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The electrophysiological correlates of recent and remote recollection

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ABSTRACT

Research using event related potentials (ERPs) to explore recognition memory has linked late parietal old/new effects to the recollection of episodic information. In the vast majority of these studies, the retrieval phase immediately follows encoding and consequently, very little is known about the ERP correlates of long term recollection. This is despite the fact that in other areas of the memory literature there is considerable interest in consolidation theories and the way episodic memory changes over time. The present study explored the idea that consolidation and forgetting processes operating over a moderate retention interval can alter the ERP markers of recollection memory. A remember/know test probed memory for stimuli studied either 15 minutes (recent memory) or 1 week (remote memory) prior to the test phase. Results revealed an attenuated late parietal effect for remote compared to recent remember responses, a finding that remained significant even when these recognition judgments were matched for reaction time. Experiments 2a and 2b identified characteristic differences between recent and remote recognition at the behavioural level. The 1 week delay produced an overall decline in recognition confidence and a dramatic loss of episodic detail. These behavioural changes are thought to underlie the ERP effects reported in the first experiment. The results highlight that although the neural basis of memory may exhibit significant changes as the length of the retention interval increases, it is important to consider the extent to which this is a direct effect of time or an indirect effect due to changes in memory quality, such as the amount of detail that can be recollected.

1. Experiment 1

1.1. Introduction

Recollection memory involves identifying a previously studied stimulus and additionally recalling at least one episodic detail occurring when it was first presented. This differs from familiarity memory which is experienced when an item is recognised but no such details can be recalled. In an attempt to separate these forms of memory, researchers often make use of the remember/know procedure (Tulving, 1985). Participants are instructed to give a remember response for cues that trigger recollection or a know response when a stimulus is recognised purely on the basis of familiarity.

ERPs have been used to investigate the neural processes underlying recognition judgments. A general and reliable finding initially reported was that compared to correctly rejected new items, hits produced broadly distributed, enhanced positivity from approximately 300 ms post stimulus, lasting for several hundred milliseconds (Rugg, 1995). It was recognised early on that the extended time course of the so called old/new effect likely reflected multiple aspects of memory processing (Duzel, Yonelinas, Mangun, Heinze, & Tulving, 1997; Rugg et al., 1998; Smith, 1993). When the remember/know procedure is employed in conjunction with ERP methodology, results support the view that recollection is associated with qualitatively different neural activity from that underlying familiarity based know judgments (Curran, 2004; Duarte, Ranganath, Winward, Hayward, & Knight, 2004; Duzel et al., 1997; Rugg & Curran, 2007; Rugg & Yonelinas, 2003; Smith, 1993).

More specifically, an early onsetting (300–500 ms) old/new effect, typically maximal at midfrontal sites, is thought to index familiarity by some researchers (e.g. Azimian-Faridani & Wilding, 2006; Rugg & Curran, 2007). An alternative proposal, however, is that the midfrontal effect is an ERP correlate of implicit memory in the form of conceptual priming (e.g. Paller, Voss, & Boehm, 2007). Distinguishing between these two views has been problematic given that familiarity and conceptual priming are confounded during the majority of recognition tasks. Later in the post-stimulus epoch, between approximately 500–800 ms, correctly recognised old items are more positive than correct rejections, particularly at left parietal sites (the late parietal old/new effect). These old/new amplitude differences also tend to be larger for remember responses than know responses, supporting the idea that this effect underlies processes important for

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recollection (Curran, 2004; Woodruff, Hayama, & Rugg, 2006; Yu & Rugg, 2010). A third ERP effect supporting recognition has also been reported in some studies in the form of late onsetting positivity from approximately 800 ms onwards, maximal across right frontal sites (Curran, Schacter, Johnson, & Spinks, 2001; Ranganath & Paller, 2000; Wolk et al., 2009). This appears to be driven by post-retrieval processing or monitoring and is not necessarily contingent upon retrieval success (Hayama, Johnson, & Rugg, 2008).

