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Introduction

Declarative memory refers to memories for facts and events that can be consciously brought to mind and "declared" (Cohen & Squire, 1980). Declarative memory comprises both semantic memory for knowledge and facts as well as episodic memory for events. The loss of declarative memory, particularly episodic memory, is one of the hallmarks of the amnesic syndrome and declarative episodic memory is what people typically mean when using everyday terms such as "memory" and "remembering".

Recognition memory is an important part of declarative episodic memory; most people are familiar with the situation where something cannot be recalled but "I'll remember when I see it". Indeed, the ability to recognise people, objects and places that we have encountered before is a vital cognitive function and has been the focus of numerous studies of memory. In particular, the role of the hippocampus in recognition memory has been the subject of intense debate, with neuropsychological studies from different laboratories frequently reporting conflicting findings. It is therefore somewhat surprising that there is actually broad agreement as to the contribution of the hippocampus to declarative memory. The dominant position is that the hippocampus plays a critical role in processing the relationships between discrete items, particularly in binding representations of items to contextual information (Eichenbaum et al., 1994; Davachi, 2006; Diana et al., 2007; Bird and Burgess, 2008a; Olsen et al., 2012). Several authors have associated the binding processes underpinned by the hippocampus with the concept of episodic *recollection*, whilst recognition memory for individual items can be accomplished by *familiarity* processing in extrahippocampal regions (Aggleton and Brown, 1999; Rugg and Yonelinas, 2003; Montaldi and Mayes, 2010).

Studies of the neuroanatomy of recognition memory started with studies of non-human primates. In this review I will first summarise the findings from these studies, which suggested that performance is only normal following hippocampal damage if trial-unique stimuli are used. I will then summarise dual process theories of recognition memory which have been partly based on the findings from animals. Conflicting evidence that item recognition memory is spared following hippocampal damage in humans will then be presented. I will then argue that unfamiliar face recognition memory is consistently spared in the context of human hippocampal damage and I will suggest that tests using unfamiliar faces are analogous to trial-unique recognition tests used in animal studies. In the final section I will review the arguments for why recognition memory following hippocampal damage is impaired for some materials but not others. Overall I will conclude that the evidence does indeed support a role for the hippocampus in binding item representations to other contextual information. Furthermore, extrahippocampal regions can support the ability to judge whether or not an item has ever been experienced before on the basis of a familiarity-like process. However, there are only very limited instances when these extrahippocampal processes support normal recognition memory and they likely make a relatively minor contribution to real-world declarative memory processes.

Animal models of recognition memory

Following the famous case of HM and others (Scoville and Milner, 1957), there was a concerted effort to develop a suitable analogue of amnesia in non-human animals, particularly primates. Whilst healthy humans are able to remember objects, faces, places and other items after a small number of

exposures, amnesics are profoundly impaired in this ability. Nevertheless, non-declarative priming effects and the ability to acquire new motor skills and classically conditioned responses are intact in amnesia (Squire, 1992). Because of this, any viable animal model of amnesia had to replicate these effects, requiring a test that could only be performed using declarative memory processes. A major breakthrough was the development of the delayed match-to-sample (DMS) and the delayed nonmatch-to-sample (DNMS) tasks for use in primate studies of recognition memory (Gaffan, 1974; Mishkin, 1978).

DMS and DMNS tasks present the subject with a single object and then after a variable delay, the object is presented with a second, unstudied, object and the subject is required to indicate either the previously studied item (DMS) or the unstudied item (DNMS). The test specifically requires visual recognition memory and the overwhelming number of studies investigating recognition memory for single items use visually presented material (the main exception being studies in humans that use verbal material presented auditorily).The key point of both DMS and DNMS tasks was that large stimulus sets of novel, "junk" objects could be used, so that gradual learning of the targets over multiple trials could not occur. These tasks were therefore thought to provide an assay of declarative recognition memory processes.

The earliest primate studies of the effects of lesions to the hippocampus or related areas found inconsistent results. The fornix is a major output pathway of the hippocampus and it is usually thought that damage to the fornix produces a memory impairment that is similar to that caused by damage to the hippocampus itself. It is therefore surprising that one study found that transection of the fornix impaired DMS performance (Gaffan, 1974), but a later study reported that bilateral hippocampal lesions did not impair performance on DNMS task (Mishkin, 1978). Subsequent studies have used more sophisticated lesion techniques, such as injections of ibotenic acid to cause localised neuronal damage whilst leaving the white matter fibres that pass through these regions intact. Despite this, contradictory findings are still obtained. For example, Murray and Mishkin (1998) and Nemanic et al. (2004) demonstrated completely intact performance on the DNMS task following bilateral hippocampal damage. By contrast, Beason-Held et al. (1999), and Zola et al. (2000), found that similar lesions impaired performance.

Primate DMS and DNMS experiments commonly use "pseudo-trial-unique" objects rather than truly trial-unique objects; since experiments involve thousands of trials, objects are repeated from time to time. When reviewing the role of the hippocampus in object recognition in rats, Mumby (2001) stated that, "it will be assumed that pseudo-trial-unique and truly trial-unique procedures engage the same recognition processes". Most researchers appear to tacitly endorse this position. However, as Charles and colleagues (2004) pointed out, the size of the pool of objects used in different studies, and therefore the extent to which the stimuli are truly novel, may play an important role in determining whether damage to the hippocampus or related brain regions causes a recognition memory impairment.

