

Rolls reviews the substantial body of evidence, much of it from his own laboratory, on the neuroanatomy of emotion. Although the coverage of this area in the book is somewhat idiosyncratic (e.g., much of it might better be described as dealing with motivation), many important issues in the field are discussed in an accessible manner. A particular strength of the book is its message that we can define emotions in terms of the reaction of the animal to rewards and punishments. This is a convincing argument for monkeys and rats, and is a useful starting point for extending our understanding of emotion generally. In this commentary, I will concentrate on one aspect of the book, the role of the amygdala in emotion. More specifically, I will argue that Rolls's proposal that the amygdala is critical for the association of visual objects with reward is not consistent with recent experimental evidence from ablation studies.

Rolls's proposal is that the ventral visual system projects via the inferior temporal visual cortex to the amygdala and orbitofrontal cortex, which together determine the reward or punishment value of the object, as part of the process of selecting which goal is appropriate. He states that "Lesions of the macaque amygdala impair the learning of both stimulus-reward and stimulus-punisher associations." (Précis, sect. 5.2.2). This statement is not supported by current evidence from lesion studies. A series of elegant and thorough experiments in rat by LeDoux and colleagues have convincingly established the importance of the amygdala in stimulus-punisher learning (for review, see LeDoux 1996), in agreement with Rolls's proposal that "the crucial site of the stimulus-reinforcement associative learning that underlies the responses of amygdala neurons to learned reinforcing stimuli is probably within the amygdala itself" (Précis, sect. 5.2.1). However, the same cannot be said for the importance of the amygdala in stimulus-reward association learning (SRAL). Whilst early evidence from aspiration ablation studies suggested a role for the amygdala in SRAL (see Gaffan 1992, for a review), a very different consensus has now been reached on the basis of two recent sets of findings.

First, the recent work of Murray and colleagues has established that many of the functions previously ascribed to the amygdala are in fact functions performed by the adjacent rhinal cortex (for reviews see Baxter & Murray, in press; Murray 1992), and that the amygdala itself has little or no role in stimulus-reward memory. However, the amygdala does have a role in reinforcer devaluation. In this experimental paradigm the monkey has previously learned that one set of positive objects are rewarded with one type of food and the remaining objects rewarded with a second, equally palatable food. After a selective satiation with one of the foods, normal monkeys will choose far more of the other food than is their normal preference. This effect is abolished in monkeys with excitotoxic amygdala lesions (Malkova et al. 1997). The conclusion that can be taken from this is that the amygdala itself is important to reward association memory only on occasions when an abrupt change in the current value of a reinforcer that has an already-established value is required, in order to produce an adaptive response. This conclusion can also be applied to the functional relationship between the amygdala and the orbital prefrontal cortex (Parker et al. 1999).

Second, recent work of Gaffan and colleagues has established that bilateral transection of the amygdala and anterior temporal stem disconnects inferior temporal cortex from its afferent connections in the basal forebrain (Gaffan et al. 1998; submitted). This disconnection severely impairs SRAL, an effect that was previously ascribed to amygdala damage (see Gaffan 1992; Easton & Gaffan 2000, for reviews), and now can be ascribed to interruption of fibres of passage through the amygdala. This conclusion has been strengthened by experiments which use crossed unilateral lesions, in which a heat lesion in the basal forebrain in one hemisphere is combined with a lesion of contralateral inferior temporal cortex. A very similar deficit in SRAL is observed in monkeys with this pattern of lesions to the animals with bilateral amygdala plus anterior temporal stem transection (Easton & Gaffan 1997;

submitted), and a similar equivalence between surgical groups in recognition memory deficits can also be seen (Gaffan et al. 1998; submitted; Easton et al., submitted). We can therefore conclude that the basal forebrain, rather than the amygdala, is the crucial structure which modulates memory storage in inferior temporal cortex in SRAL.

