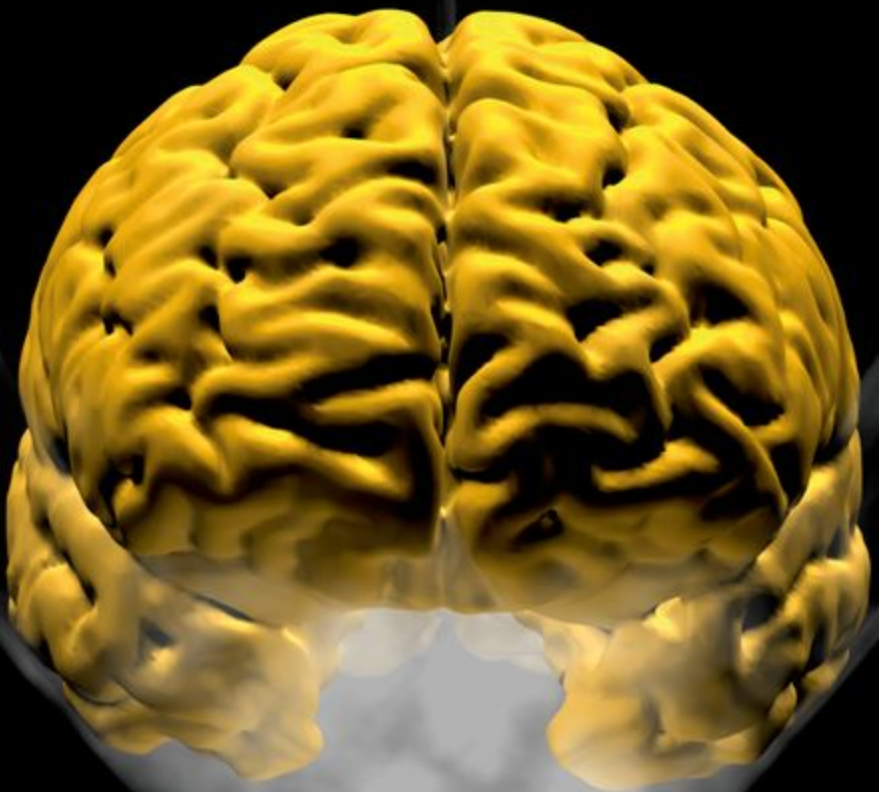
PLEASURES OF THE BRAIN



Edited by
Morten L. Kringelbach and Kent C. Berridge

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and

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PLEASURES OF THE BRAIN

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Introduction: The Many Faces of Pleasure

MORTEN L. KRINGELBACH AND KENT C. BERRIDGE

The American writer John Steinbeck wrote of "the tragic miracle of consciousness" and how our "species is not set, has not jelled, but is still in a state of becoming" (Steinbeck and Ricketts, 1941). He wrote about how consciousness offers us pleasures, desires, and the freedom of choice, but how this freedom is always accompanied by the certainty of the end. The negative side of this sentiment was emphasized by the French philosopher Jean-Paul Sartre who memorably wrote that "hell is other people" (Sartre, 1947).

Life may ultimately meet a tragic end, but the pleasure along the way is what makes it worthwhile. Pleasure is central to our sense of well-being. The very survival of every large-brained creature as an individual and the evolutionary survival of each species have depended on the pleasures afforded by its hedonic neural systems. We are rewarded by food, sex, and many other sensory and abstract incentives, and as members of a very social species, we also take great pleasure in the company of other people.

A better understanding of the pleasures of the brain might thus offer us fundamental insights into our own nature, into how brains work in daily life, and even into better ways to enhance our quality of life. Pleasures are of many sorts and occur in many different brains. The purpose of this book is set them together in one place, and as far as possible come to an understanding of how diverse pleasures arise from neural systems. While some of this pleasure is clearly consciously experienced, there are also nonconscious components, as convincingly shown by the some of the chapters in this book.

We were encouraged to begin this attempt to capture pleasure in a scientific net by the enormous progress in recent years of affective neuroscience as an important and exciting discipline (LeDoux, 1996; Panksepp, 1999). Through the studies of animals as well as humans, many important insights have been made regarding the brain mechanisms of pleasure, and related motivation and emotion.

It has become increasingly apparent that pleasure and reward are at the heart of affective neuroscience and the psychology of well-being (Berridge, 2003; Berridge and Kringelbach, 2008; Kahneman, 1999; Kringelbach, 2005; Leknes and Tracey, 2008). Pleasure is essential to a normal healthy life. The loss of pleasure, anhedonia, is a common theme in many mental illnesses such as depression, schizophrenia, and addiction, and any progress in understanding the functional neuroanatomy of pleasure thus holds the promise of better treatments.

At the same time, pleasure has sometimes been seen in psychology and neuroscience as perhaps a bit too subjective to be studied scientifically. But pleasure exists as a natural phenomenon, and we believe that what exists can be studied scientifically. While it is certainly true that pleasure is linked with our most subjective states of consciousness, at the same time, it is equally true that pleasure is a multifaceted psychological phenomenon with many constituent nonconscious components. A large part of the failure to

make progress in understanding the psychological and neural properties of pleasure may have simply been the reluctance of the scientific community to devote attention and effort to the task. This book is a beginning to redress this omission.

A multifaceted view of pleasure (and of emotion in general) can be helpful in studying pleasure in people and certainly in other animals—and crucially without having to determine whether consciousness is present in these animals (Kringelbach, 2004). As shown in this book, many highly successful experimental paradigms have been developed, which have subsequently given us new insights in the nature and mechanisms of pleasure.

In this book, we have asked many experts to present the state-of-the-art of their neuroscientific research into pleasure and reward. Ground-breaking developments have occurred on several fronts, and recently, there has been a convergence of interesting new data on pleasure coming from many disparate fields. The time seems ripe to present these important findings in a single volume. We hope this book will come to serve both as a starting point and as a reference volume to graduate students and scientists who are fresh to the world as well as to scientists coming from other related and unrelated fields.

The Chapters of this Book

The many faces of pleasure and reward raise interesting questions. We believe that it can be a strength rather than a weakness to have disagreements about certain fundamental concepts, as is the case with many emerging fields, in order to eventually develop the best concepts. To reflect the many different views, we have therefore opened the book with a special section designed extract, distill, and contrast alternative views on fundamentals. We invited the authors of the book to provide us with their answers to a number of common "fundamental questions" regarding the role of pleasure in the brain. It was optional for the authors, and some contributed to the section while others did not.

Contributing authors were encouraged to provide answers to only the questions they felt most passionate about. In other words, the "fundamental questions" section is an opportunity to see at a glance what various authors think are the bedrock conceptual foundations and guiding principles for their scientific studies of pleasure. We hope that this question section will be of great interest to readers on its own.

The rest of the chapters of the book are divided into three sections: animal, human, and clinical applications. This organization is merely for convenience; many issues span the sections and alternative groupings could easily be imagined.

Animal Pleasures

In the opening chapter of the first section, Smith, Mahler, Peciña, and Berridge offer a overview of some affective neuroscience research on finding hedonic hotspots in the rodent brain. The authors show how activity in cubic-millimeters of certain brain areas such as the nucleus accumbens and ventral pallidum can be manipulated to change the generation of pleasure 'liking'. They also discuss some aspects of the distinction 'liking' and 'wanting' of the same pleasure and show how dopamine is clearly more linked to the latter rather than the former.

In the next chapter, Burke, Miller, and Schoenbaum investigate the role of specialized corticolimbic circuits linked to pleasure in rats. These corticolimbic circuits connect together limbic forebrain structures to mediate conditioned reinforcement. They focus especially on three important brain regions: the basolateral amygdala, the orbitofrontal cortex, and the nucleus accumbens, and use devaluation paradigms and selective lesions to study how these three brain regions interact in a coherent circuit.

The chapter by Aldridge and Berridge focuses in more detail on the nature of the neural coding for pleasure in the hedonic hotspot of the ventral pallidum. Interestingly, neurons here code the hedonic impact of a pleasant taste and lesions to this brain region can abolish 'liking' reactions completely. The authors propose that neuronal events in this brain region may play a central role in applying the pleasure gloss to stimuli that makes them rewarding.

Dickinson and Balleine offer an overview and a hedonic interface between pleasure and cognition in their chapter. They show how the function of hedonic and affective experience may be to act as a goal interface between cognitive and motivational systems, interface that is required because these systems use incommensurate psychologies embedded in their somewhat separable neural systems. Aspects of this theory have, in their own words, many "similarities to of the Freudian process of *cathexis*," and reveal a remarkable subtlety in the psychology of pleasure that is shared by humans and other animals.

The animal section concludes with a chapter by Watson, Shepherd, and Platt who investigate the

neuroethology of pleasure in nonhuman primates. In particular, the authors show how neuroeconomics and neuroethology can come together to inform the research in pleasure and reward.

Human Pleasures

The second section begins with Frijda's thoughtful chapter on the nature and function of pleasure in daily human life. The chapter is a thorough investigation of the psychology of pleasure. The following chapter by Cabanac provides an overview of the physiological and philosophical investigations of pleasure by the chief originator of the scientific study of "alliesthesia" that has played such an important role in studies of the affective neuroscience of pleasure. Cabanac takes an evolutionary approach to pleasure and discusses links among primary sensory and social pleasures linked to survival and procreation.