Gaffan (1974), Beason-Held et al. (1999) and Zola et al. (2000) who all found a recognition memory impairments, used a pools of 300, 400 and "over 400 items" objects respectively. Since the studies involve several thousands of trials, this necessitates the frequent reuse of the objects. By contrast to these studies, Mishkin and Murray (1998) and Nemanic et al. (2004), who found that ibotenic acid lesions to the hippocampus had no effect on DNMS performance, used pools of "over 1120" and 1200 objects respectively. Both studies stated that any particular object was reused only once per month.

Charles et al. (2004) directly tested whether the size of the stimulus pool influenced whether fornix transection in monkeys impaired recognition memory. The authors used three different variants of a standard DMS task; (1) the sample was paired with another object seen within the same session, (2) the sample was paired with another object unseen in the same session, but which had been used in a previous session, (3) the sample was paired with an "absolute" novel object (or "truly trial-unique"), which had never been seen before. The results were striking. Fornix transection had no impact on the ability to match the sample object when the foil object was absolutely novel. However, fornix damage impaired object recognition when either the foil object was from the same session or when the object had been previously seen in an earlier session. Importantly, the latter condition is similar to a DMS test using pseudo trial-unique stimuli when there is a relatively small stimulus pool.

Whilst the effects of hippocampal damage on DMS / DNMS tests have been mixed, there is agreement that selective damage to another medial temporal lobe (MTL) region, the perirhinal cortex, is sufficient to cause a severe impairment in recognition memory (Meunier et al., 1993; Buckley et al., 1997).

To summarise the findings from non-human primate research into the effects of hippocampal damage on recognition memory: when the stimulus pool is large enough that items are only used again very infrequently or are truly trial-unique, hippocampal damage appears to have little or no impact on recognition memory. However, when stimulus pools are smaller and objects are reused over the course of the experiment, damage to the hippocampus or fornix is more likely to impair recognition memory performance. It is beyond the scope of this review to describe the effects of hippocampal damage on object visual recognition in rodents. However, the weight of evidence appears to support the position that selective hippocampal damage does not impair this type of recognition memory [(Mumby, 2001; Winters et al., 2004) but see (Prusky et al., 2004)]. It therefore should be the case that at least some forms of recognition memory should be preserved in patients with selective hippocampal damage.

Dual-process theories of recognition memory

It is widely believed that there is a division of labour in declarative memory processes supported by the hippocampus and extrahippocampal cortical regions (Eichenbaum et al., 1994; Davachi, 2006; Diana et al., 2007; Bird and Burgess, 2008a; Olsen et al., 2012). Primate studies demonstrated that visual recognition memory can be spared following selective hippocampal damage but is impaired by perirhinal cortex damage. Furthermore, data from various sources has consistently shown the hippocampus to be critical for memory for (allocentric) spatial information, memory for associations between different types of stimuli and binding items to the contexts that they were experience in (e.g. O'Keefe and Nadel, 1978; Eichenbaum et al., 1994; Gaffan, 1994; Aggleton and Brown, 1999). The importance of the perirhinal cortex for object recognition memory has also been supported by several convergent techniques including electrophysiological studies (Brown and Xiang, 1998) as well as studies using immediate early gene expression (Aggleton and Brown, 2005).

From the 1970's some experimental psychologists have argued that recognition memory can be underpinned by either a feeling of familiarity or by recollecting specific contextual information about an item (Atkinson and Juola, 1974; Mandler, 1980; Jacoby and Dallas, 1981; Tulving, 1985; Yonelinas, 1994). These theories argued that familiarity and recollection are independent memory processes. Nevertheless, both recollection and familiarity are both declarative memory processes in that they give rise to conscious knowledge that can be declared.

Many researchers have associated the hippocampal role in binding or relating items to contexts with recollection, while item recognition processing supported by the perirhinal cortex has been linked to familiarity (Aggleton and Brown, 1999; Rugg and Yonelinas, 2003; Eichenbaum et al., 2007; Montaldi and Mayes, 2010). Irrespective of whether extrahippocampal memory processing is equivalent to "familiarity", all theories that argue for a division of labour between MTL structures (henceforth, "dual process" theories) predict that recognition of discrete items should be relatively independent of the hippocampus. However, as reviewed in the following section, the evidence in favour of this position is far from conclusive. It should be noted that most dual process theories are domain general, such that the specific type of material is not considered important. Studies that have investigated the predictions of dual-process theories have used words, faces, scenes, objects and many other types of memoranda, often averaging performance across tests to obtain global measures of recognition.

Testing dual-process theories in patients with hippocampal damage

A straightforward prediction of all dual process theories is that recognition memory of single items should be relatively preserved following selective hippocampal damage, whether or not item recognition is supported by familiarity processes. By contrast, performance on tests of recall, for which recollection of associative information is necessary, should be impaired. A number of studies have found this pattern, even when using tests that have tried to match the overall difficulty of the recall and recognition tasks (Vargha-Khadem et al., 1997; Baddeley et al., 2001; Mayes et al., 2002; Adlam et al., 2009; Patai et al., 2015). Furthermore, in a large group study, damage to the fornix and subsequent shrinkage of the mammillary bodies was found to selectively correlate with decreases in recall but not recognition (Aggleton et al., 2000; Tsivilis et al., 2008). Despite this other studies have found recognition memory to be impaired by hippocampal damage (Manns et al., 2003; Kopelman et al., 2007). Some of the discrepancies between the different studies are likely to be attributable to differences in the patients' aetiologies, in the extent of their hippocampal damage and the age of lesion onset. Nevertheless, there are instances where patients seem to be quite closely matched in terms of these dimensions, and yet recognition memory has been spared in some and impaired in others. In fact, one study explicitly highlighted the variability between apparently similar patients (Holdstock et al., 2008).

