



Special issue: Discussion forum

Emotion and decision-making explained: Response to commentators



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All the commentators are thanked for the insightful and interesting issues that they raise, and for opening up the scientific analysis of emotion and its brain mechanisms for discussion in a forum. In the context of this forum (Rolls, 2014c), I am pleased to respond to all the commentaries in the spirit of taking our understanding forward.

1. Multiple routes to emotion-related responses

One of the themes of *Emotion and Decision-Making Explained* (Rolls, 2014c) is that there are multiple routes to emotion-related responses, with some illustrated in Fig. 1. Brain systems involved in decoding stimuli in terms of whether they are instrumental reinforcers so that goal directed actions may be performed to obtain or avoid the stimuli are emphasized as being important for emotional states, for an intervening state may be needed to bridge the time gap between the decoding of a goal-directed stimulus, and the actions that may need to be set into train and directed to obtain or avoid the emotion-related stimulus. In contrast, when unconditioned or classically conditioned responses such as autonomic responses, freezing, turning away etc. are required, there is no need for intervening states such as emotional states. These points are covered in Chapters 2–4 and 10 of the book.

Ono and Nishijo (2014) raise the issue of the extent to which subcortical pathways are involved in the elicitation of some of these emotion-related responses. They describe interesting research that pulvinar neurons in macaques may respond to snakes, and may provide a route that does not

require cortical processing for some probably innately specified visual stimuli to produce responses. With respect to Fig. 1, the pathway is that some of the inputs labeled as primary reinforcers may reach brain regions including the amygdala by a subcortical route. LeDoux (2012) provides evidence in the same direction, in his case involving a ‘low road’ for auditory stimuli such as tones (which do not required cortical processing) to reach, via a subcortical pathway, the amygdala, where classically conditioned e.g., freezing and autonomic responses may be learned. Consistently, there is evidence (Chapter 4) that humans with damage to the primary visual cortex who describe themselves as blind do nevertheless show some responses to stimuli such as a face expression (de Gelder, Vroomen, Pourtois, & Weiskrantz, 1999; Tamietto et al., 2009; Tamietto & de Gelder, 2010). I agree that the elicitation of unconditioned and conditioned responses to these particular types of stimuli (LeDoux, 2014) is of interest (Rolls, 2014a).

However, in *Emotion and Decision-Making Explained*, I emphasize that there are massive cortical inputs to structures involved in emotion such as the amygdala and orbitofrontal cortex, and that neurons in both structures can have view-invariant responses to visual stimuli including faces which specify face identity, and can have responses that are selective for particular emotional expressions (Leonard, Rolls, Wilson, & Baylis, 1985; Rolls, 1984, 2007, 2011, 2012; Rolls, Critchley, Browning, & Inoue, 2006) which reflect the neuronal responses found in the temporal cortical and related visual areas, as we discovered (Perrett, Rolls, & Caan, 1982; Rolls, 2007, 2008a, 2011, 2012; Sanghera, Rolls, & Roper-Hall, 1979). View invariant representations are important for

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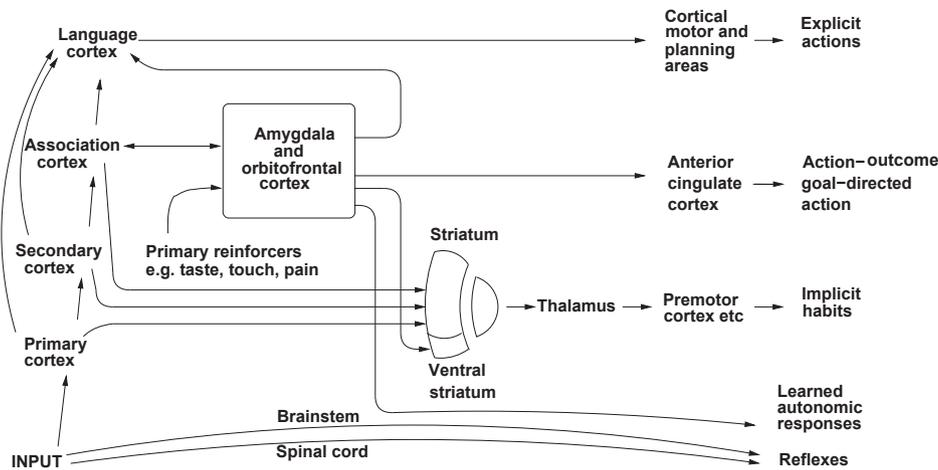


