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Limbic systems for emotion and for memory, but no single limbic system

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ABSTRACT

The concept of a (single) limbic system is shown to be outmoded. Instead, anatomical, neurophysiological, functional neuroimaging, and neuropsychological evidence is described that anterior limbic and related structures including the orbitofrontal cortex and amygdala are involved in emotion, reward valuation, and reward-related decision-making (but not memory), with the value representations transmitted to the anterior cingulate cortex for action–outcome learning. In this ‘emotion limbic system’ a computational principle is that feedforward pattern association networks learn associations from visual, olfactory and auditory stimuli, to primary reinforcers such as taste, touch, and pain. In primates including humans this learning can be very rapid and rule-based, with the orbitofrontal cortex overshadowing the amygdala in this learning important for social and emotional behaviour. Complementary evidence is described showing that the hippocampus and limbic structures to which it is connected including the posterior cingulate cortex and the fornix-mammillary body-anterior thalamus-posterior cingulate circuit are involved in episodic or event memory, but not emotion. This ‘hippocampal system’ receives information from neocortical areas about spatial location, and objects, and can rapidly associate this information together by the different computational principle of autoassociation in the CA3 region of the hippocampus involving feedback. The system can later recall the whole of this information in the CA3 region from any component, a feedback process, and can recall the information back to neocortical areas, again a feedback (to neocortex) recall process. Emotion can enter this memory system from the orbitofrontal cortex etc., and be recalled back to the orbitofrontal cortex etc. during memory recall, but the emotional and hippocampal networks or ‘limbic systems’ operate by different computational principles, and operate independently of each other except insofar as an emotional state or reward value attribute may be part of an episodic memory.

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1. Introduction

The concept of the limbic system has a long history, and is a concept that has endured to the present day (Catani, Dell'acqua, & Thiebaut de Schotten, 2013; Mesulam, 2000).

In this paper I describe evidence that there are separate systems in the brain for emotion and for memory, each involving limbic structures, but that there is no single limbic system. We might term the system for emotion the 'emotional limbic system', and the system for memory the 'memory limbic system', but there are non-limbic components to both systems. The important concept I advance here is that the systems for emotion and for episodic memory involve largely different brain structures and connections, and different computational principles of operation, which are described. I argue here that of course some links from the emotional system into the memory system are present, for often an emotional state is part of an episodic memory, and when that episodic memory is recalled, the emotional state must be included in what is recalled. These concepts are important not only within neuroscience, but also for neurology (Catani et al., 2013; Mesulam, 2000), neuropsychology (Aggleton, 2012), and psychiatry.

2. Historical background to the concept of a limbic system

The use of the term 'limbic' has changed over time, but the concept of a limbic system is still in use (Catani et al., 2013). The term 'limbic' was introduced by Thomas Willis (1664) to designate a cortical border encircling the brainstem (limbus, Latin for 'border'). Paul Broca (1878) held the view that 'le grand lobe limbique' was mainly an olfactory structure common to all mammalian brains, although he argued that its functions were not limited to olfaction. Limbic structures are frequently taken to include cortical structures such as the hippocampus and cingulate cortex, and structures to which they are connected such as the mammillary bodies, septal area, and amygdala (Isaacson, 1982). After Broca's publication, the accumulation of experimental evidence from ablation studies in animals broadened the role of limbic structures to include other aspects of behaviour such as controlling social interactions and behaviour (Brown & Schäfer, 1888), consolidating memories (Bechterew, 1900), and forming emotions (Cannon, 1927). Anatomical and physiological advances led James Papez (1937) to describe a neural circuit for linking action and perception to emotion. The Papez circuit consists of the hippocampus connecting via the fornix to the mammillary body, which connects via the mammillo-thalamic tract to the anterior nuclei of the thalamus and thus back to the cingulate cortex. According to Papez, emotion arises either from cognition entering the circuit from the cortex through the hippocampus, or from visceral and somatic perceptions entering the circuit through the hypothalamus. Some of Papez' evidence on his circuit and emotion was that in rabies where the disease appears to have a predilection for the hippocampus and cerebellum, the patient is subject to anxiety, apprehensiveness, and paroxysms of rage or terror. Papez held that 'the cortex of the cingular gyrus may be looked on as the receptive region for the experiencing of emotion as the result of impulses coming from the hypothalamic region or the hippocampal formation' (Papez, 1937). A decade later, Paul Yakovlev (1948) proposed that the orbitofrontal cortex, insula, amygdala, and anterior temporal lobe form a network underlying emotion and motivation. Paul MacLean crystallised previous works by incorporating both Papez' and Yakovlev's views into a model of the limbic system (MacLean, 1949, 1952). MacLean concluded that the limbic cortex, together with the limbic subcortical structures, is a functionally integrated system involved especially in emotion. Robert Isaacson assembled evidence on the functions of this system in emotion and memory in a book entitled *The limbic system* (Isaacson, 1982).

In the remainder of this paper I describe evidence that there are separate systems in the brain for emotion and for episodic memory, each involving limbic structures; introduce a hypothesis about the nature of the links between these systems; show that the computations in the two systems are very different; and argue that there is no (single) limbic system.

3. Brain systems involved in emotion: the orbitofrontal cortex, amygdala, and anterior cingulate cortex (ACC)

3.1. *Emotions defined*

A very useful working definition of emotions is that they are states elicited by rewards and punishers, that is, by instrumental reinforcers (Gray, 1975; Rolls, 2005, 2014; Weiskrantz, 1968). Instrumental reinforcers are rewards and punishers that are obtained as a result of an action instrumental in gaining the reward or avoiding the punisher. This approach is supported by many considerations (Rolls, 2014), including the following three. First, the definition is conceptually acceptable, in that it is difficult to think of exceptions to the rule that rewards and punishers are associated with emotional states, and to the rule that emotional states are produced by rewards and punishers (Rolls, 2014). Second, the definition is powerful in an evolutionary and explanatory sense, in that the functions of emotion can be conceived of as related to processes involved in obtaining goals, and in states that are produced when goals are received. Indeed, my evolutionary Darwinian account states that the adaptive value of rewards and punishers is that they are gene-specified goals for action, and that it is much more effective for genes to specify rewards and punishers, the goals for action, than to attempt to specify actions (Rolls, 2014). Examples of such primary (i.e., unlearned or gene-specified) reinforcers include the taste of food, pain, stimuli that promote reproductive success, and face expression. Other stimuli become secondary reinforcers by learned associations with primary reinforcers in parts of the brain involved in emotion such as the orbitofrontal cortex and amygdala. An example is the sight of food, which by learned association with a primary reinforcer, taste, becomes a secondary reinforcer. Third, this approach provides a principled way to analyse the brain mechanisms of emotion, by