A potential resolution to these conflicting findings was that the studies did not directly test the contribution of recollection and familiarity to recognition performance. A variety of techniques have been developed in the experimental psychology literature for separating recollection- and familiarity-based processes. These might involve explicitly asking participants if they retrieved any additional information about an item or if they simply judged it to be familiar (the "Remember/Know" paradigm; Gardiner, 1988). Alternatively, recognition confidence judgements can be plotted as receiver-operating characteristic curves (ROCs) and fitted to a dual process model to estimate the contribution of recollection and familiarity to performance (Yonelinas, 1994). Using these techniques, some patients with hippocampal damage were identified who indeed showed the predicted impairment of recollection- but not familiarity-based processes (Bastin et al., 2004; Aggleton and Brown, 2005; Turriziani et al., 2008). Similarly, patients with presumed hippocampal damage or with shrinkage of the mammillary bodies following damage to the fornix appeared to be selectively impaired in recollection but not familiarity (Yonelinas et al., 2002; Vann et al., 2009). However, again a number of studies failed to replicate these findings using the same techniques in apparently similar patients (Cipolotti et al., 2006; Wais et al., 2006; Bird et al., 2007; Bird et al., 2008).

While this review is focussed on the role of the hippocampus in recognition memory, it should be noted that there have been reports of patients with unilateral damage to the perirhinal or entorhinal cortex who show a reversed dissociation; impaired familiarity with spared recollection processes (e.g. Kohler et al., 2002; Brandt et al., 2016). Such double dissociations lend support to dual process theories.

There has been much debate about the reasons for these discrepant results across studies but no consensus has emerged (e.g. Montaldi and Mayes, 2010; Wixted et al., 2010). Several studies have suggested that the assumptions underpinning some versions of dual process theory might be incorrect. For example, it has been questioned whether recollection is all-or-none rather than varying in strength like familiarity (Wixted et al., 2010; Didi-Barnea et al., 2016). Others have argued that recollection and familiarity are not independent of each other (Moran and Goshen-Gottstein, 2015). It is also the case that small differences in the data, such as the number of highly confident false alarms, can cause small differences to the shape of the ROC curve, which, when fitted to a dual process model, lead to large differences in the estimates of recollection and familiarity. Thus, apparently large differences between studies might reflect rather small differences in the underlying raw data.

In sum, studies from different laboratories have found contradictory evidence for the preservation of item recognition or of familiarity-based recognition processes following hippocampal damage. However, as reviewed in the next section, there are some instances when recognition memory is spared following hippocampal damage and, importantly, the findings have been replicated across many different laboratories.

Recognition memory for unfamiliar faces is spared in humans with hippocampal damage

Most studies of the neuroanatomy of human recognition memory have not considered the nature of the to-be-remembered material to be important. However, there has been a long history of investigation of material-specific memory impairments, such as verbal versus nonverbal materials (Milner, 1971; Warrington, 1974; Kim et al., 2003), or faces (Maguire and Cipolotti, 1998; Tippett et al., 2000) or scenes (Incisa della Rocchetta et al., 1996). There is now considerable evidence demonstrating material specific recognition memory impairments following hippocampal damage in humans.

Cipolotti et al. (2006), reported the case of an amnesic man (VC) with a severe recognition memory impairment for (familiar) words as well as pictures of (unfamiliar) outdoor buildings and landscapes. By contrast, he was able to perform a demanding test of unfamiliar face recognition as well as controls. VC sustained extensive bilateral hippocampal damage as a result of a period of anoxia (Kartsounis et al., 1995). Although the degree of extrahippocampal damage to VC's brain has been debated (Kapur et al., 1999; Bayley et al., 2006), the striking finding was the sparing of performance on the face recognition task in the context of an otherwise global amnesic syndrome. Interestingly, both familiarity and, more importantly, recollection, as estimated using the ROC procedure, both appeared to be contributing to his preserved performance. Rather similar findings had been described previously by Carlesimo and colleagues (2001) of a man with bilateral hippocampal atrophy and lesions to the globus pallidus bilaterally. The patient demonstrated spared face recognition memory in the context of an otherwise global memory impairment including recognition memory for words and buildings.

The finding of spared face recognition but impaired scene recognition was replicated in a group of three patients with hippocampal damage (Taylor et al., 2007). Furthermore, two further single-case studies of patients with hippocampal damage demonstrated sparing of both recollection and familiarity processes for unfamiliar faces, whilst scene recognition memory was impaired (Bird et al., 2007; Bird et al., 2008).

All of these studies suggested that face recognition could be preserved in the context of damage to the hippocampus that resulted in other declarative memory impairments. To test how general these findings were, we carried out a secondary analysis of published data from patients with hippocampal damage who had been administered Warrington's Recognition Memory test (Warrington, 1984), which assesses recognition memory for both words and faces (Bird and Burgess, 2008b). The findings were clear-cut; within the population of 10 patients, word recognition memory was impaired but face recognition memory was intact (see Figure 1).