Fig. 1 – Multiple routes to the initiation of emotion-related responses. The inputs from different sensory systems to brain structures such as the orbitofrontal cortex and amygdala allow these brain structures to evaluate the reward- or punishment-related value of incoming stimuli, or of remembered stimuli. One type of route is via the language systems of the brain, which allow explicit (verbalizable) decisions involving multistep syntactic planning to be implemented. The other type of route may be implicit, and includes the anterior cingulate cortex for action–outcome, goal-dependent, learning; and the striatum and rest of the basal ganglia for stimulus–response habits. Outputs for autonomic responses can also be produced using outputs from the orbitofrontal cortex and anterior cingulate cortex (some of which are routed via the anterior insular cortex) and amygdala.

inputs to structures involved in emotion and memory (Rolls, 2014b), for what is learned in one trial to for example a particular person's front view of a face, will transfer to another view, for example the same person in profile view. Moreover, these invariant representations must be not of any face, but must be of a particular person's face [implemented with a sparse distributed neuronal representation (Rolls & Treves, 2011)]. Moreover, this type of invariant representation of the identity of a face must be combined with the particular expression on a face, for emotional and social actions and responses depend on whose face it is, and on the emotional expression on that face. Massive cortical computations are needed to solve view invariance and face and object identity representation (Rolls, 2008b, 2012; Rolls & Treves, 2011), and as these are important in many human and other primate emotions, cortical inputs to the orbitofrontal cortex and amygdala become very important in primates including humans. In this context, behavioral including autonomic responses to a snake or to a tone or to a face (without identity or invariance) are indeed of interest (LeDoux, 2014), but are not at the heart of most primate including human emotions, and may produce more typically responses, even species-specific responses [cf Panksepp (1998)], rather than goal-directed emotional behavior.

2. Insula and emotion

Tom Scott, whose studies of neuronal activity in the taste pathways are of great interest, raises the issue of the functions of the insula in taste, and also its other functions including visceral (Scott, 2014). Scott agrees that taste neurons in the primate anterior insula and adjoining frontal operculum

represent the identity of different taste stimuli (Scott & Plata-Salaman, 1999) and are not influenced by satiety (Rolls, Scott, Sienkiewicz, & Yaxley, 1988; Yaxley, Rolls, & Sienkiewicz, 1988), so do not represent reward value or pleasantness. Indeed, activations in the corresponding region in the human are correlated with the intensity of taste stimuli, and not their pleasantness (Grabenhorst & Rolls, 2008). Insular primary taste cortex neurons in macaques also represent the texture and temperature of what is in the mouth, but do not respond to olfactory or visual stimuli (Kadohisa, Rolls, & Verhagen, 2005; Verhagen, Kadohisa, & Rolls, 2004). Olfactory stimuli do influence a more anterior part of the insula, the agranular insula, where taste and odor are combined to produce flavor (de Araujo, Rolls, Kringelbach, McGlone, & Phillips, 2003). Given that oral somatosensory stimuli do activate the primary insular taste cortex (Kadohisa et al., 2005; Verhagen et al., 2004), and that single neuron tuning to a set of odors (Critchley & Rolls, 1996a, 1996b; Rolls, Critchley, Mason, & Wakeman, 1996; Rolls, Critchley, & Treves, 1996) cannot be directly measured with functional magnetic resonance imaging (fMRI), activations to olfactory stimuli, especially all those with trigeminal components, in the insular taste cortex must be interpreted with caution.