The sensory pleasures of food, taste, and smell and their brain bases are the subject of the next two chapters in the human section. The chapter by Gottfried provides an authoritative overview of the human olfactory system. In particular, the author presents recent neuroimaging data on olfaction, which have confirmed that smells are intimately linked to hedonics, pleasure, and emotion. Similarly, the following chapter by Veldhuizen, Rudenga, and Small provides an overview of the human taste system, and in particular describes important new neuroimaging data that help reveal human brain bases of flavor pleasures and show the close links between taste and smell in food hedonics.

Sexual pleasures are also a prominent sensory hedonic experience that has been shaped by evolutionary selection pressures on brain systems, and the book has two chapters devoted to our current understanding of this all-too often taboo subject. In one chapter, Komisaruk, Whipple, and Beyer investigate how sex is good for our health and describe studies in particular of the neural systems and neurotransmitters involved in sexual excitement and in orgasm. Next, Georgiadis and Kortekaas review in their chapter an array of important functional neuroimaging studies to bring together what is known about brain mechanisms of sexual pleasure in people and describe neuropsychological and pharmacoendocrinological anomalies that affect human sexuality.

Both food sensory pleasure and sexual pleasure are compared and linked to research on the social pleasures in the chapter on fundamental pleasure systems by Kringelbach, which proposes a general theory for the mechanisms and functional neuroanatomy of pleasure. Kringelbach gives a special analysis of the role of orbitofrontal cortex in human hedonic reactions, a prefrontal region in cortex that has sometimes been viewed as the apex of pleasure processes in the brain.

Dopamine has long been a favorite topic for neuroscientists interested in pleasure and reward, but it has only recently become possible to link pharmacological and neuroimaging studies together in penetrating experimental designs that reveal whether dopamine actually produces pleasure in humans. Leyton's work leads the way in these efforts, and his chapter links the animal research on dopamine with his exciting new neuroimaging research in people to show how dopamine is implicated in the regulation of mood and motivational states in humans but perhaps not pleasure per se. In particular, the chapter shows how dopamine strongly influences sustained interest and approach, weakly influences positive emotions, yet elegantly shows that dopamine affects human pleasure ratings only tenuously, if at all.

Higher pleasures such as monetary, artistic, musical, altruistic, and transcendent pleasures can perhaps be studied only in people, and recent neuroimaging studies have made some headway in exploring these important human pleasures. The chapter by Vuust and Kringelbach explores the pleasures evoked by music. It traces what is known about brain activity patterns during musical enjoyment and shows how much remains to be discovered about this powerful, and perhaps unique human, positive reward. In a related analysis of human art, the emerging field of neuroesthetics is described in the chapter by Skov. The author in a sense links artistic and social pleasures in a proposal that creating art always involve a desire to affect some hedonic impact in an observer.

Finally, many of the strands of what humans know about their own pleasure are pulled together in the chapter by Schooler and Mauss. The authors describe the psychological research on the experience and meta-awareness of pleasure. They show how many of our most pleasurable experiences occur with little meta-awareness of the fact that we are experiencing pleasure and how conscious attention to pleasure can distort or even destroy the underlying hedonic process.

Clinical Applications

The final section consists of three chapters describing how our current knowledge of pleasure can come to impact on our understanding and treatment of pain. The clinical chapter by Petrovic describes

neuroimaging studies of how placebo modulates pain and relates these findings to the underlying processes of pain relief, i.e., pleasure, in the human brain.

Next, Green, Pereira, and Aziz explore the important topic of pleasure electrodes and brain stimulation therapy in human patients, describing growing evidence of how deep brain stimulation can give pain relief to patients with severe chronic pain from, for example, phantom limbs.

The final chapter by Leknes and Tracey provides a conceptual and empirical overview of pleasure in mind and brain. They revisit the important questions raised by the English philosopher Jeremy Bentham about whether pleasure and pain are in fact the "masters of mankind," and link those questions to many of the new scientific developments described by earlier chapters.

The Future of Pleasure in Affective Neuroscience

We hope that the reader will come to enjoy the richness of the chapters in this book. A book on pleasure ought to give some. We hope readers might obtain at least the pleasure of seeing progress in understanding of how hedonic psychological processes are instantiated in brain mechanisms and of a sense that scientific perspectives are gaining a better handle on the slippery topic of pleasure. The contributors here are all leaders in their fields of hedonic psychology and the affective neuroscience of pleasure. They each provide important pieces to the puzzle, which constitutes our current knowledge of the nature of the many faces of pleasure as embedded in our biological brains.

Neuroscientists, psychologists, and related investigators have come a long way in this exploration though our current state of knowledge could equally well be described as a state of only slightly mitigated ignorance. Ignorance is, we all agree, not bliss when it comes to pleasure and brain, and we hope that a better understanding of the functional neuroscience underlying hedonic impact will ultimately come to help more people who live currently without pleasure in their lives. At the very least, we hope that the challenges and opportunities of this exciting scientific adventure will attract many other neuroscientists and lead to further progress in the affective neuroscience of pleasure and insight into the very core of what makes us humans.

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Fundamental Pleasure Questions

Basic Pleasures

1. Is pleasure necessarily a conscious feeling? Or can hedonic reactions ever be unconscious?

Berridge: Surprisingly, hedonic reactions can be unconscious, even though a conscious feeling of enjoyment is central to traditional definitions of pleasure. For example, unconscious 'liking' reactions can occur in people without any subjective awareness at all of the reaction at the moment it is caused (by a subliminal happy face), yet go on to influence later consumption behavior and evaluative ratings of a valence-laden ingestive target (e.g., Winkielman et al., 2005), presumably by directly activating brain limbic systems (Morris et al., 2001). It seems fair to say that there is an unconscious pleasure when a brain generates a positive hedonic 'liking' reaction of which the introspecting mind remains unaware.

My answer does not mean that all instances of behavioral positive reinforcement must entail pleasure, regardless of pleasure reports (Rolls, 2005). There are other routes to behavioral reinforcement besides pleasure, conscious or unconscious (e.g., pure 'wanting' without any 'liking' at all; procedural habits, etc.). But independent evidence for unconscious 'liking' reactions, even if rare, must force us to expand our definition of pleasure.

Cabanac: Yes, which implies the answer to the question that follows is … no.

Aldridge: I assume that pleasure requires consciousness. Hedonic reactions might not require consciousness (e.g., reflexive taste reactions). Hedonic reactions, which an observer might interpret as indicating a pleasure, may or may not be "actual pleasure" in the subject.

Frijda: Pleasure, if not defined as conscious feeling, is not necessarily conscious. That is, pleasure as a feeling is based on pleasure processes that by themselves are nonconscious and can remain so. Felt pleasure is but one of the outputs of those processes.

Leknes: It is certainly possible to exclude unconscious feelings from one's definition of hedonic reactions such as pleasure. In my opinion, such a definition would miss most of the processing underlying conscious hedonic feelings. Who has never felt their attention drawn away from the task at hand due to a feeling of discomfort, which, upon introspection, has been mounting over time without one's awareness? If this is the case for unpleasant sensations, I can see no reason why pleasant feelings should be different in this respect.

Dickinson: Yes, pleasure is necessarily a conscious experience because this experience grounds the attribution of incentive value to objects, people, and events. However, behavioral responses that accompany pleasure may well be mediated through unconscious processes.

Shizgal: Yes and yes. In common parlance, pleasure refers to a component of conscious experience.

In this view, pleasure is a conscious feeling by definition, and an unconscious pleasure is an oxymoron. The experience of pleasure depends on higher levels of the hedonic apparatus. In contrast, processing at lower levels may operate in the absence of awareness.

An analogy to visual processing serves to illustrate the distinction between the more limited meaning of the first part of the question and the broader meaning of the second one. Information flows from the retina through the multilevel thalamo-cortical division of the visual system. The crucial work performed by cells at lower levels of the pathway, in the retina and visual thalamus, appears to be beyond the ken of the conscious processor. For example, such cells fail to show the lightness constancy that allows our conscious perception of surface reflectance to remain so remarkably stable under varying ambient illumination. In contrast, the responses of cells in the primary visual cortex do show lightness constancy and are thus correlated with visual experience (Shimojo et al., 2001).

The conscious processor is typically described as serial in nature, severely bandwidth limited, and slow. In order to allow a huge number of computations to be performed in parallel by the nervous system, most must occur below the waterline of awareness, and only certain signals are capable of gaining access to consciousness. We are incapable of bringing a retinal image into consciousness, and we should be grateful for this inability—the two-dimensional retinal image is highly ambiguous and contains high spatial resolution only in a small portion of the central field. Extensive lower-level processing is required to organize edges, surfaces, and the results of numerous eye movements into what ultimately emerge as stable, conscious percepts of objects arrayed in a three-dimensional visual world. If the conscious processor had to worry about the details of these crucial lower-level processes, it would be overwhelmed. The bandwidth limitation of the conscious processor is also evident in the hedonic domain. We close our eyes when experiencing intense pleasure and may do so as well when making demanding hedonic evaluations such as determining the relative merits of different wines. However, when distraction undermines the experience of pleasure, hedonic processing at lower levels continues unabated. No matter how engaging the dinner conversation or how breathtaking our companion, we don't tend to eat distasteful items on our plate. Habitual users will continue to work for injections of weak doses of an addictive drug even when unable to accurately report the presence of the drug in the injected solution (Lamb et al., 1991). Thus, hedonic signals can be divided into a class that cannot enter into awareness and a second class that can; whether or not a signal in the latter class succeeds in entering consciousness depends on its fate in the competition for attentional and working-memory resources.