Figure 1 about here

In 2010, Aly and colleagues replicated the main finding of intact face recognition compared with impaired word recognition in a small group of patients with presumed hippocampal damage as a result of a period of mild hypoxia (Aly et al., 2010). However, the results of this study were inconsistent with Cipolotti et al. (2006), Bird et al. (2007) and Bird et al. (2008) in that only estimates of familiarity but not recollection were spared.

Insert Figure 2 about here

More recently, Smith and colleagues demonstrated intact face recognition memory over short retention intervals in a group of 5 patients with hippocampal damage (Smith et al., 2014; see Figure 2). The same patients were impaired at both word and unfamiliar buildings recognition memory when tested within a few minutes. Smith et al., went on to extend the findings of previous studies in a number of important ways. First, they demonstrated that after around 2 hours, face recognition was as impaired as recognition memory for other memoranda. Second, confidence ratings for responses on the face recognition memory tasks and ROCs derived from these were similar between the patients and controls, suggesting that both recollection and familiarity processes were underpinning the spared performance. Third, in their experiment 3, Smith et al. used famous faces as memoranda. Importantly, each participant (both the controls and patients) indicated which of the faces they thought were famous or not. In general, pre-experimental familiarity with faces boosts recognition memory (Klatzky and Forrest, 1984; Bird et al., 2011) and this effect was present in the healthy controls. Critically, the patients with hippocampal damage were only impaired in their recognition memory for faces that they identified as being famous (see Figure 3).

Insert Figure 3 about here

A recent study further clarified the limits of unfamiliar face processing following hippocampal damage. Olsen and colleagues (2015) described a patient who was able to recognise faces that were studies from a single viewpoint but was impaired at recognising faces that had been studied from variable viewpoints. The authors concluded that the patients was impaired at binding the features of the faces across different repetitions. It is noteworthy that patients with hippocampal damage are able to perceptually match faces from different viewpoints (Lee et al., 2005a), suggesting that the critical hippocampal role is in binding features across time.

Lastly, it is noteworthy that some studies that have averaged data across different recognition memory tests actually find material specific effects. For example, the patient YR who has been described by Mayes, Holdstock and colleagues (Holdstock et al., 2002; Mayes et al., 2002) performed significantly better on 7 recognition tests involving unfamiliar faces (mean z-score = +0.32) than she did on 8 recognition tests involving words (mean z-score = -1.30) and 6 recognition tests involving unfamiliar scenes (mean z-score = -0.75; Mayes et al., 2002). Also, Tsivilis et al. (2008) reported data from 35 patients with variable damage to the fornix and found that word recognition memory correlated with the extent of fornix damage, but word recognition memory did not.

The hippocampus supports recognition memory for pre-experimentally familiar items

There are a number of factors in which recognition memory for unfamiliar faces is unlike recognition memory for other materials that are commonly used in clinical and experimental settings. These are: (1) the faces are unique, in that the specific faces have never been seen before, (2) related to (1), none of the faces is associated with any pre-existing conceptual knowledge, (3) faces are perceived as single items or units. In all of these respects, they are similar to the "junk" objects used in DMS / DNMS tests for trial unique items. Each of these factors will be discussed below.

Although humans have very extensive experience with perceiving and recognising faces, each individual face in a recognition memory test is being seen for the very first time. Thus, the test is one of absolute familiarity detection; *have you ever seen this item before*? However, as Charles et al. showed in monkeys with fornix damage, when objects are repeated and the task becomes "have you seen this item before *during this trial*?", performance suffers. It therefore follows that individuals with hippocampal damage would perform poorly if tests of face recognition were repeated using exactly the same items.

If a face has never been seen before, then it follows that no details associated with that person will be retrieved (unless they happen to resemble someone else). As a result of this, recognition judgements are likely to be made solely on the visual features of the face. Again, this is similar to DMS/DNMS tasks that use objects that are unfamiliar to the animals being tested. By contrast, a familiar face will likely cue the retrieval of pre-existing conceptual information. This associated information enhances the memory traces created at encoding and sets up a richer set of retrieval cues to be exploited by a hippocampally-mediated memory system at test (see also Trinkler et al., 2009). Consistent with this, recognition memory for known faces is better than for unknown faces (Klatzky and Forrest, 1984; Bird et al., 2011) and, critically, damage to the hippocampus abolishes this advantage (Smith et al., 2014). The proposed role of the hippocampus in supporting conceptually rich representations of known items is consistent with the finding that person-specific conceptual knowledge is encoded by single neurons in the human hippocampus (Quiroga et al., 2005; Quiroga, 2012).

Recognition memory for words is consistently impaired by hippocampal damage. Words used in recognition tests are almost always pre-experimentally known. This means that during a recognition test each word has to be judged as having been seen *during the test*. Furthermore, words are likely to be recognised in terms of the concept that the word refers to, rather than as a perceptual item. In some studies, this is necessarily the case, as words are presented auditorily during study but visually during test (Yonelinas et al., 2002; Vann et al., 2009). Therefore, words are similar to the case of famous faces discussed above. Each word has its own unique set of associated specific and general associations which may be activated during study and aid subsequent retrieval. It is also noteworthy that recognition of odors is impaired by hippocampal damage (Levy et al., 2003; Levy et al., 2004). In these studies, the odors were all familiar, such as garlic powder and shoe polish. Again, similarly to words and famous faces, these odors have pre-existing associations which provide a richer set of cues to base recognition memory judgements. The evidence suggests that recognition memory for items that have well-established conceptual representations is mediated in part by the hippocampus.