In what is probably a nearby part of the anterior insula, which receives inputs from the visceral thalamus (Carmichael & Price, 1995), activations are related to viscer-autonomic activity (Critchley & Harrison, 2013). The issue considered in Section 4.9 on the insula is whether the activations also found in the insula to disgust face expressions and other emotion-provoking stimuli are due to autonomic-visceral responses being produced as a result of insular inputs from regions such as the orbitofrontal cortex and amygdala known to be involved in such processing, or are due to some special

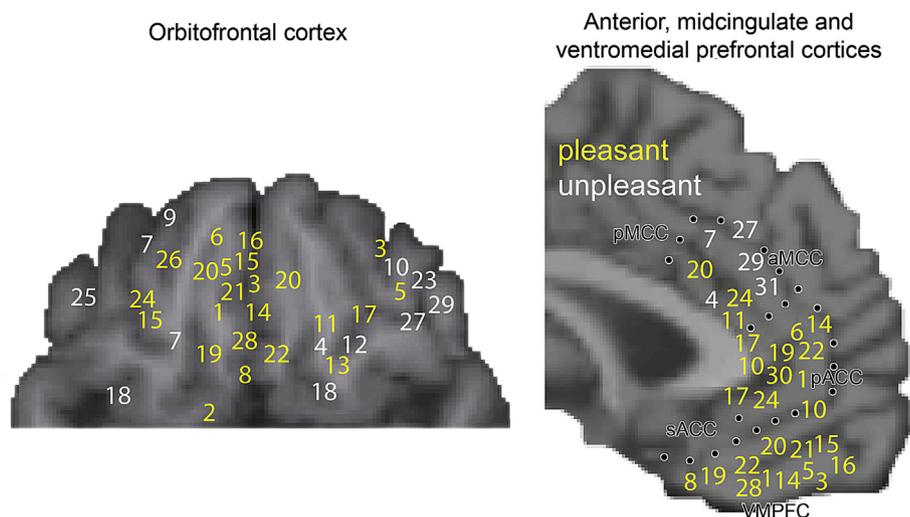


Fig. 2 – Maps of subjective pleasure in the human orbitofrontal cortex (ventral view) and anterior cingulate and ventromedial prefrontal cortex (sagittal view). Yellow: sites where activations in functional neuroimaging studies correlate with subjective pleasantness. White: sites where activations correlate with subjective unpleasantness. The numbers refer to effects found in specific studies listed by Grabenhorst and Rolls (2011). Taste: 1, 2; odor: 3–10; flavor: 11–16; oral texture: 17, 18; chocolate: 19; water: 20; wine: 21; oral temperature: 22, 23; somatosensory temperature: 24, 25; the sight of touch: 26, 27; facial attractiveness: 28, 29; erotic pictures: 30; laser-induced pain: 31. pMCC – posterior midcingulate cortex; aMCC – anterior midcingulate cortex; pACC – pregenual anterior cingulate cortex; sACC – subgenual anterior cingulate cortex; VMPFC – ventromedial prefrontal cortex. This figure is modified from Grabenhorst & Rolls, 2011. Value, pleasure and choice in the ventral prefrontal cortex *Trends in Cognitive Sciences* 15: 56–67, by the addition of labels for the different regions of the cingulate cortex in collaboration with B. Vogt.

emotion-related computation being performed in the insula. The parsimonious view is adopted in Section 4.9 (until direct evidence shows otherwise) that such activations to emotion-related stimuli in the insula (including for example responses to odors) reflect input from other brain areas involved in emotion-related computations that produce visceromotoric output.

More posteriorly in the insula is a somatosensory representation of the body (Section 4.9) that provides information about one's own body in that there is no response to the sight of someone else's body being touched (McCabe, Rolls, Bilderbeck, & McGlone, 2008), and here too the representation is related to the intensity and not the pleasantness or affective value of thermal stimuli applied to the hand (Rolls, Grabenhorst, & Parris, 2008).