Gottfried: Yes, pleasure is necessarily a conscious feeling, if that is how one wishes to define pleasure. Such a definition would seemingly limit pleasure to the rarefied society of humankind. Certainly the scientific challenges of determining whether a nonhuman animal has feelings, or is conscious of them, have not yet been overcome.

On the other hand, no. Pleasure does not have to be a conscious feeling, if one considers it more simply as a hedonic reaction to particular sensory inputs without reference to consciousness or feelings. Importantly, by this standard, hedonic reactions can be measured. Being measurable they have been shown to influence behavior at an unconscious level. Putative pheromones are one example in which hedonic reactions occur outside of conscious awareness. These chemosensory signals can operate at subthreshold concentrations and have been shown to influence human behavior, mood, and perhaps even mating selection. In the visual domain, studies of affective blindsight and unconscious emotional learning also indicate that the affective content of unseen pictures and faces alter physiological and neural indices of hedonic processing. I favor this more inclusive definition of "pleasure" as it embraces human animals and nonhuman animals alike.

Kringelbach: Pleasure can be defined as the conscious experience of reward but it is questionable whether such a narrow definition is meaningful or useful. Much of our brain activity is not available for conscious introspection and neuroscientific evidence from humans and other animals has made it clear that nonconscious brain activity is essential for controlling our behavior. Some of this nonconscious brain activity is related to hedonic processing and may lead to hedonic reactions, where we are not conscious of their origin but where we are nevertheless happy to confabulate about the causes.

In a similar way to how it is has proven useful to divide emotion into the nonconscious and conscious subcomponents of emotions and feelings, it might be more useful and meaningful to divide pleasure into both nonconscious and conscious subcomponents of evaluative hedonic processing. Such a definition would hold that while pleasure plays a central role for emotions and conscious feelings, it is not itself a conscious feeling.

2. Is pleasure simply a sensation, like sweetness? Or is the hedonic impact of sweetness and other sensory pleasures somehow added to the pure sensation signal?

Berridge: Pleasure is more than the sensation that causes it. Pleasure is an additional niceness gloss painted upon the sensation (as Frijda puts it). Pleasure always must be actively generated by brain hedonic circuits to transform a mere sensation such as sweetness into something nice.

Aldridge: Given my answer to question 1 (above), I would say pleasure is more than a sensation. Hedonic reactions may be responses to simple sensations and may look to an observer like pleasure, but they are only reactions. In this view, "pleasure" requires a human to report it.

Frijda: Pleasure is not a sensation. It is a "pleasantness gloss" added to whatever is pleasant. Pleasure is always pleasantness of something. When the feeling is focused on, it disappears (it is "evanescent").

Leknes: It is likely that the pleasantness of chocolate is related to our perception of its sweetness, fattiness, etc. Eating chocolate is not pleasurable to a sated subject, however, although it is probably safe to assume that the sensory properties remain unchanged (Small et al., 2001). A simple model would propose that pleasure arises from a weighted combination of the sensory signals and of signals about homeostatic state (i.e., how useful the stimulus is for the organism).

Dickinson: No, pleasure is not a sensation, but an affective experience that accompanies but is usually also integrated with sensation in experience.

Shizgal: No and no. The purpose of sensory systems is to provide facts about the world. These systems are engineered to function as objectively as possible. Thus, the lightness constancy mechanism to which I referred in my answer to question 1 does a remarkable job of accurately reporting the reflectances of surfaces, regardless of whether they are in full sunlight or deep shadow. Similarly, the color-constancy mechanism largely compensates for the spectral changes in the illuminant over the course of the day, preventing a forager from confusing an unripe fruit viewed at dawn with a ripe one viewed at noon.

Hedonic systems provide a subjective commentary on the information provided to them by sensory systems. Both a warm stimulus encountered when one is hypothermic and a cool stimulus encountered when hyperthermic are experienced as pleasant. As Michel Cabanac has argued, their subjective meaning is similar—they are both good for us and are sought out because they help return a crucial physiological variable to its regulated value. Nonetheless, we do not confuse the sensations arising from the two stimuli. We perceive them as objectively different even if their subjective hedonic values are the same.

Mixing the objective and subjective signals could prove harmful. For example, if judgments about the sugar and fat content of prey items depended on the hedonic experience that accompanies their consumption, a forager could make errors in trading off amount, procurement costs, and quality, thus failing to maximize net energy intake. Thus, accurate sensory assessment is crucial to determining the relative value of prey items. However, hedonic signals, which depend on the physiological and ecological state of the forager, could provide information about absolute value and thus adjust key decision variables such as risk appetite.

Kringelbach: Pleasure does not fit most common definitions of sensations, as pointed out by Ryle (1954). Instead, pleasure would appear to be part of the subsequent valuation of sensory stimuli needed in decision making, including most importantly the hedonic valence.

The pleasure or hedonic impact of sweetness will elicit what has been termed "acceptance wriggles" by Frijda (see this volume), which adds the hedonic gloss to the sensation, which we experience as conscious pleasure. These pleasure-elicited behaviors are also present in other animals including rodents who will lick their lips to sweet foods as convincingly described by Berridge (see this volume) and can be taken as an objective measure of the pleasure elicited. While human infants initially exhibit similar kinds licking of their lips for sweet foods, these stereotyped behaviors disappear after a while. Humans still, however, exhibit much pleasure behavior from the carefree smiles and laughter of pleasant social interactions to the deep groans of sensory and sexual pleasure. Most people would instinctly feel that our pleasure would somehow not be quite the same without these pleasure-elicited behaviors and the case could be made that it would in fact not be pleasure but "false" pleasure. Consciously engaging the pleasure-elicited behaviors even without conscious or nonconscious elicited pleasure may start a positive feedback loop, which recruits hedonic processes, as in the experiments of Strack et al. (1988) where affective responses became stronger when participants were required to hold a pen in their mouth in ways typically associated with smiling without requiring them to pose in a smiling face—and significantly less strong when not engaging these smiling muscles.

3. Is human pleasure similar to or different from that of other animals?

Berridge: The answer is yes, both. Human pleasure is unique in the sense that unmatched human cognitive capacities transform our mental representation of pleasant events into accompanying elaborate thoughts. Human cognition adds richness and alters the attention we pay to pleasures, elaborates our plans to get them, vastly expands the range of events that can trigger pleasure to include cognitive and cultural sources (art, music, social rewards, etc.), and provides new top-down regulatory ways to amplify or dampen a pleasure or displeasure.

But as an affective neuroscientist trying to find out how brains generate basic sensory pleasures, my answer is: human pleasure is essentially the same as other animals (at least other mammals, and possibly beyond). Humans and animals share the same limbic brain circuits and likely have the same hedonic hotspots to generate pleasure. Those hedonic limbic circuits operate as far as we know by the same neurochemical signals and circuit rules in humans and nonhumans alike.

Cabanac: May I answer that question with another question? Is YOUR pleasure similar to or different from MY pleasure? Or with a similar question: is female orgasm similar to male orgasm? Yet we know that pleasure fulfils the same function in animals and humans: optimization of behavioral decisions.

Aldridge: It is not possible to determine if pleasure is the same in animals and humans. Hedonic reactions may appear to an animal observer to be similar. Neuroscientists may be able to demonstrate that hedonic reactions involve homologous brain systems. Scanning or pharmacological experiments may also demonstrate similarities between neurochemically defined brain systems of animals and humans. Neither of these would prove that pleasure is the same in animals and humans.

Frijda: Human pleasure is similar to and different from that of other animals, like a glass is both half full and half empty. The reason is simple. See my answer to question 2: what pleasure is about is different between humans and other animals because animals do not know that they are feeling pleasure, but functionally (e.g., in evoking acceptance wriggles). I assume they are the same.

Komisaruk: I think pleasure is not unique to humans. Therefore, I think that pleasure does not require language ability. When my sons come home, I would say that their dogs greet them happily. If and when they scold their dogs, their dogs do not look happy. A dog wagging its tail looks to me like a happy dog—that is, a dog that is feeling pleasure (I sense my animal behavioral, anti-anthropomorphizing colleagues gritting their teeth). Similarly, when my cat purred, she looked to me as if she were content, that is, feeling pleasure. She never purred if she appeared to be disturbed in any way. It would perhaps be useful to see whether purring and tail-wagging could be used as valid indicators of pleasure—pharmacologically speaking. Questions such as these, while difficult to answer, are far more manageable than the question of which and how neurons produce any bit of awareness. However, still more difficult is the question of which and how neurons produce a bit of the feeling of pleasure.

Dickinson: Depends on what animals—ape, rat, or cockroach? My view would be that any cognitive animal (i.e., one capable of true goal-directed action) experiences states of pleasure that are similar to our own.

Kringelbach: Pleasure serves a central role in fulfilling the evolutionary imperative of survival and procreation. This means that for all animals the sensory pleasures linked to food intake is likely to be a basic pleasure. Similarly, the social interactions with other members of the same species, which could potentially lead to the propagation of genes, have probably been selected for, which means that social pleasures must also be basic. Also progeny may elicit social pleasure as in the very important social bond between parents and infants. In social species such as most mammals, it might be that social interactions are at least as pleasurable as the sensory pleasures related to food intake.