The hippocampus supports recognition memory for stimuli comprised of multiple items

Dual process theories of memory propose that the hippocampus does not process discrete items. Unfortunately, there is often little discussion as to what an "item" is. Cohen and colleagues (e.g. Cohen et al., 1997) have argued that items are the outputs of processing modules and use the example of faces to illustrate this. Although faces are comprised of numerous individual features, they are almost invariably perceived as a unified item. A compelling line of evidence for this is that illusions that can dramatically affect face perception are weakened or eliminated by inverting the face (e.g. Maurer et al., 2002). This suggests that inverted faces are perceived as configurations of individual features rather than discrete items and is consistent with the finding that familiarity contributes to associative recognition of upright, but not inverted, unfamiliar faces (Yonelinas et al., 1999). It is therefore of interest that the patients described by Smith et al., (2014) were impaired at a recognition test for inverted unfamiliar faces.

Hippocampal damage consistently impairs recognition memory for scenes (Cipolotti et al., 2006; Bird et al., 2007; Taylor et al., 2007; Bird et al., 2008; Smith et al., 2014). Scenes comprise individual features, but unlike faces, the identify and spatial arrangement of the features is unpredictable and unique to every scene. There is a large body of evidence that the hippocampus processes large-scale spatial information (O'Keefe and Nadel, 1978; Bird and Burgess, 2008a; Clark and Maguire, 2016) and several studies have shown that the hippocampus plays a role in representing spatial information over very short lags (Hannula et al., 2006; Hartley et al., 2007) and even in spatial perception (Lee et al., 2005b; Aly et al., 2013). It is likely that pictures of scenes are particularly good examples of the type of visual material that the hippocampus processes. This may be because a picture of a scene inevitably triggers the formation of a representation of its spatial layout and the representation of scenes is known to require the hippocampus (Byrne et al., 2007; Hassabis and Maguire, 2007). Pictures of other materials, such as doors, have yielded mixed findings with respect to the effects of hippocampal damage (Manns and Squire, 1999; Adlam et al., 2009). Pictures of doors might be recognised on the basis of either the arrangement of individual elements or on the recognition of a single diagnostic feature, and the strategy used might dictate the degree to which the hippocampus supports performance.

To date, there are no clear-cut examples of materials other than faces that can be recognised using extrahippocampal familiarity processes. However, it is possible that there are other unfamiliar materials which are perceived as single units and whose recognition would not depend on the

hippocampus. Voss and colleagues (Voss et al., 2008) showed that healthy adults can perform very well on recognition memory tests for abstract patterns, despite feeling that they were only guessing when performing the task. The authors concluded that "forced-choice recognition tests for stimuli of low conceptual content might not scrutinize explicit memory in humans" (Voss et al., 2008). This is different from the situation with faces, which can be explicitly recognised even in the context of severe memory problems. However, this may reflect a degree of expertise in face recognition processes, imbuing feelings of familiarity with high levels of confidence, which may not be the same for unfamiliar complex abstract patterns. It should be noted that one study of abstract pattern recognition in patients with hippocampal damage, did report an impairment (Levy et al., 2003). However, the stimuli used in this study could have been verbally labelled (e.g. "red star") and it has also been shown that apparently meaningless patterns may nevertheless elicit contextual associations (Voss and Paller, 2007). It therefore remains a possibility that recognition of genuinely meaningless and non-verbalizable stimuli might be supported by extrahippocampal regions.

Taken together there are a number of conditions that are likely to dictate when normal recognition memory can be independent of the hippocampus. In many situations, not all of these conditions are likely to be met, and therefore recognition will be subserved in part by hippocampal-mediated memory processes. However, the fact that there are situations where recognition memory is entirely intact following hippocampal damage is supportive of dual process models and argues against earlier theories whereby different MTL structures subserved all types of declarative memories (e.g. Squire et al., 2007).

Re-evaluating dual process theories of recognition memory

Theories of the role of the hippocampus in declarative memory highlight its importance in processing relationships between items and in binding representations of items to contexts. By contrast, recognition of items in isolation is thought to be mediated by extrahippocampal regions although this has not always been supported by the neuropsychological evidence.

The concept of familiarity was proposed by experimental psychologists as a process that underpinned recognition judgments when no associated information could be recalled. As such, it seems natural to associate familiarity processes with visual object processing known to be subserved by the perirhinal cortex. However, the psychological term familiarity refers to domain-general processing which may act on conceptual representations as well as perceptual representations. Indeed, studies in healthy adults have suggested that familiarity processes underpin a large proportion of recognition judgements irrespective of the nature of the materials used (Gardiner and Parkin, 1990; Parkin et al., 1995). Consequently, most studies investigating dual process theories in patients have not considered potential material specific effects and have focussed on isolating the contributions of recollection and familiarity using different behavioural paradigms. As reviewed above, the results from different laboratories have been inconsistent.