3. Cingulate cortex and emotion

Brent Vogt, a leading expert on the anatomy and functions of the cingulate cortex, and the editor and indeed author of much of the excellent *Cingulate Neurobiology and Disease* (Vogt, 2009), considers the role of the cingulate cortex in emotion (Vogt, 2014). The points that he makes about cytoarchitectonic (his Fig. 1A) and functional divisions of the cingulate cortex are very constructive and helpful. When we put together functional neuroimaging studies of the anterior cingulate cortex, we found that many reward-related, positively affective, stimuli are mapped to the pregenual cingulate cortex

(pACC) (Grabenhorst & Rolls, 2011) in regions that include areas p24 and p32 in Vogt's Fig. 1A (see Fig. 2). In contrast, many unpleasant stimuli are mapped just posterior to this in the anterior midcingulate cortex (aMCC) above the corpus callosum (Grabenhorst & Rolls, 2011) (see Fig. 2), which includes area 24c' as shown in Vogt's Fig. 1. Most of these representations produced by unpleasant stimuli (Grabenhorst & Rolls, 2011) are in aMCC where pain produces activations (Rolls et al., 2003; Vogt, 2009).

The hypothesis considered in *Emotion and Decision-Making Explained* is that these reward- and punishment-related representations in these anterior cingulate cortex regions are relayed from the medial and lateral orbitofrontal cortex, and are used in the cingulate cortex for action-outcome learning (Rolls, 2014a). In this type of learning, associations must be learned between actions that are made, and the rewards and punishers (the outcomes) that are obtained. Importantly for this function, actions, movements, are represented in the midcingulate cortex [MCC, in which there are two cingulate motor areas (Vogt, 2009)], and not in the orbitofrontal cortex which is primarily concerned with value representations and not with actions (Rolls, 2014a), and so the anterior and midcingulate cortices are appropriate regions for action-outcome learning, which could not be performed by the orbitofrontal cortex. In performing this type of learning, the anterior and midcingulate cortices need to be able to remember actions just made until the outcome is known, which may be seconds later, and therefore it is proposed that attractor networks in these cingulate regions hold in short-term memory the

actions just made, so that an association can be made to the outcome when it becomes known, probably using associative (Hebbian) synaptic modification. However, an important frontier for research is the development of a more precise computational model of this, and measurement by single neuron recordings of which areas within the anterior and midcingulate cortices are involved in the action memory and association with outcome processes, and enable the benefits and costs of actions to be learned.

It has been argued recently that these reward, punishment, and action-related functions of the anterior and midcingulate cortices and their close connections with the orbitofrontal cortex and amygdala are separate from the more memory-related functions of the posterior cingulate cortex (PCC) and its closely related areas (Rolls, 2014b). For this reason, it has been proposed that we should no longer adhere to the concept of a limbic system, but that if we are to continue with 'limbic' terminology, we should accept that there are two (or more) limbic systems (Rolls, 2014b). The PCC has connections via parahippocampal areas with the hippocampus which is involved in episodic memory (Dere, Easton, Nadel, & Huston, 2008; Rolls, 2008b, 2010), and with parietal regions involved in the representation of space, which is usually a component of an episodic memory. The question then arises of why the hippocampus has some connections to the orbitofrontal cortex and amygdala; and for that matter why there may be some connections between the anterior cingulate cortex and the PCC (Vogt, 2009). The answer that is proposed is that emotional or affective states may be part of an episodic memory, and must therefore be connected to the hippocampal system, both for storage of an episodic memory; and for retrieval of the emotional component of an episodic memory back to the orbitofrontal and anterior cingulate cortex (Rolls, 2014b).

Not only the functions performed by, but also the computational styles of the two limbic systems, are very different (Rolls, 2014b). The hippocampal system is involved in storing a whole memory with all its parts, and then restoring all the components of the episodic memory from any of the parts, and in this computation autoassociation or attractor networks are important (Rolls, 2008b, 2010). In contrast, to decode whether a sensory stimulus is associated with a reward to provide a representation of value, and then to associate actions with these value representations to lead to the generation of correct actions in future, is inherently a much more feed-forward, pattern association, process (Rolls, 2008b, 2014a, 2014b).