Careful neuroscientific experimentation in humans and other animals have shown that evolution appears to have preserved many brain circuits between species. Some of these brain networks must be involved in pleasure and pleasure-elicited behaviors. Thus it is likely that human pleasure will share many features with other animals and particular those closest related such as other mammals and primates. Yet, it may well be that human conscious experience of pleasure is different not only in degree but also in kind from other animals. Activities combining sensory and social pleasures such as those involved in a dinner party could have a synergistic effect on the higher-order pleasures experienced in humans, which might be hard to find in other animals.

4. Is pleasure simply the experience of getting what you want? Are liking and wanting simply two words for the same pleasure process? Or can pleasure liking or pleasure wanting exist without the other?

Berridge: Getting what you want is different from liking what you got. Getting what you want is not always pleasurable. And even when it is, its pleasure is quite different from the wanting and getting. Taking pleasure in what you get requires the additional 'liking' gloss, a distinctive and hedonic brain process of its own. If that hedonic process is lacking, then getting what you want will produce no true pleasure.

Aldridge: *First question:* I don't know. *Second question:* The Berridge scheme divides 'liking' and 'wanting' into two separate psychological processes. In that scheme, it doesn't make sense to call them the same thing and there is good evidence that 'liking' and 'wanting' can be manipulated independently. It is yet to be determined how 'liking' and 'wanting' map onto pleasure. In my view, pleasure is a process involving all brain systems processing reward information (cortical and subcortical) so 'liking' and 'wanting' would be combined. *Third question:* I don't know what "pleasure liking" or "pleasure wanting" are or how they differ from 'liking' and 'wanting'.

Frijda: Pleasure does not consist in getting what you want but, more generally, meeting what befits you (since pleasure signals "well-functioning"), which includes getting what you want, but also many other things (like perhaps getting what you want, or meeting what you might want, or what allows you to do what you can do). And pleasure exists without any wanting, such as walking in the sunshine when you are twenty and healthy and reasonably well-fed (the same for when you are eighty).

Dickinson: It depends upon what you mean by 'wanting'. In the nontechnical sense (i.e., not in the Berridge–Robinson sense), the pleasure or liking induced by an experience brings about a wanting for that experience through the process of incentive learning.

Kringelbach: Many theories of desire have taken pleasure to simply be the fulfilment of desire. Spinoza wrote that "pleasure is the transition of a man from a less to a greater perfection," where perfection is the completeness of which an individual has realized her desires. Schroeder (2004) has argued against such standard accounts of desire, since getting what you might desire does not always lead to pleasure, and he has instead proposed a theory, which links intrinsic desire directly with the reward systems of the brain. Berridge (see this volume) has convincingly argued that the hedonic impact, 'liking', and the incentive salience, 'wanting' are partly dissociable in terms of their underlying neural circuitry and pathways. In terms of neurotransmitters, it has been shown that dopamine is more related to the 'wanting' or the desire, while opioids are more related to the 'liking' or the pleasure. Malignant desires such as addiction can then be conceptualized as 'wanting' without 'liking' as argued by Robinson and Berridge (1993). Similarly 'liking' without 'wanting' would be akin to what has been described by some world religions as bliss or "true" happiness. Whether such a state truly exists has not yet been demonstrated but the aforementioned conceptualization may offer the scientific tools to test it.

5. Can pleasure be measured by objective physiological or behavioral techniques? (e.g., facial reaction or EMG, pupil dilation, GSR, neuronal firing, neurotransmitter release, neuroimaging)

Berridge: Yes, at least, basic or core 'liking' reactions to pleasure can be measured by objective neural or behavioral techniques. Conscious liking, admittedly, is more difficult to objectively measure (though even here, properly constructed rating scales can provide replicable and meaningful measures of subjective pleasure).

The measurement glass is more than half full. Psychologists and neuroscientists can use objective hedonic measures of core 'liking' reactions to discover which neural systems generate the brain's basic pleasure gloss. Eventually they may be able to recognize reliable electrophysiological–neuroimaging brain signatures of 'liking'. Scientists can also explore psychological features of the core pleasure process, including the relation of hedonic 'liking' to motivational 'wanting'. And they can compare basic 'liking' reactions to subjective rating measures of conscious pleasure, perhaps uncovering commonalities and differences in the underlying mechanisms.

Cabanac: Two words from the question may be answered separately: "Reliably," yes. Our body reacts to pleasure and these physiological responses such as hypertension, tachycardia, fever, etc. can be reliably recorded.

"Measure," definitely no. The word measure implies quantifying parametrically a mental event that takes place at the same time of a physiological response. The latter can be parametrically measured. The former can be quantified, but not parametrically. There always remains a doubt about a mental event report by any participant, even when the experimenter is self-testing.

Aldridge: Neural activity, neuroimages, and other physiological responses correlated with hedonic reactions can be measured. If humans report pleasure when they are scanned or being measured, then one could say that the scans or physiological responses are correlates of pleasure. It is likely, however, that the same regions of the brain may be active or the same physiological responses might occur in other contexts apart from reported pleasure. Based on my assumption that pleasure requires consciousness, physiological correlates of pleasure can only be measured in humans who report pleasure. Hedonic reactions can be measured at other times, but these may or may not be correlated with "pleasure."

Frijda: Can pleasure be measured objectively? I do not know whether all pleasure can, when the criterion is subjective report. But I suppose one can get fairly close by behavioral techniques: remaining longer with a stimulus or event than necessary for identification or preparation of escape.

Petrovic: Certainly pleasure cannot be measured. We know for fact that physiological responses correlating with the report of pleasure can be measured, including various muscular reactions, sweating, activation of certain regions in the brain and involvement of specific neurotransmitter systems. We can only study the mirror image of pleasure. However, our problem is that none of these responses are involved in just pleasure, thus the specificity is low. So in a way studying pleasure systems is a complex task relying on putting together a large amount of bits of a puzzle and trying to see the big picture.

Dickinson: No. Only indirectly.

Kringelbach: The pleasure-elicited behaviors can be measured in animals and include stereotyped behaviors such as facial expressions, pupil dilations, and orgasms. These behavioral changes must correspond to physiological changes in brain activity such as the temporal unfolding of neural activity and neurotransmitter release linked to specific brain regions, which then presumably can be used as objective measurements. In order to establish the relevant physiological changes, causal interventions are needed such as those carried out by Berridge and colleagues in the nucleus accumbens and ventral pallidum, where they shown that microinjections of opioids can change the hedonic gloss on subsequent pleasure-elicited behaviors.

We have used the causal technique of deep brain stimulation (DBS) in humans to show pain relief when stimulating the periacqueductal gray. At the same time, we have used magnetoencephalopathy (MEG) to measure the whole brain activity associated with this intervention (Kringelbach et al., 2007a,b). This is a promising technique for studying pleasure in the human brain where different brain targets can be switched on and off and the effects measured on the whole-brain activity and on pleasure-elicited behaviors, which can be compared to subjective conscious reports.

6. Are pleasure and pain on a continuum?

Berridge: Controversy persists on how positive affect relates to negative. The brain often seems to produce affective responses as if it generated pleasure and pain (or displeasure) along a single continuum. For example, increases in positive 'liking' expressions typically are accompanied by decreases in 'disliking' expressions for the same target and vice versa. Reciprocity between pleasure and pain has led many psychologists to posit a single continuum for affect.

And yet, teasing bits of evidence from psychology and neuroscience continue to support a contrary argument that pleasure and pain–displeasure may have separable mechanisms. Pleasure and displeasure may be capable of being produced independently and perhaps even sometimes simultaneously by the same target. If so, two separate dimensions would seem in order. In short, the evidence remains a bit contradictory, and our field still needs a more conclusive proof.

Aldridge: Pain systems activate brain regions not usually included in those thought to be processing hedonic reactions and/or reward. Thus, it seems unlikely that pleasure and pain are on a continuum.

Frijda: Like the half full, half empty glasses. They are on a continuum in some regard (objects can be placed on a continuum with reasonable confidence, or on some preference continuum), but they also and always differ in some regards, like the discontinuity or categorical jump between credit and debt. And they are not on a continuum in the sense that both can exist simultaneously, as in mixed feelings, hedonic uncertainty, and nostalgia.

Leknes: In everyday speech (and in the writings of philosophers (Bentham, 1907)), pain and pleasure often represent opposite sides of a hedonic continuum, where pains describe unpleasant and unwanted feelings as varied as boredom, pain in a medical sense, or embarrassment. The scientific literature usually refers to these pains and pleasures as punishments and rewards. In general, pleasurable feelings are usually rewarding and pain is usually a punishment. There are some notable exceptions to this heuristic, such as pleasurable pain in sexual masochism, and also interesting

mixtures like the bittersweet quality of unrequited love or the guilty pleasure of eating the last piece of pie.

Petrovic: Some studies indicate that there is a continuum at least in the involvement of specific neurosystems. We know that activation of the opioid neurosystem will induce a sensation of pleasure but also suppress pain. It has also been shown that induction of sadness will suppress the opioid system. It seems that several neurosystems work antagonistically in this way, for example, activation of the cholecyctokinin (CCK) system induces anxiety (and even panic attacks in larger doses), and moreover this system will make pain to be perceived as more intense and unpleasant. Also, if the opioid system is inhibited, the CCK systems will be more active and vice versa. In this way, these systems seem to work together in a continuum stretching from pleasure and suppression of unpleasantness to anxiety and increased unpleasantness.