Novelty assessment is often proposed to be an important precursor of memory formation, and Rolls and his colleagues have found cells in several key areas of the brain that respond preferentially to novelty. As with the discussion of SRAL above, however, evidence from single cell recording studies alone do not provide a convincing explanation of the relationship of novelty-related processing to memory formation. Rolls, citing the research of Wilson and Rolls (2000), proposes that the amygdala is filtering information about whether visual stimuli are either novel or reward-related, and making decisions about output based on these evaluations (Rolls 1999a, p. 105). In support of this, he states that lesions of the amygdala in macaque negatively affect this process (specific experiments unspecified). This lesion effect is more likely to be due to the effect of damage to the rhinal cortex than to damage to the amygdala itself. Using a series of memory tasks which manipulate the relative novelty of visual stimuli, we have found that aspiration lesions of the amygdala which do not damage rhinal cortex do not abolish the advantage for novel visual stimuli seen in normal monkeys (Parker et al. 1998). In contrast, crossed unilateral lesions of perirhinal cortex and prefrontal cortex do abolish this novelty advantage (Parker et al. 1998), as do bilateral ablations of the perirhinal cortex (Buckley et al. 1999). It therefore seems unlikely that the amygdala is crucial for the novelty-related processing that precedes visual object-reward associations.

Awareness may be existence as well as (higher-order) thought

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Abstract: Rolls attributes to consciousness the functions of reflection, planning, and error-correction. Neuropsychologically grounded cybernetic theory provides an analogous, broader conceptualization: consciousness constructs goals (and plans), alters the valence of goal-related phenomena, registers error-signals, and explores unexpected circumstances (reconfiguring goals and plans as necessary). Consciousness plays a fundamental unrecognized ontological role, as well, conferring the status of "discriminable object" on select aspects of otherwise indeterminate "being."

Rolls identifies consciousness particularly with higher-order thought, describing it as "the state which arises in a system that can think about . . . thoughts" (p. 248). He believes consciousness has two primary functions. The first, potential for reflection on past events, has a corollary, planning for future events. The second, integrally related to the first, is correction of error made by lower-order processes.

Rolls suggests that higher-order thoughts intervene when lower-order-thought-predicated plans fail (p. 250). Higher-order thoughts perform this operation (linguistically) by analyzing the structure of lower-order plans, identifying specific weak links, and replacing those with potentially better alternatives. Rolls's theoretical model can therefore be assimilated to the cybernetic viewpoint (Wiener 1948) (and psychological elaborations thereof). Such assimilation is advantageous because it unites Rolls's work with a well-developed alternative body of theory, and allows his ideas regarding consciousness further integration with current theories of emotion (not excluding his own).

The plans that organisms formulate include goals, from the cy-

bemetic perspective (Wiener 1948). Goals are hypothetical future world-states similar to those currently obtaining, but modified in a manner both attainable and beneficial. The desired future state may be viewed as an (imaginal) template, against which current insufficient states of the world are compared, as behavior is undertaken (Peterson 1999). A "plan," in this scheme, is that sequence of behavioral steps posited as necessary to produce the desired future condition (Carver & Scheier 1998). Plan-formulation may be the responsibility of the higher-order thought system described by Rolls – but so (explicitly) must be abstract goal-formulation. Higher-order thought systems performing this latter function may modulate emotional valences directly (may affect the "reinforcing value" of stimuli) as well as formulating or altering plans (Peterson 1999). This valence-modulating capacity constitutes a major extension of the role of consciousness, even when defined in a manner otherwise similar in all regards to that proposed by Rolls.

Rolls (p. 61) presumes that emotions are states produced by "instrumental reinforcing stimuli," and suggests that this presumption allows for "operational definition of what causes an emotion." However, what might be instrumentally reinforcing in one situation (whether "subjective" or "objective") may not be in another. This implies that Rolls's definition is less than optimally "operational." All sophisticated behaviorists recognize that the current status of an animal in part determines the reinforcing nature of a given "stimulus" (Rolls in fact admirably details the mechanisms by which such determination occurs, when he describes brain control of feeding and reward). But there is a cognitive component of "current status," analogous to higher-order control and modification of current plans. Formulation of an abstract goal (a future "desired state") instantaneously transforms that goal into something equivalent in all essential features to a consummatory reward (Peterson 1999). It is in this manner that higher-order cognition and emotion meet. A cognitively constructed "consummatory reward" may be something as abstracted away from instinctive significance as a goal scored during a soccer game (an occurrence for which individuals will work, and one whose possibility also colors all other game-events: opposing players and their maneuvers become "threats" or even "punishments," assuming they interfere with scoring chances or score themselves; scoring opportunities are "incentive rewards," indicating progress towards a consummatory goal – and all this in the absence of conditioning!) This means that emotions may be more operationally considered "states produced by stimuli whose reinforcing properties derive from their relationship to some explicitly formulated goal"; and means further that the notion of stimulus-valence is not meaningful, unless current organismal goals are explicitly specified (although sometimes valence evaluation may indeed take place in the absence of higher-order thought; see LeDoux 1996, pp. 161–69).