4. Rolls' theory of emotion compared to appraisal theory

I agree with Brosch and Sander (2014) that my theory of emotion and appraisal theory are quite close and complementary, and not in disagreement. Both theories involve appraisal, and in my theory this is clearly operationally defined as decoding whether a stimulus is a reward or a punisher or neither. In my theory, part of the utility of this decoding of instrumental reinforcers is that instrumental actions can be influenced, whereas in more traditional appraisal

theory fixed action patterns as the fixed responses were emphasized (Frijda, 1986; Scherer, Schorr, & Johnstone, 2001).

What Brosch and Sander argue in their interesting commentary is that the significance of an event for an individual's core values is an important determinant of emotional responses and decisions (Brosch & Sander, 2013). Core values in this approach include self-direction, stimulation, hedonism, achievement, power, security, conformity, tradition, benevolence, and universalism. I simply note that as these are 'values', they are instrumental reinforcers, and are probably useful extensions to or examples of the set of reinforcers that I set out in Table 2.1 of *Emotion and Decision-Making Explained*.

However, some care is needed in the interpretation of the underlying factors that explain why these core values are reinforcers. Brosch and Sander indicate that one underlying dimension reflects the conflict between outcomes for the individual versus outcomes for the social group. I argue in *Emotion and Decision-Making Explained* that many of the rewards and punishers that guide our behavior are related to the reproductive success of genes that specify rewards and punishers, and that even in the case of altruism this is still often the case, through the processes of kin and reciprocal altruism. Values encoded by genes that facilitate reciprocal altruism may include sensitivity to one's reputation in society, and individual variation in genes that specify values such as this may underlie the dimensions described by Brosch and Sander. The point here is that genetic variation in how rewards and values are specified may underlie differences between individuals in apparently selfish versus social behavior, one of the dimensions identified by Brosch and Sander as underlying core values. An interesting point made in *Emotion and Decision-Making Explained* is that humans and other animals with a reasoning system can reason their way into not following what their genes specify. For example we may choose on the basis of reasoning not to choose sweet and fatty foods such as ice cream, in the interests of maintaining health. Thus reasoning, as well as genes, can influence our value systems.

5. Conscious emotional feelings

Chapter 10 of *Emotion and Decision-Making Explained* is about emotional feelings and consciousness. The whole issue of consciousness is different from the other topics considered in the book, for the normal scientific methods of experiment and theory do not appear, at least at present, able to fully address how subjective feelings (phenomenal consciousness) arise. Indeed, this topic is one where philosophers do not appear to have an agreed way forward. For these reasons, it is made clear that what is described in this chapter should not be held to have practical implications.

Given this proviso, but also the inherent interest of how emotional feelings do arise, a theory of consciousness that involves higher order syntactic thoughts is described. This theory applies especially to humans, for we have direct access to at least our own subjective conscious thoughts, and the issue is left open for other animals. The approach of LeDoux (2008, 2012, 2014) is quite close to my approach (Rolls, 2008a, 2014a).

Jaak Panksepp, in his commentary (Panksepp, 2014), puts the case that we should start with affective feeling states, and use those as building blocks for theories and investigations of emotion. A problem with this approach starting with the subjectivity of affect is that scientists and philosophers are not sure how to test for these subjective states in many animals. Part of the progress in understanding the brain mechanisms of emotion that followed the publication of *The Brain and Emotion* (Rolls, 1999, 2000) was because many scientists accepted that at least pro tem an operational definition of emotions, as states elicited by rewards and punishers (i.e., instrumental reinforcers), provided a tractable scientific way forward in the study of emotion that provided for objective tests of hypotheses.