Green: Pleasure and pain can certainly be regarded as two opposite extremes. On the one hand, pleasure is associated with a feeling of well-being as opposed to the feeling of misery or doom associated with pain. However, the subjective feeling of pain has tangible benefits for the survival of the organism. For example, a limb that feels pain will withdraw from a hot stimulus. On the other hand, what are the tangible benefits of pleasure to an organism's survival? Is pleasure simply the conscious awareness of a higher being's state of safety or a recognition that direct actions do not need to be taken to aid survival?

Pleasure actually appears much more complex than "the opposite of pain." If it is simply "the opposite," how do we explain the fact that some people derive pleasure from pain? One extreme example may be masochistic sexual experiences. However, a more subtle example involves the experience of pain that will eventually lead to a benefit. For example, training for a marathon can be very painful and difficult, but the individual will derive pleasure from the satisfaction that they are becoming physically stronger and knowing that they will be able to undertake the race. Does this "no pain–no gain" phenomenon disprove the continuum hypothesis or is it that we are prepared to put up with pain in order to defer a greater pleasure?

Dickinson: No. They are on orthogonal continua but usually with a mutual inhibitory interrelationship.

Kringelbach: Pleasure and pain are closely linked with each other but opinions differ over whether they are opposites or different kinds. As with most controversies, the answer depends primarily on focus and definition. Pain is not exactly the same as the lack of pleasure and does not necessarily solely correspond to displeasure. While pleasure is mostly stable, pain is more unstable and calls out for change. A stimulus will rarely make animal both approach and avoid it at the same time, but it is nevertheless clear that at least humans can feel both pleasure and displeasure as part of mixed feeling states. One example of such a mixed feeling is the Portuguese word *saudade*, which is akin to nostalgia but not fully translatable as such. Both words describe bittersweet emotions that are linked to painful memories from pleasures past, which at the same time are also pleasant memories. In addition, the word *saudade* also includes future expectations by evoking the pleasant and painful feelings of longing for pleasures past, which might return in a distant future.

Reward and punishment are intimately connected to pleasure and pain. Some scientific evidence would seem to indicate that there are different pathways involved in reward and punishment. At the same time, there is also evidence that reward and punishment make use of shared pathways. Depending on which levels of the brain processing one is focusing on, the answer could be one of opposition or difference of kind and most likely a combination of the two—but more evidence is needed.

7. Does pleasure have an evolutionary function?

Berridge: Yes, pleasure has an evolutionary function—probably more than one. Brain evolution cannot afford to wastefully dispense the massive amounts of neural machinery that process pleasure on major psychological processes that have no fitness benefit. Pleasure and displeasure reactions are so prominent in our own lives and in the behavior of other animals, and the underlying limbic neural mechanisms for generating affective reactions so well developed in the brains of both, that we are forced to conclude the capacity for pleasure reaction is an evolutionary trait that was selected and conserved. It is difficult to imagine an evolutionary scenario that would have led to such prominent and similar limbic brains in so many species if pleasure were not adaptive.

How could pleasure have had evolutionary functions? Basic core pleasure reactions have always had objective consequences for an individual's behavior, physiology, and eventual gene fitness. In a sense, hedonic reactions have been too important to survival for hedonia to be exclusively subjective. And subjective pleasure itself, in creatures that have it, carries an additional function: providing a declarative goal to guide flexible cognitive systems that operate at least partly

in conscious modes (see Dickinson and Balleine, this volume). Brains have had to actually do many things based on hedonic impact, and the doing of those things has given evolutionary functions to pleasure.

Cabanac: Any answer to that question belongs to the realm of belief, because it is not possible to "prove" anything regarding evolutionary usefulness. Yet, I believe that the answer is *yes*. The emergence of pleasure in the Amniotes gave them such an efficacy that this property remained and most likely contributed to the evolution from reptiles to birds and mammals.

Aldridge: It seems likely. Pleasure focuses behavior toward evolutionary useful ends, for example, eating, drinking, sex.

Frijda: Pleasure has the evolutionary function of signaling functioning well of any function that impacts overall function monitoring (either in consciousness or state of well-being).

Petrovic: The conscious part of pleasure must have a similar function as other conscious phenomena. It has been suggested that consciousness may be a way of selection of the very most important information processes going on in the brain, and that this "hyper-attention" has a direct evolutionary benefit. Possibly, the same idea may be suggested for conscious experience of pleasure. Pleasure may "simply" represent an extreme form of motivation and learning of what is good in our surroundings to drive complex behavior in the future.

Dickinson: Yes—that of allowing the control of behavior by cognitive process by supplying these processes with their goal values.

Kringelbach: As mentioned above, pleasure is likely to play a central role for the central evolutionary principles of survival and procreation of the species. The function of the basic sensory and social pleasures could be to help optimize our decisions such that survival and procreation remain possible. This is demonstrated by those individuals temporarily without pleasure which is common in depression and mental illness. The suicides involved in these afflictions would seem to indicate that without pleasure even survival and procreation become meaningless.

Brain Pleasures

8. What brain substrates actually cause pleasure?

Berridge: The brain is surprisingly frugal in its number of neural substrates able to directly cause pleasure. Pleasure causation implies that the substrate is either a sufficient cause to increase hedonic impact, or a necessary cause that must remain intact for normal hedonic impact. The causation question is especially knotty because several putative brain pleasure substrates have turned out to probably not cause pleasure after all (for example, mesolimbic dopamine systems and many so-called "pleasure electrodes").

Only a few subcortical brain substrates so far have compelling positive evidence for pleasure causation. For example, hedonic hotspots in nucleus accumbens, ventral pallidum, and brainstem have been found where opioid or related neurochemical activation causes increases in natural 'liking' reactions to sweet pleasure. Conversely, damage in some hotspots may disrupt normal pleasure reactions. But not many other sites can be listed yet for which necessary or sufficient criteria are met by strong evidence. Other limbic sites, and especially cortical sites, need a closer look regarding pleasure causation.

Aldridge: I don't expect that we will find that a single brain region "causes" pleasure. Rather, I expect that distributed patterns of activity across sets of brain regions may "represent" a pleasure state. When that representation is engaged, a subject may report pleasure. It seems likely that many sites including cortical and subcortical regions are activated during pleasure. One might find that particular patterns of activated sites are correlated with reports of pleasure or with observations of hedonic reactions. If a stimulus triggers activation in these same sites in a human, it is reasonable to predict that it would be reported as pleasurable. Further, depending on the flow of activation through brain circuits, experimentally stimulating one brain site directly may lead to activation in an entire set of sites; however, stimulation in this one site should not be viewed as causal. The stimulus would just be triggering the representation.

Petrovic: I believe that complex networks of regions are involved in processing what we experience as pleasure. I think that it is possible to dissociate specific subcomponents of pleasure. If we again study where the opioid system (highly associated to the experience of pleasure) is located in the brain, it is spread out over many different, but specific, regions from the brainstem and the nucleus accumbens to the anterior insula and the anterior cingulate cortex. Possibly, nucleus accumbens is relevant for the motor response in pleasure such as smiling while the insula may be involved perceiving secondly derived bodily feelings when we experience pleasure and the anterior cingulate cortex may be involved in the interaction between pleasure and cognition.

Schoenbaum: Pleasure seems to be an extraordinarily subjective and complex emotion. Presumably, pleasure emerges from signaling across multiple brain areas (VTA, amygdala, accumbens, ventral pallidum, hypothalamus, etc.) that are intimately involved in processing information about biological rewards. Humans and almost certainly animals are able to recognize a particular neural state in these circuits with the attainment of biological goals/rewards. We would speculate that this recognition, perhaps occurring in cortical regions (prefrontal?), would be what we'd call pleasure. Because it can be recognized, that neural state can then be mapped on to higher constructs or more abstract goals, so that it can be evoked by them. The fact that these constructs/goals are a step (or more) removed from the biological goal/reward triggering the original state may explain why pleasure derived from attaining these secondary goals may be variable, less intense, more abstract, and different in subtle ways from pleasure derived directly from meeting biological needs. Thus pleasure, whether it is derived from a primary reward or secondary reward, may be processed in both several regions of the brain, both cortical and subcortical.

Leknes: Here, I will restrict my comment to substrates of human pleasure. It is notoriously difficult to experimentally induce pleasure in an MRI scanner environment, and usually fMRI studies of pleasure rely on an experimentally induced homeostatic imbalance such as hunger, thirst, or, in my own work, a pain state. The good news is that it is easy to measure pleasure in these studies since subjects can give subjective reports on pleasure rating scales. To my knowledge, not a single area implicated in pleasure in the human literature has failed to be implicated in aversive processing as well. Examples are the amygdala (Becerra et al., 2001; Gottfried et al., 2003; Paton et al., 2006) and the nucleus accumbens (Menon and Levitin, 2005; Zubieta et al., 2005).

Komisaruk: Pleasure for me is like what Associate Justice of the Supreme Court Potter Stewart once said about pornography: "I could never succeed in intelligibly defining [it]…but I know it when I see it." The question of what brain systems produce pleasure raises the nasty question of which neurons produce consciousness and how they do it. With brain imaging, we see particular brain regions activated during orgasm, which is pleasurable. The nucleus accumbens and the hypothalamic paraventricular nucleus become particularly activated at orgasm. This indicates that the neurons that respond to dopamine and those that secrete oxytocin are both activated during this intensely pleasurable experience. However, we have (yet) no way of knowing whether the activation of these two groups of neurons themselves is what produces the feeling of orgasmic pleasure, or whether it is activity that they relay to other neurons that creates the feeling of pleasure. If it is to other neurons, then which ones, and even so, how does *their* activity produce the feeling of pleasure? That, of course, raises the question of how *any* neuron activity produces *any* feeling or cognitive experience, and the different qualities thereof, such as pleasure, pain, red, cold, sweet, or melody.