Surprisingly, the best evidence for dual process theories comes from studies that explicitly varied the materials used to test recognition memory, rather than attempted to quantify recollection and familiarity processes. Such studies have shown that unfamiliar face recognition being consistently preserved even in patients with very dense amnesia. Furthermore, a number of studies have suggested that both recollection and familiarity contribute to the preserved ability of patients with hippocampal damage to recognise faces (Cipolotti et al., 2006; Bird et al., 2007; Bird et al., 2008; Smith et al., 2014). These findings agree with several researchers who have argued that the concepts of recollection and familiarity, at least as defined by experimental psychologists, do not map simply

on to anatomical brain regions, and that brain regions that represent particular stimuli may underpin both familiarity and recollection for those stimuli (Davachi, 2006; Cowell et al., 2010; Graham et al., 2010; Wixted and Squire, 2011).

I have interpreted these findings as evidence that recognition memory for items may be completely preserved following hippocampal damage provided that, (1) the items are completely unfamiliar, (2) the items do not have any pre-existing contextual associations, and (3) the items are processed as individual units. Arguably, this parallels DMS /DNMS tests using trial-unique stimuli that have been used in animal studies of recognition memory. Although these conclusions are based on evidence solely from studies using visual material, I would predict that the same principles would apply to other modalities, such as unfamiliar sounds.

Outside of the laboratory, these conditions are unlikely to be met and therefore declarative memory usually depends to some degree on hippocampal processing. Furthermore, preserved face recognition memory in patients appears to be fragile, decaying after a few hours (Smith et al., 2014) and affected by changes in orientation of the face (Olsen et al., 2015). As such, the usefulness of extrahippocampal processes for supporting declarative memory by themselves is very limited. This is due to the simple fact that, in the real world, declarative memory *is* associative and almost always involves a certain degree of binding between items. Furthermore, in most situations the people, places and objects that we interact with usually are familiar and meaningful to us and it is the relationships between these elements that is important. The fact that the "butcher on the bus" phenomenon is used to describe familiarity-based recognition likely stems from the fact that recognising faces is one of the very few instances when familiarity does directly evoke a declarative memory.

None of this should be taken to mean that item processing outside of the hippocampus is unimportant. Representations of items are the building blocks of declarative memories and the perirhinal cortex plays a critical role in visual object processing (Bussey and Saksida, 2005; Taylor et al., 2006). Furthermore, perirhinal cortex and other anterior temporal lobe regions support conceptual representations of objects (Wang et al., 2010; Clarke and Tyler, 2015). Therefore, these regions likely play a key role in the rapid perception, categorisation and interpretation of the contents of the world around us.

Conclusions

Studies of the effects of hippocampal damage on recognition memory are broadly supportive of dual process theories which propose a division of labour between MTL structures to support declarative memory processing. Under these theories, the hippocampus plays a critical role in binding item and contextual information and in processing the relationships between items, whereas extrahippocampal regions such as the perirhinal cortex process discrete items. Some of the clearest support for this proposal comes from primate studies on the effects of MTL lesions on recognition memory for trial-unique objects. Within the human literature, convergent findings have come from studies of recognition memory for unfamiliar faces. In both of these cases the stimuli are discrete items and are not associated with any pre-existing contextual information. Therefore, recognition judgements can be based on a feeling of whether the stimulus has ever been seen before.

In general, dual process theories have not considered the nature of the material to be important; test "items" might be faces, names , pictures, etc. However, this has a profound impact on whether hippocampal damage impairs recognition memory. When items are already associated with

concepts or contexts, as is the case with words, famous faces and even stimuli that have been used in previous tests, recognition memory is supported by hippocampal processing. In addition, recognition memory for scenes and perhaps other visual memoranda that are comprised of multiple elements also depends on the hippocampus.

While material-specific effects of hippocampal damage on recognition memory have been consistent, studies that have attempted to quantify the effects of hippocampal damage on recollection-based and familiarity-based recognition have produced more variable results. It is likely that the psychological constructs of recollection and familiarity do not map directly on to the processing carried out in different regions of the MTL. Despite this, there is now a greater consensus as to the processing roles of the hippocampus and other regions in declarative memory than there has been for many decades. As long as future studies consider the precise nature of the representations and processes necessary to perform different tasks, then our progress towards understanding the neuroanatomical substrates of declarative memory looks set to continue.