It then becomes of real interest to understand how subjective emotional states, measured directly in humans by reports of subjective experience, are related to states elicited by rewards and punishers, and this is considered in Chapter 10 and elsewhere in *Emotion and Decision-Making Explained*. Of particular relevance are investigations that test whether subjective, conscious, emotional feelings are always associated with emotions that are produced by rewards and punishers, for there is a great deal of evidence that much human information processing including some related to emotional responses can take place without subjective awareness (phenomenal consciousness) (Dijksterhuis, van Knippenberg, Holland, & Veling, 2014; Finkbeiner & Coltheart, 2014; Gazzaniga, 1988, 1995; Gazzaniga & LeDoux, 1978; LeDoux, 2008; Phelps & LeDoux, 2005; Weiskrantz, 1997, 1998). In the context of emotion, an emotion-related face expression can be correctly identified in patients with blindsight who report not having seen the face, and can trigger fast emotional reactions (de Gelder et al., 1999; Tamietto et al., 2009; Tamietto & de Gelder, 2010). Further, identification of or responses to emotional and other stimuli can be triggered in humans with stimuli that do not reach the threshold for conscious report (Persaud & McLeod, 2008). Indeed, we showed that in a backward masking paradigm macaque inferior temporal cortex neurons respond for 30 msec to visual stimuli that humans do not consciously report seeing yet can guess at much better than chance, and respond for 50 msec or more when humans do consciously see the stimuli, providing evidence that there is much and stimulus-selective information processing that can take place in the brain even when the firing is insufficient to reach the threshold for conscious report (Rolls, 2003; Rolls & Tovee, 1994; Rolls, Tovee, & Panzeri, 1999). The evidence that some responses to emotion-provoking stimuli can be elicited in such experiments even in the absence of subjective awareness suggests that awareness may not always be associated with behavioral responses that are taken as evidence for emotions, and indeed a theme of *Emotion and Decision-Making Explained* is that there are multiple routes to behavioral responses including responses to emotion-related stimuli. This suggests that emotional experience may be somewhat different from the ability to produce behavioral responses that may be used as measures of emotion. For these reasons, taking affective experience, phenomenal consciousness as the criterion for an emotional response may be too limiting, and instead it is of interest to explore what the relation is between phenomenal consciousness and

behavioral responses to emotion provoking, and for that matter other, stimuli, and that is an exploration that is started in Chapter 10. An implication of these points is that humans may be the best subjects in which to explore which behaviors can be produced with and without subjective conscious experience, and thus to delineate the computations in the brain to which subjective conscious states may be especially linked [Chapter 10 of *Emotion and Decision-Making Explained*, Rolls (2014a)].

The parsimonious approach taken in *Emotion and Decision-Making Explained* to the points discussed by Jaak Panksepp is thus as follows. There are multiple routes to responses, some of which are shown in Fig. 1. Unlearned responses such as autonomic responses, freezing behavior, and withdrawal from for example looming stimuli can take place without intervening states, and can be classically conditioned. An important step in evolution is when stimuli can become the goals for arbitrary actions (in the process of instrumental learning, which involves rewards and punishers for actions), for intervening states are required, for example to bridge a time interval after a stimulus before a successful action can be selected and made to obtain or avoid the goal, or to maintain behavior directed towards a goal if an expected reward is not obtained in the process of frustrative non-reward. These intervening states, which may need to persist for minutes in the absence of the stimulus, can then be described as emotional states, with supporting evidence described in Chapter 2. This provides an operational definition of emotional states (as states elicited by rewards and punishers), which does not rely on inferences about ‘affective states’ of the type about which humans can make direct reports, which matches operationally what humans describe as emotional states, and which provides a foundation for classifying different emotions, as described in Chapter 2. There is evidence from research in humans that some behavioral and autonomic responses to stimuli can take place without conscious awareness, and this provides a direct approach to what types of behavior can take place without conscious reported awareness, and what type of processing is related to conscious awareness. This issue, of conscious awareness, is an issue that is very much open to debate, and no conclusions on this are reached in *Emotion and Decision-Making Explained*, in which it is indicated that current theories are preliminary, and so do not imply practical consequences. There are many interesting scientific observations about consciousness, including the finding that the consciously reported subjective pleasantness of stimuli is linearly related to activations in the orbitofrontal cortex, but this does not imply that the awareness itself is represented in the orbitofrontal cortex, and much remains to be discovered about the processes involved, and about which we should be open-minded at present.

