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Review

Moving beyond standard procedures to assess spontaneous recognition memory

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ABSTRACT

This review will consider how spontaneous tasks have been applied alongside neuroscientific techniques to test complex forms of recognition memory for objects and their environmental features, e.g. the spatial location of an object or the context in which it is presented. We discuss studies that investigate the roles of the perirhinal cortex and the hippocampus in recognition memory using standard testing paradigms, and consider how these findings contribute to the ongoing debate about whether recognition memory is a single unitary process or multiple processes that can be dissociated anatomically and functionally. Due to the wide use of spontaneous tasks, the need for improved procedures that reduce animal use is acknowledged, with multiple trial paradigms discussed as a novel way of reducing variability and animal numbers in these tasks. The importance of improving translation of animal models to humans is highlighted, with emphasis on a shift away from relying on the phenomenological experience of human subjects.

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1. Introduction

Recognition memory is commonly impaired in neurodegenerative or brain damaged patients (Aggleton and Shaw, 1996), so it is critical to gain full understanding of brain mechanisms and neural networks that are essential for this memory function in humans. The current review will discuss the behavioural approaches used to assess different forms of recognition memory in non-human animals, and how they can be usefully applied with neuroscientific approaches, such as lesions and immediate-early gene imaging, to inform our understanding of memory function in such animals. In addition, new approaches that address the large animal use in widely used behavioural tasks will be discussed. The implications for animal reduction as well as greater reliability of these tasks are significant, and sit alongside further consideration of the 3Rs (Replacement, Refinement and Reduction), in view of how animal models can be used to inform research on human memory.

A debate which is central to our understanding of recognition memory function is whether it is a single unitary process or two distinct processes. A full discussion is beyond the scope of this review, but has been comprehensively covered elsewhere (e.g. Aggleton and Brown, 2006; Clark and Squire, 2010; Ranganath and Ritchey, 2012), so we shall begin with just a brief introductory overview to provide a basis for the behavioural work to be discussed.

2. Recognition memory – two distinct processes?

Recognition and episodic memory are forms of declarative memory whereby memories can be consciously recalled. Recognition memory may be defined as the process of identifying when something (e.g. an object, a person) has been encountered previously. Episodic memory, on the other hand, involves memory for a past experience in one's life.

Researchers have long been interested in the mechanisms underlying recognition memory. Eichenbaum et al. (1994) proposed that recognition is supported by two functionally distinct processes mediated by structures in the medial temporal lobe; the hippocampal formation, supporting recollected associations and relationships amongst stimuli, and the parahippocampal region, supporting recognition of individual items. This functional dissociation of recognition memory was further extended by Brown and Aggleton (2001) when they proposed that the hippocampus is part of an extended circuit specifically necessary for episodic recollection (associated with a feeling of 'remembering'; Tulving, 1985), while the perirhinal cortex is part of a circuit involved in familiarity and recency judgements about an encountered stimulus (associated with a feeling of 'knowing'; Tulving, 1985). Dual-process models, such as those proposed by Eichenbaum et al. (1994) and Brown and Aggleton (2001), are based on recognition processes being functionally distinct, though there is still some debate as to which regions in the medial temporal lobe are necessary to support these processes (Eichenbaum et al., 2007). According to these models, the hippocampus, fornix (subcortical fibre pathway connecting to the hippocampus) and anterior thalamus form a neural circuit that is critically involved in the process of recollection but not familiarity. On the other hand, the perirhinal and parahippocampal cortices and the medial dorsal nucleus of the thalamus are necessary for familiarity (Aggleton et al., 2005; Bowles et al., 2007; Brown and Aggleton, 2001; Eacott and Heywood, 1995; Eichenbaum et al., 2007; Fortin et al., 2004; Langston and Wood, 2010; Ranganath et al., 2004; Sauvage et al., 2008; Yonelinas et al., 2002). However, other researchers argue that recognition memory is a single process dependent on both the hippocampus and adjacent cortex (Donaldson, 1996; Haist and Shimamura, 1992; Squire et al., 2004, 2007). Such models state recognition memory is a process based on familiarity, where 'knowing' reflects weaker memory and 'remembering' is associated with strong memory.

Studies involving human amnesic patients with hippocampal damage have provided useful insight into this debate, with some reporting selective recollection impairment with spared familiarity processing (Aggleton et al., 2005; Bastin et al., 2004; Gardiner et al., 2006; Holdstock et al., 2002; Turriziani et al., 2008; Yonelinas et al., 2002), offering support to the dual-process model, whilst others have found deficits in both recollection and familiarity (Cipolotti et al., 2006; Jenson et al., 2010; Manns et al., 2003). To some extent, the inconsistent findings can be attributed to differences in testing measures and/or the specific medial temporal lobe damage varying between patients. If recognition memory is to be convincingly accepted as being supported by dual-processes, then it is necessary to localise the structures within the medial temporal lobe that mediate these processes, and specifically whether the roles of the perirhinal cortex and the hippocampus can be regarded as separate in their support of familiarity and recollection (Aggleton and Brown, 2006; Eichenbaum et al., 2007; Guderian et al., 2011; Montaldi and Mayes, 2010; Montaldi et al., 2006; Murray et al., 2007; Norman, 2010; Squire et al., 2007; Squire and Wixted, 2011; Vann et al., 2009; Vann and Albasser, 2011).

The human patient literature goes some way in determining the structures underlying recognition memory, however, a substantial amount of research has, and continues to be, focused on developing animal models of memory which can provide an insight into the functional neuroanatomy. The importance of such research is evident as animal studies not only allow for impairments after specific and localised lesions to be measured, but they also allow researchers to look at precise genetic and molecular factors involved in memory processes and the effect of pharmacological interventions (Dere et al., 2006), with the aim of developing appropriate treatment for memory impairments in neurodegenerative diseases, and neurorehabilitation for deficits in brain injured individuals.

3. Early studies on recognition memory in animals

Subjects with damage to the medial temporal lobe have been reported to experience profound memory deficits (Scoville and Milner, 1957). Early studies on recognition memory in non-human primates sought to reproduce this damage to gain an understanding of the anatomical basis for such deficits. However, the nature of a suitable task to reveal deficits which are analogous to those of patients such as H.M. was not always clear. Gaffan (1974) developed the 'delayed matching to sample' (DMS) task as a one-trial test of visual recognition memory in monkeys. The task consisted of presenting the animal with a single object in the sample phase that had to be displaced for a food reward. In the test phase, the sample object was presented alongside a new object, and the monkey was trained to select/match the object from the sample phase, thus demonstrating memory for that object. The delay between the sample and test phases of the trials could be varied to increase demand on recognition memory, and it was argued that this task was analogous to the yes/no recognition memory tasks used in human memory studies and those used to identify memory impairments in amnesic individuals (Clark and Squire, 2010).

In 1978, Mishkin modified the DMS task so that the monkeys were trained to select the new object in the test phase, rather than the object that had appeared in the sample phase. Training for this 'delayed nonmatching to sample' task (DNMS) was quicker as it capitalised on the animals' natural preference for novelty (Mishkin, 1978; Mishkin and Delacour, 1975). DNMS has been widely used as a test of recognition memory in both monkeys (e.g. Eacott et al., 1994; Mishkin and Delacour, 1975) and humans

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