Consideration of the role played by higher-order thought in goal-specification and consequent valence-determination also allows for a more comprehensive view of error detection and correction. Sokolov (1969) suggested that the orienting reflex (a complex psychophysiological response, associated with initiation of exploratory behavior) emerges automatically when the goal-directed nervous system detects an unexpected "stimulus." "Unexpected" in this context means "deviant from plan (the behavior manifested did not produce the result desired)." Orienting and more complex exploratory behavior garners new information, used either to modify the ongoing plan or, if necessary (and much more problematically), to eradicate and reconstruct the current goal (Peterson 1999). Vinogradova (1975) suggested that the comparator designed to detect such deviation/novelty resided in the hippocampus. Gray (1982; Gray & McNaughton 1996) associated the function of this novelty detection system with the emergence of behavioral inhibition and anxiety. LeDoux (1996) and others, including Rolls, associate anxiety more particularly with amygdalic function, so the relationship between hippocampal novelty-detection and behavioral inhibition/anxiety appears as of yet unclear. However, the notion that novelty is a primary source of anxiety

(and knowledge) should take center stage in any discussion of the relationship between cognition, emotion and consciousness (Peterson 1999), as initial caution (and then exploration) is so clearly appropriate, when unexpected relations emerge between desire and world.

Consciousness therefore appears as higher-order (linguistically mediated) correction of lower-order plans, as Rolls suggests, and more. Consciousness also establishes explicit goals (while informed by other brain processes indicating biological necessity); formulates plans designed to attain those goals (or arranges already automatized plans to the same end); re-evaluates the significance of ongoing events (as a consequence of establishing goals and plans); registers signals indicating emergence of unexpected events (feeling not only anxiety but "hope" and "curiosity" while doing so; Peterson 1999); and explores, gathering new information and reconstructing goals and plans in the face of failure.

One more radical attribute of consciousness may also be posited, as a consequence of operation within this expanded conceptual framework. Rolls notes that inputs from sensory systems must be registered within consciousness, for the purposes of planning (p. 251). However, the sensory plenum as such is too complicated to constitute an object (or even many objects) of consciousness (Medin & Aguilar 1999). This means that sensory awareness is selective: the world is necessarily parsed up into the limited set of "objects" functionally relevant to the operations of current goal-directed operations, and the necessarily co-existent category of "all things presently irrelevant" (and therefore "ignored" or "unconscious").

Only functionally relevant objects "exist" at any given moment – constituting figure, so to speak, instead of ground. So the very fact of discriminable things appears as something dependent upon consciousness. This makes consciousness something far more fundamental than generally supposed (makes it something far from epiphenomenal) (Peterson 1999), and helps account at least by inference for its continuing incomprehensibility.

The causal status of emotions in consciousness

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Abstract: Rolls demonstrates how reward/punishment systems are key mediators of cognitive appraisal, and this suggests a fundamental, causal role for emotion in thought and behaviour. However, this causal role for emotion seems to drop out of Rolls's model of consciousness, to be replaced by the old idea that emotion is essentially epiphenomenal. We suggest a modification to Rolls's model in which cognition and emotion activate each other reciprocally, both in appraisal and consciousness, thus allowing emotion to maintain its causal status where it matters most.

Although Rolls covers a wide area of neuroscience research, there are two themes that come to the fore. First is the review and integration of a large amount of basic research on the structure and organization of the brain systems that are central to the production of emotional behaviour. The second theme is the thesis that all emotions are caused by reward/punishment contingencies and that this formulation is consonant with appraisal theories of emotion.

We will argue that Rolls's version of appraisal theory places the two themes, one integrative, and one reductive, at odds. This becomes most evident in Rolls's consideration of the nature of consciousness, where the causal role of emotions is blurred. Finally, we will sketch a solution to the dilemma that is predicated on the idea that emotions inform appraisals even while they are initiated and constrained by those appraisals.

Rolls situates his definition of emotion within the existing frame-