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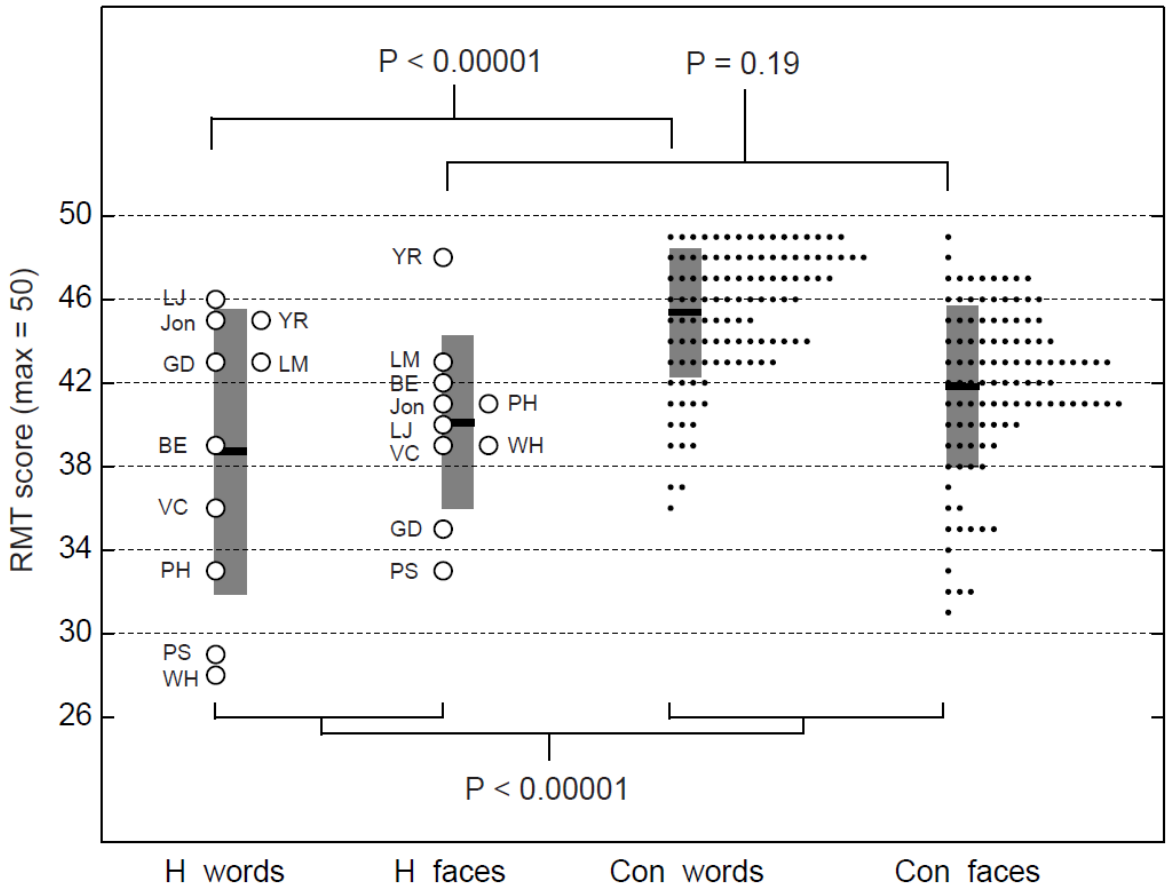

Figure 1

Legend: The hippocampal (H) patients' scores on the Words and Faces subtests of the Recognition Memory Test are on the left, controls' (Con) scores on the right. The H patients performed lower than Con when considering both recognition tests together (significant effect of group: $F(1, 117) = 22.9$, $P<0.001$). Importantly, there was a significant group by subtest interaction ($F(1, 117) = 8.4$, $P=0.004$); the H patients performed better on the faces than on the words subtest, whilst the Con showed the opposite pattern. Direct comparisons between the groups' performance on each subtest revealed a difference only on the words subtest (words; $t=5.76$, $d.f.= 117$, $P<0.001$. faces; $t=1.33$, $d.f=117$, $P=0.185$). Individual patient's data points are labelled. Bold lines indicate mean group performance, shaded bars indicate ±1SD.