Dickinson: No idea but suspect that there is a major cortical involvement—insula?

Kringelbach: Berridge and colleagues (see this volume) have convincingly shown that in rodents subcortical regions such as the nucleus accumbens and ventral pallidum have hedonic hotspots where the activity modulates the pleasure-elicited behaviors related to food intake. They have also shown that dopamine is mostly related to 'wanting' and opioids are most likely linked to 'liking.' There is also some evidence that direct stimulation of the PAG in humans can elicit pain relief, which is reported as pleasurable (Kringelbach et al., 2007a,b), presumably linked to the engagement of the opioid system but not exclusively (see Green and Aziz, this volume).

These subcortical structures interact with cortical structures such as the orbitofrontal cortex (OFC), the insula, and anterior cingulate cortex (ACC; both anterior and posterior parts). The directionality of this causation has not been demonstrated but it is known that in mammals the structures of the basal ganglia are mainly on the output side of the OFC (see Schoenbaum, this volume). Using MEG, it has been demonstrated that the pain relief obtained from direct stimulation of the periacqueductal gray (PAG) in humans will elicit activity in the mid-anterior OFC (Kringelbach et al., 2007a,b). Other human neuroimaging experiments have shown that this part of the OFC is the most likely candidate for the subjective hedonic experience of pleasure (Kringelbach, 2005). It is currently not known whether this brain region causes pleasure or whether it is the point of integration between nonconscious and conscious hedonic processing.

9. Do the same brain substrates mediate conscious pleasure and trigger basic behavioral–physiological hedonic reactions? Or is conscious pleasure mediated separately?

Berridge: Conscious pleasure must be mediated separately from basic or core 'liking' reactions. Behavioral–physiological hedonic reactions

can sometimes occur unconsciously even in normal people, thus separating conscious and basic forms of hedonic reaction. Independent phenomena must have separable causes, and so only two conclusions are possible about the relevant brain substrates. One is that diverging anatomical brain circuits must mediate subjective conscious pleasure versus objective core 'liking' reactions. The other is that, at the very least, if the same neural substrates mediate both conscious pleasure and unconscious pleasure reaction, then conscious (subjective plus basic) and unconscious (basic only) hedonic reactions must correspond to different modes of activation for that substrate.

Aldridge: Behavioral–physiological hedonic reactions are responses to sensations. I would not define hedonic reactions as pleasure. Given my answer above (question 8), I expect that activation in circuits related to hedonic reactions could be a subset of circuits activated during conscious pleasure. Basic behavioral–physiological hedonic reactions are not pleasure on their own, although they may occur during pleasurable activation and may even trigger patterns of activation in more widespread areas.

Small: There is very strong evidence that the conscious pleasure associated with eating is encoded in the OFC but not the amygdala. Neuroimaging studies in humans, in which perceived pleasantness can be ascertained with rating scales, consistently demonstrate strong positive correlations between perceived pleasantness ratings of taste (O'Doherty et al., 2001; Small et al., 2003), smell (Anderson et al., 2003), flavor (de Araujo et al., 2003), and food reward (Kringelbach et al., 2003; Small et al., 2001) and activation of OFC. This is true whether pleasantness is derived from variation in stimulus attributes or internal state.

Additionally, in a recent study from our laboratory, we asked subjects to evaluate several dimensions of sweet, sour, salty, and tasteless solutions (Bender et al., 2005). Activation of the caudolateral OFC was selectively associated with evaluation of stimulus pleasantness, and this region was preferentially connected to earlier taste relays when a taste compared to a tasteless solution was experienced. This suggests that the caudolateral OFC organizes retrieval of sensory information from earlier taste relays in the service of computing perceived pleasantness. Neural responses in the amygdala do not correlate with perceived pleasantness of taste, flavor, and food reward (Anderson et al., 2003; de Araujo et al., 2003; Small et al., 2003), nor are they sensitive to alliesthesia (Kringelbach et al., 2003; Small et al., 2001)—the reduction in food pleasantness associated with satiety (Cabanac, 1971). Instead, the amygdala responds to food cues (LaBar et al., 2001; O'Doherty et al., 2002) and its response is sensitive to devaluation (Gottfried et al., 2003), indicating that it encodes the incentive value of food cues and that it is sensitive to changes in the incentive value related to internal state.

However, despite its critical role in encoding predictive food reward, there is preliminary evidence from the laboratory of Marci Pelchat that it does not mediate the conscious perception of desire or food craving (Pelchat et al., 2004). Pelchat and colleagues examined neural response to food cues that did or did not elicit subjective cravings. They found that although the amygdala responded to food cues, it was the insula and dorsal striatum that respond during time periods in which subjects reported experiencing cue induce cravings. Together, these findings suggest that neural representation of conscious pleasure experienced during eating and conscious desire experienced during food anticipation is at least partially segregated from the encoding of the predictive value of food cues.

A related issue is whether emotion and affect consist of explicit hedonic feelings, such as perceived pleasure, as well as "implicit affect," and whether these two components of emotion are represented by separable neural systems. Berridge and Robinson (2003) have argued that implicit affective reactions can exist objectively without necessarily being experienced subjectively. For example, subliminally perceived happy and angry faces produced opposite effects on the value of a beverage despite no change in reported feelings (Winkielman et al., 2005). In a landmark study, Morris et al. (1998) showed that the amygdala distinguished sensory stimuli solely based upon whether they had been previously associated with a subliminal happy or angry face. In our recent study, referred to above, we found that the amygdala preferentially communicated with the primary gustatory cortex during passive perception of taste compared to active evaluation (when a judgment about a stimulus feature was required). This contrasts with preferential connectivity between primary gustatory regions and OFC during the conscious evaluation of pleasantness. Thus, although these findings are a long way from providing proof of concept, given the role of the amygdala in encoding subliminally presented faces, they at least hint at the existence of separable systems for explicit and implicit emotion.

Schoenbaum: We would speculate that subcortical areas intimately involved in reward processing are the substrate or detector of situations in which pleasure is possible. In other words, these regions must signal by

their activity pattern that critical needs have been met. However the actual experienced emotion of pleasure is derived from cortical recognition of this state. For this reason, we can have pleasure imposed upon us to some extent by external circumstances (such as winning the lottery), but we almost always have substantial control over it (i.e., we can ruin it). Moreover, we can anticipate pleasure, which may involve cortical areas invoking a pleasure-like state in these downstream regions (either in reality or virtually in their own local synapses that retrieve information from these areas). Finally it may also be possible for cortical areas to selectively influence different parts of these circuits, perhaps due to there own anatomical specificity, leading to different forms of pleasure (e.g., satisfaction vs. joy).

Dickinson: My own view is that conscious pleasure result from a re-entrant transformation of basic behavioral–physiological hedonic reactions?

Shizgal: The signals that give rise to behavioral–physiological hedonic reactions may also trigger an accompanying experience of pleasure. However, awareness of these signals depends on whether they have gained access to working memory. Thus, the brain substrates appear to be organized hierarchically. Conscious experience arises from the higher levels of the system.

According to Baars' global workspace theory, the cognitive architecture consists of a multitude of specialized modules that can work independently and locally. Signals must gain access to consciousness in order to be broadcast simultaneously to many different modules and thus to coordinate their activity. When we sail on a brisk day, local modules adjust our posture and exposure to sun and wind without requiring the intervention of consciousness. However, when thermal discomfort crosses a threshold, we become aware of our predicament, a state than entails broadcast of the information. This enables the recruitment of the multiple modules required to formulate and execute a plan to go below and fetch a windbreaker.

Kringelbach: Given the demonstrations of nonconscious hedonic processing, it would seem likely that there is a separation and perhaps part overlap of brain mechanisms and substrates. In terms of correlation, it would appear from various neuroimaging experiments that the mid-anterior OFC correlates with conscious subjective pleasure reports as shown in an experiments involving "selective satiety" (Kringelbach et al., 2003). This evidence has recently been corroborated by causal evidence when combining the causal intervention of deep brain stimulation with MEG, which showed that pain relief (which was reported as more pleasant) through stimulation in the PAG elicited brain activity in this region. It is unlikely that the mid-anterior region of the OFC is the only node in what is likely to be an extended network of cortical and subcortical regions mediating conscious pleasure, which is also likely to include the cingulate cortex and the insular cortex (e.g., Craig, 2003).

10. Is there common currency for all sensory pleasures (food, sex, drugs, etc)? Or are different sensory pleasures mediated by different neural circuits?

Berridge: Brain hedonic mechanisms probably overlap heavily, at least for sensory pleasures. This is only a guess; admittedly these are still early days regarding evidence. But from what we know so far, many of the same cortical and subcortical substrates participate in pleasures as diverse as food, drugs, sex, parental, romantic and social interaction, money, music, and various cultural rewards. Of course, individual pleasures might also have their own pockets of unique neural substrate within the brain. Yet even if sweet-unique, sex-unique, or other pleasure-unique pockets exist, the general rule for mediation of sensory pleasures seems likely to be brain overlap and a neural common currency.