6. Reward, emotion, and motivation elicited by brain stimulation

Panksepp (2014) raises the issue of the emotional and related effects elicited by electrical stimulation of the brain, an approach that he has used extensively in animals (Panksepp, 1998). Research in this area was described by Rolls in *Emotion*

Explained (Rolls, 2005) in Chapter 7 entitled Brain-Stimulation Reward, and was not included in *Emotion and Decision-Making Explained* (Rolls, 2014a) so that the latter book could focus on newer findings. Evidence was described that electrical stimulation of the lateral hypothalamus and orbitofrontal cortex can act as a specific natural reward (for example with stimulation selected at one site when hungry, and at another site when thirsty), and acts to do this by activating neurons activated by natural rewards such as food or water (Rolls, 2005; Rolls, Burton, & Mora, 1980). In humans, subjective states of pleasure or mood elevation may be elicited rapidly by electrical stimulation at some of these or related brain sites in the subcallosal cingulate cortex, the stimulation may be useful in the long term in raising mood and relieving depression, and neurons in these regions may be activated by emotion-provoking stimuli (Laxton et al., 2013; Lozano et al., 2012). Of course the fact that an emotional experience can be triggered by electrical stimulation of a brain area does not mean that the experience itself is implemented in that brain area (in the same way that a pin prick in a finger does not imply that the awareness is implemented in the neurons in the finger that are firing), for the electrically stimulated brain area is connected to many other brain areas (Rolls, 2005; Rolls et al., 1980).

The situation is a little more complicated for some of the behaviors elicited by stimulation of at least the hypothalamus/medial forebrain bundle region (Rolls, 2005). Electrical stimulation at some brain sites can elicit feeding, drinking and other types of behavior (Valenstein, Cox, & Kakolewski, 1970). The behavior may be called ‘stimulation-bound’ because it occurs during the electrical stimulation, or ‘stimulus-bound’ because the behavior is associated with a particular goal object, for example food pellets. If small-tipped stimulation electrodes are used relatively specific behaviors are elicited, such as drinking with electrodes near the zona incerta, and feeding with electrodes in the lateral hypothalamus (Huang & Mogenson, 1972; Olds, Allan, & Briese, 1971).

A frequently observed feature of such behavior is plasticity, that is stimulus-bound feeding can develop into stimulus-bound drinking if food is removed from the environment and replaced with water (Valenstein et al., 1970). It is as if the stimulation activates the animal and the behavior that is elicited depends on which environmental stimuli are available for the animal to respond to, for example, food to chew or water to lap. This type of interpretation receives support from the observation that a mild continuous tail-pinch (with, for example, a paper clip) leads to ‘stimulus-bound’ types of behavior such as eating in the rat (Antelman & Szechtman, 1975). Because of such findings, it is difficult to interpret stimulus-bound behavior produced by brain stimulation as a proof of activation of a hunger or thirst mechanism – rather it could be a more general type of behavioral activation.

7. Conclusion

Emotion and Decision-Making Explained provides a foundation for understanding what emotions are; why we have them; their brain mechanisms; how there are many types of value that differ between individuals; how these value systems are

related to neuroeconomic value and the implications for microeconomics; how decision-making is implemented in the brain; how there are different routes to behavior with some that organize behavior for the success of an individual's genes, and others that allow reasoned routes to decisions and actions that can be in the interests of the individual and/or of others. The commentators are thanked for the interesting issues that they raised. There is much exciting research that will be of great interest and that has potential application to medical issues that remains to be performed.

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