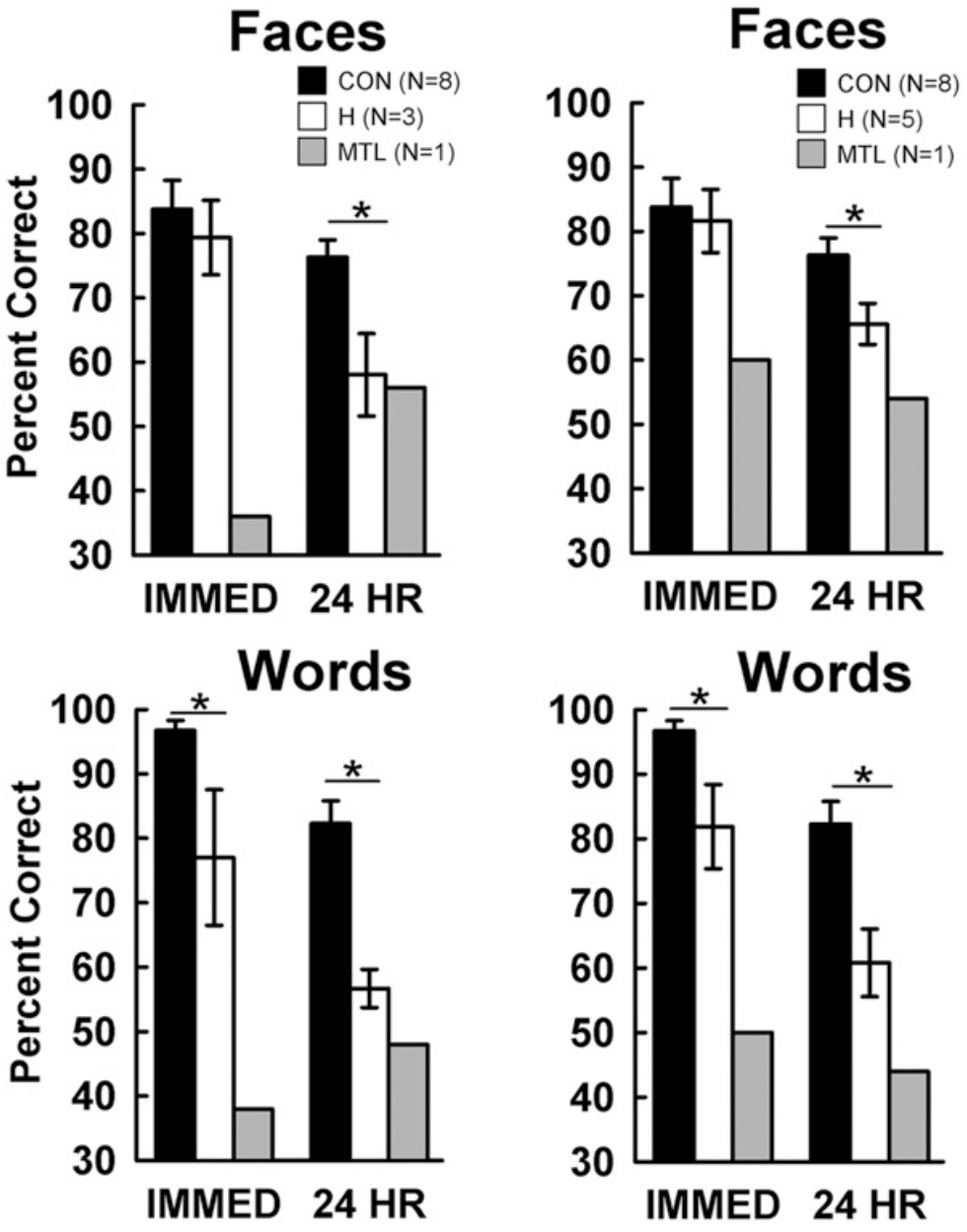

Figure 2:

Legend: Performance of a control group (CON) and memory impaired patients with damage limited to the hippocampus (H) or larger lesions of the MTL on the Words and Faces subtests of the RMT. Testing occurred either immediately after study (IMMED) or 1 d later (24 HR). (Left) Patients whose lesions have been characterized by postmortem histology. (Right) Patients whose lesions were estimated from quantitative structural neuroimaging. For H patients, memory for faces was intact when tested immediately after study but impaired when tested the next day. Memory for words was impaired regardless of the retention interval. MTL patients (EP on the left, GP on the right) were impaired in all conditions. Asterisks indicate a significant difference between patients and controls (*$P < 0.05$). Brackets indicate SEM.

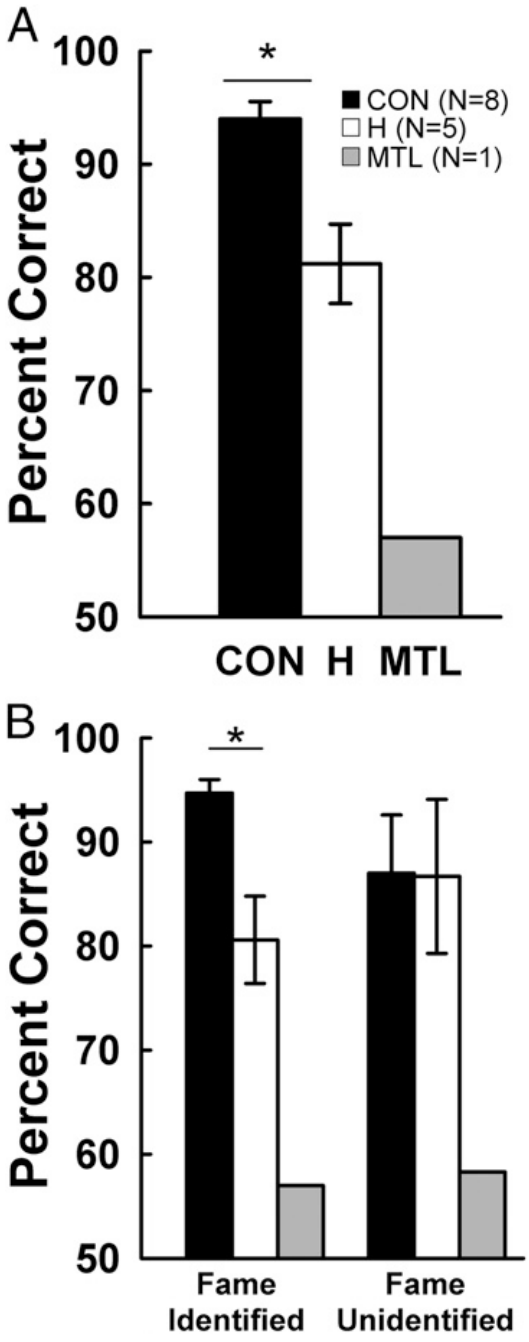

Figure 3:

Legend: Performance on a recognition memory test for famous faces for a control group (CON) and for memory-impaired patients with damage limited to the hippocampus (H) or larger lesions of the MTL. Participants studied 50 famous faces and then immediately took a recognition memory test involving the 50 previously studied faces and 50 new famous faces. (A) Both H and MTL patients were impaired. (B) Accuracy was examined separately according to whether the faces could be identified as famous. H patients were impaired for known famous faces but performed as well as controls for faces that they did not identify as famous. The MTL patient was impaired regardless whether he could identify the faces as famous. Asterisks indicate a significant difference between H patients and controls (*$P < 0.05$). Brackets indicate SEM.