Cabanac: The term "common currency" implies that we are dealing with a mental mechanism that allows to compare, sort, and rank the various motivations present at a given time, in order to satisfy the most urgent. Such an emergence into cognition does not necessarily mean that the nervous substrate is common to all motivations. Especially, positive and negative hedonic impacts may result from the activation of different nervous substrates.

Aldridge: I predict there will be separate circuits for food, sex, drugs and, rock 'n' roll; however, I also predict that there will be extensive overlap between these different circuits. It may be that some circuits such as ventral basal ganglia or cortical regions are activated in all pleasure responses.

Frijda: I do not see that common currency and involving common neural circuitry are the same. As to common currency: I think it is an open question to what extent pleasures are substitutable. Pleasures in part are pleasures that contribute to higher order pleasure (also known as sense of well-being); but they can also give contour to absence of other pleasures; since all pleasures are pleasures of/about something.

Leknes: Surely there can be a common currency without the neural circuitry of different pleasures overlapping completely? People make decisions about gains

and losses even when these are in different modalities; just think about guilty pleasures, when the addition of a mere touch of extra guilt can cause the pleasure to vanish altogether.

Dickinson: My theoretical prejudice is to answer yes to this question.

Shizgal: Yes and yes. As Michel Cabanac has argued, sensory pleasures are often tied to the capacity of a stimulus to redress a physiological imbalance. Multiple physiological variables are regulated and different sets of physical resources in the world must be procured to keep each of these variables within the required range. For example, the macronutrients required to maintain the short- and long-term energy store are of little use in maintaining hydromineral balance, and no amount of salt or water will provide an energy source for metabolism. Thus, local currencies are required to evaluate the energy and hydromineral content of prey items, and each may be reflected in hedonic signals. Given that both types of resources are found in the same prey, a mechanism is required to translate the local currencies into a more global (common) one. This is what microeconomists call a substitution problem. Salt and fat are considered complements in microeconomic parlance because they satisfy different needs; one cannot substitute for the other. Carbohydrates and fats are partial substitutes; both are energy sources, but the former is better suited to replenishing the short-term store and the latter, the long-term store. In order to obtain an optimal combination of resources that are not perfect substitutes, a nonlinear combinatorial rule is required. This is a fundamental problem that has long been neglected by students of hedonic processing. Once again, the answer to the question depends on the level of processing under consideration. At the early levels, local currencies are employed. At a higher level, the local currencies are converted into a common one. This argument can be generalized readily to a broader class of objectives and sources of hedonic signals.

Kringelbach: From a computational point of view, it would seem to make sense to have a common currency, which could be used for the comparisons of sensory stimuli needed for decision-making. Kahneman et al. (2003) proposed a distinction between "experience utility" and "decision utility," where the "experience utility" is the degree of like or dislike of the choices or the hedonic value involved—and as such a measure of pleasure. In contrast, the "decision utility" relates to whether the object of choice is wanted or unwanted and this concept thus shares features with desire. These decision-making processes are related to the present, while the memories and expectations of these are called "remembered utility" and "predictive utility." These processes can be thought of as beliefs about the wants and likes involved in the past and future decisions.

The neuroscientific data are currently inconclusive about the possible nature of such a common currency. I would include social pleasure as a basic pleasure at the same level as sensory pleasures, and my hunch is that the basic pleasures use partly overlapping neural circuits on which the higher-order pleasures are parasitic. I have proposed a model where some these functions are served by the OFC in humans (Kringelbach, 2005). The OFC is one of the most polymodal regions of the brain. Sensory information from all the senses is received and combined in multimodal integration in the posterior parts of the orbitofrontal cortex. The reward value of the stimuli is assigned in more anterior parts of the orbitofrontal cortex, from where it can be used to influence subsequent behavior (in lateral parts of the anterior orbitofrontal cortex with connections to the anterior cingulate cortex), stored for monitoring/prediction/learning (in medial parts of the anterior orbitofrontal cortex) and made available for subjective hedonic experience (in mid-anterior orbitofrontal cortex). The reward value and the subjective hedonic experience can be modulated by hunger and other internal states. Human neuroimaging experiments have shown that affective sensory and social stimuli affect the activity in various regions of the OFC in similar ways to higher order stimuli such as monetary and esthetic stimuli.

11. Do brain substrates for basic sensory pleasures also participate in mediating higher social, esthetic, or intellectual pleasures?

Berridge: Yes, I think many of the pleasure mechanisms activated in the brain by basic sensory pleasures also participate in at least some higher human pleasures. This reflects the brain's conservation and common currency of neural circuitry for hedonic reaction. However, human higher pleasures also undoubtedly have their own complicated and unique brain signatures and certainly unique routes to activation. Higher cognitive mechanisms of induction are quite different from direct sensory pleasures. It is even conceivable that some few higher pleasures might turn out to be entirely separate from sensory pleasures, involving no overlap at all. But in the end, my bet is on substantial overlap for virtually all pleasures.

Aldridge: If there can be esthetic or intellectual assessments of food, sex, drugs and, rock 'n' roll, and

I believe there are these kinds of appreciation, then I expect that brain representations of these esthetic pleasures would invoke activity in the same pleasure circuits. Perhaps one could make the same kind of argument for social pleasures.

Frijda: I do not know whether brain substrates for "basic sensory pleasures" also participate in "higher" pleasures. There are too many presuppositions in this question. Sensory pleasures seem to me no more basic than the pleasures of behaving without impediment or social pleasures.

Kringelbach: As stated above, it would seem likely that the basic sensory pleasures form building blocks for higher-order such as esthetic and intellectual pleasures. Note also that I regard social pleasure as a basic and necessary pleasure in the mammalian brain. By including the social pleasures in the basic building blocks, it becomes possible to see how higher-order pleasures such as schadenfreude or killjoy can be extracted from the higher-dimensional space of basic sensory, sexual and social pleasures.

12. What are the relative roles in pleasure of subcortical limbic structures versus cortex?

Berridge: Perhaps it is a blow to our cerebral self-image, but the subcortical limbic brain probably contains the chief generating circuitry for many of our most intense pleasures. So far the most effective sensory pleasure generators, at least, have been found by experiments that manipulate subcortical brain structures, such as subcortical nucleus accumbens and connected limbic subcortical sites. For example, activating opioid or related neurochemical signals in those sites is sufficient to directly cause increases in hedonic 'liking' reactions to a sweet pleasure. Likewise, only subcortical lesions (e.g., ventral pallidum) appear to eliminate normal 'liking' reactions to sweetness and to replacing them with negative 'disliking' reactions that are usually associated with bitter or other nasty tastes.

Similar evidence about the causation of pleasure does not yet exist for any region of cortex as far as I know. Even many "anhedonia" patients with cortical lesions may still retain most basic pleasures, despite deficits in how they act on their emotions. However, impressive neuroimaging and electrophysiological activation studies have shown that orbitofrontal and related cortex limbic regions do clearly code pleasure (described by Kringelbach, Small, Schoenbaum, and other authors in this book). And the cortex is undoubtedly a controller of subcortical structures, so that, like a domino falling earlier in the chain, downward causation may give cortex a once-removed role in triggering pleasure via activation of subcortical hedonic circuits. Finally, nearly everyone agrees that the cortex is important to conscious pleasure feelings and to cognitive representations of pleasant events. But it might be truer to characterize the cortex role in subjective feelings as causing the consciousness of an underlying pleasure reaction, rather than causing the basic pleasure reaction itself.

Aldridge: I expect that cortical and subcortical structures cooperate and interact extensively. The anatomy suggests that cortical inputs might "enable" or "gate" activity in subcortical circuits, which can in turn drive activity in cortical circuits. By the patterns of cortical gating, subcortical circuits might have differential levels of access to inform the cortex. In a way then, cortical circuits can control their own inputs. I predict that pleasure can't exist without both cortical and subcortical circuits. Hedonic reactions may not proceed without activity in both.

Gottfried: In some ways, this question captures the basic distinction between emotion and feeling. If pleasure is taken to reflect a biologically meaningful emotional state, then subcortical limbic structures may play the major role. However, if pleasure is taken to reflect subjective positive feeling, then the cortex would have a more prominent role. In all likelihood, the answer is that there is a role for both systems. A neurological syndrome known as "pseudobulbar affect" or "pathological laughing and crying" sheds some light on the topic. This condition was noted by Darwin as long ago as 1872 and characterized in detail by the eminent neurologist Kinnear Wilson in 1924 (for review and discussion, see Schiffer and Pope, 2005). Patients with pseudobulbar affect exhibit spontaneous, intense emotional outbursts, typically laughing or crying, which are usually incongruent to their mood and inappropriate to the immediate situation. This disorder is often observed with bilateral hemispheric lesions of the frontal cortex or internal capsule, and it is thought that the interruption of descending (inhibitory) motor information onto subcortical brainstem structures causes a release (disinhibition) of motor programs underlying emotional expression. Thus, the clinical and pathological features of pseudobulbar affect suggest a heuristically useful dichotomy between emotional control (cortical) and emotional output (subcortical).

Kringelbach: The data suggests that the ancient evolutionary developed brain structures can override our cortical structures. Yet, it is also clear that the cortex, and especially the OFC and ACC regions can also

drive subcortical structures. More empirical evidence for the interactions is needed.

Higher Pleasures

13. What is the relation of pleasure to cognition?

Berridge: Pleasure is essentially affective, whereas cognition is not. Cognition and affect are mutually intertwined but never wholly identical. They trigger and modulate each other, but remain distinguishable at least in principle.

Cabanac: Mental objects of cognition possess four dimensions: 1. quality (nature), 2. intensity (magnitude), 3. duration (time), and 4. hedonicity (pleasure/displeasure). Dimensions 1–3 cannot be nil, but dimension 4 can. In that case, hedonicity is indifference.

Aldridge: Pleasure requires cognition. Hedonic reactions don't require cognition. I am assuming that cognition means consciousness.

Frijda: What is the relation of pleasure to cognition? It is like asking what is the relation of one person to another. But if the question means: "is there pleasure without any cognition" the answer depends on the meaning of "cognition" and if cognition means information processing the answer is: no pleasure without information processing because all pleasure is of/about something, including assessment of one's current overall state of functioning.

Shizgal: The machinery of cognition is required in order to produce the experience of pleasure, and pleasure may result from various cognitive activities, such as problem solving. I will address the first of these statements, which relates to my answers to other questions.

In Baars' global workspace theory, we become conscious of a signal, such as a sensation, only once it has gained entry to working memory. Attention plays a crucial role as a gatekeeper to this evanescent, capacity-limited, mnemonic store. Thus, thinking hard about something else should negate the experience of pleasure. Once in working memory, a signal can be accessed by executive processes involved in goal selection and is broadcast to the numerous special-purpose components of the cognitive apparatus that operate outside of awareness. This is essential to the formulation and execution of plans for maximizing, prolonging, and re-initiating pleasurable experiences. These objectives can be attained, to a more limited degree, by lower-level modules (c.f., the example of the sailor described in my answer to question 10), but the crucial element of a stable, long-term plan would be missing, without the intervention of executive processes.

Kringelbach: Some psychologists have tended to see cognition as separate from pleasure, emotion, and motivation. Yet it is difficult to see how cognition could proceed without these processes. Pleasure clearly influences cognition. Take the example of the human dorsolateral prefrontal cortex, which is the structure that many psychologists would point to as the main brain region involved in cognition and higher-order cognitive concepts like working memory and selection for action. It turns out that this brain region also has valenced representations of taste, which could aid higher cognitive processes in guiding complex motivational and emotional behavior (Kringelbach et al., 2004).

Similarly, neurophysiological recordings in a reward preference task have demonstrated that neurons in the dorsolateral prefrontal cortex encode both the reward amount and the monkeys' forthcoming response, while neurons in the orbitofrontal cortex more often encode the reward amount alone (Wallis and Miller, 2003). It would seem high time to integrate pleasure, motivation, and emotion into the cognitive neurosciences. As an example, Dickinson and Balleine (in this volume) have argued that subjective pleasure may allow animals to have declarative goals with can come to guide flexible cognition.

14. What is the relation of pleasure to social cognition?

Berridge: Social cognition is a distinctive trigger, though I think its pleasure shares brain circuitry with nonsocial pleasures.

Cabanac: The relation is the same as with other cognitive objects. Hedonicity indicates what is (or what was in the evolutionary past of our species) useful. With sensations, pleasure indicates physiological usefulness; with social cognition, pleasure indicates social usefulness. In the case of aggressiveness, passive behaviors and highly aggressive behaviors arouse displeasure. But medium-intensity aggression can be agreeable (to the aggressor).

Aldridge: I don't know.

Kringelbach: Pleasure is central to social interaction, which in its simplest form is not a higher pleasure but a basic pleasure, as argued above. Our liking of infant faces is an example of such a basic social pleasure. Darwin pointed out that in order for infants to survive and to perpetuate the human species, adults

need to respond and care for their young and Lorenz proposed that it is the specific structure of the infant face that serves to elicit these parental responses. Using MEG, we have recently found a key difference in the early brain activity of normal, nonparental adults to infant faces compared to adult faces (Kringelbach et al., 2008). Only infant faces elicited early activity at around 130 milliseconds in the medial OFC, which has previously been shown to reflect the reward value of a wide variety of stimuli, where the brain activity was correlating with their reported pleasantness. Higher-order social cognition such as theory of mind arises later in primate development but it is likely to build on combinations of the basic pleasures.

15. What is the relation between language and pleasure?

Berridge: The way we talk about pleasure is perhaps why the conscious feeling traditionally has been its defining feature. But dictionary definitions are never the last word on the true nature of any psychological process.

Cabanac: As with any other mental experience, pleasure indicates what to decide. We have evidence that participants selected the grammatical formulas that gave them pleasure and avoided those that arose displeasure. Thus, grammatical optimization is achieved through the maximization of pleasure.

Aldridge: I don't know. Perhaps language is important for representations of some kinds of pleasure such as intellectual or esthetic pleasure.

Frijda: There is pleasure without language. Ask my cat (she can't talk but can purr).

Kringelbach: Pleasure is possible without language as argued above. Human language and our subsequent linguistic reports of subjective experience may, however, come to change our pleasure. The evidence also suggests that we have limited conscious access to nonconscious processing and that at least some subjective linguistic reports are post hoc and confabulatory (e.g., Johansson et al., 2005).

16. How do sensory pleasures relate to higher positive affects generated by social-cognitive (social pleasures, money) or esthetic (art, music) or moral (altruistic or transcendent loves)?

Berridge: Again, I think that overlap exists. Even unique human cultural pleasures may be pleasurable precisely because they act as new psychological keys in the same old brain hedonic locks that generate sensory pleasure. Of course, massive differences also exist between sensory pleasure and some higher pleasures, and a few higher affects might turn out to entirely different from sensory pleasures. Still, overlap is the rule for many.

Cabanac: These pleasures permit to rank the behavioral responses in terms of which to satisfy first. The hedonic dimension of consciousness is what triggers decisions in that realm of activity also. Pleasure is the common currency that ranks the urgencies. The most pleasant (or least unpleasant) is always ranked first. If sensory pleasure is more intense than esthetics, then physiology will be satisfied first. If altruistic pleasure is more intense than money, then moral behavior will be accomplished first.

Aldridge: One may like the feel of money, the sound of music, the sight of paintings. These sensations might trigger pleasure representations in the brain.

Frijda: Interesting question. I do not know.

Gottfried: What sets these higher positive affects apart from the "lower" sensory pleasures is that by and large they represent "civilized" pleasures unique to humans. Frequently these higher-order pleasures are abstractions of biologically salient stimuli or affective states. After the manner of learning theorists, with their models of S-S (stimulus–stimulus) and S-R (stimulus–response) learning, one could reasonably think of these distinctly human pleasures as a form of "I-S learning," whereby a positive stimulus (S) is effectively linked to an idea (I). These ideas could be concrete or abstract, and might take the form of symbols, signs, multisensory perceptual events, mental states, concepts, or thoughts, such as pounds sterling, or sonatas, or sapphires, or love. In this framework, any organism with the capacity for abstractive learning (what one might call I-S learning) needs to be able to satisfy certain criteria. First, it needs to be able to have a central nervous system, for the high level of integrative processing necessary for I-S learning could not be accomplished without a brain. This basic stipulation would disqualify many animals (and perhaps some humans). Second, it needs to be able to store and retain (neural) representations of ideas.

Third, it needs to be able to form associations between idea representations and pleasurable sensory (or affective) representations. Based on the distinctive evolutionary features of the human brain, I would speculate that the prefrontal cortex is critical for the development and realization of these civilized pleasures. As a final note, insofar as the experience of pleasure has biological (survival) value, it follows that higher positive affects should be behaviorally beneficial. Some of the

earliest examples of abstract pleasure are found in the cave paintings at Lascaux, circa 15,000 B.C. Here, the cavemen's depiction of bison and woolly mammoths probably had less to do with esthetic contemplation, and more to do with finding ways of overcoming their innate fears of these large beasts, in order to improve their chances on the hunt.

Kringelbach: Higher-order pleasures are likely to be higher-dimensional combinations of the basic sensory and social pleasures and as such may re-use some of the same brain mechanisms. The inclusion of social pleasures in the basic pleasures makes this into a higher-dimensional space of which it becomes easier to form even apparently maladaptive pleasures such as schadenfreude and killjoy.

17. In what ways are pleasure and happiness linked?

Berridge: Happiness cannot be reduced to pleasure alone. But the attainment of happiness must surely include the ready capacity for pleasure reactions.

Cabanac: There is a fundamental misunderstanding with the word "happiness". Because hedonicity is the common currency that allows motivations to "talk" to one another, the mechanisms must be homologous to all motivations. Thus happiness (general) must follow the same rules as comfort (physiology). In physiology, comfort is the absence of hedonic experience. Thus, comfort is indifference and can be stable. On the other hand, pleasure indicates that a stimulus is useful, and maximizing pleasure optimizes behavior. But, as soon as we have maximized pleasure, we thus reduce the physiological need and usefulness disappears. Thus, pleasure is always transient, while comfort is stable and can be permanent.

The general case follows the same rules as sensation and physiology. The equivalent of pleasure is joy; the equivalent of comfort is happiness. Thus joy is hedonically positive but transient and happiness is indifferent and stable.

Aldridge: I don't know. Maybe they are the same thing.

Frijda: There is no happiness without pleasure; there is much pleasure without happiness. Pleasure is a core evaluative process; happiness is an emotion or long-term evaluation.

Kringelbach: Pleasure is but a fleeting moment in the state which is happiness. It is possible that "true" happiness or bliss might be a state of 'liking' without 'wanting', which with the current available neuroscientific evidence is becoming a testable hypothesis.

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