One question that remains to be addressed is how recognition and the corresponding electrophysiological response changes as the delay between encoding and retrieval increases. It is well established that a considerable amount of information is lost from memory during the delay between study and test and there is general agreement that the rate of decay is maximal immediately after learning and then gradually declines (Wixted, 2004). Exploring recognition memory, Dudukovic and Knowlton (2006)reported that many stimuli that originally supported a remember response after a 10 minute retention interval were given a know response when tested for again 1 week later. This suggests that although there is information loss over a week, for many stimuli, recognition memory remained in a degraded, acontextual form. It is also the case, however, that many memories appear to be stable and long lasting. The term slow or systems consolidation refers to processes involved in this stabilisation into long-term memory stores, comprising significant neurological changes (Dudai, 2004). For example, evidence suggests that memory retrieval becomes less dependent on the hippocampus and more likely to involve neocortical activation over time (Moscovitch, Nadel, Winocur, Gilboa, & Rosenbaum, 2006; Squire & Bayey, 2007). These gradual processes play out over the length of the retention interval following a time course that is poorly defined (Meeter & Murre, 2004). However, prospective studies show changes start to emerge after remote delays spanning 1 to 90 days and the first period of sleep following learning appears to be particularly important (Gais et al., 2007; Takashima et al., 2006, 2009).

The identified ERP old/new effects are thought to underlie long-term memory processes but research in this area has very rarely tested memories that are even an hour old. In a rare attempt to characterise more remote recognition memory, three previous studies made use of a 24 hour retention interval (Curran & Friedman, 2004; Jaeger, Johnson, Corona, & Rugg, 2009; Wolk et al., 2006). Studies by Wolk et al. and Curran and Friedman reported reliable early midfrontal and late parietal old/new effects for recognised stimuli but these effects were not modulated by delay. Importantly, the interval of 24 hours in these studies also had minimal impact on the behavioural data suggesting that the memory representations had not changed appreciably over this period of time.

In contrast to these studies, Jaeger et al. (2009) tested memory for object stimuli previously presented during encoding on emotionally negative or neutral backgrounds. At the immediate delay, hits for items that had been paired during study with an emotional background were more positive than those previously presented on a neutral background but this pattern was reversed at the long delay. The authors suggest that these ERP differences may be a consequence of systems consolidation processes, i.e. a qualitative change in the neural basis of these memories over the 24 hour period. However, this study made no attempt to separate memories that were largely familiarity-driven from those that were recollection-driven. ERP data showed that late parietal old/new effects at the long delay were significant for neutral but not emotional hits suggesting a reduction in recollection that was specific to stimuli encoded in a negative context. As Jaeger et al. identified, it is feasible that the delay-driven differences between emotional and neutral hits are caused largely by differential contributions of recollection and familiarity to overall hits, rather than emotionality dependent consolidation processes.

To summarise, findings regarding delay effects on recognition ERPs have been mixed and relevant data are available from only a small number of studies employing modest remote intervals. The present study questioned whether there would be any differences in how typically observed old/new effects manifest at longer delays when attempts are made to separate recollection and familiarity based recognition judgments.

A remote delay of 1 week was examined because this represents a considerable extension of the 24 hour delay, which has previously been explored (Curran & Friedman, 2004; Jaeger et al., 2009; Wolk et al., 2006). However, 1 week is not so long that we can no longer expect robust recognition memory (Gardiner & Java, 1991).

Under the assumption that midfrontal and late parietal old/new effects represent correlates of familiarity and recollection respectively, it is expected that they should persist for as long as reliable behavioural measures of these processes can be obtained. However, it is hypothesised that there will be considerable forgetting over the 1 week period, which may lead to attenuation of old/new amplitude differences. A more tentative suggestion, however, is that by comparing the ERPs produced after recent and remote delays, we may reveal qualitative changes due to a shift in the neural basis of memory over time. As suggested by Jaeger et al. (2009), recognition ERPs may be sensitive to consolidation processes.

1.2. Method

1.2.1. Participants

Twenty-two right-handed students participated in the experiment. Data from 6 participants were rejected due to insufficient trials (<15) in the critical conditions. This left a sample of 16 subjects (7 male), mean age 20.8 (SD=2.6). All volunteers were paid £15 for their time or received course credit if relevant. The study was approved by The University of Manchester research ethics committee.

1.2.2. Materials

A total of 450 colour photographs of objects were selected from the Hemera Photo Objects Collection, Volume I (Hemera Technologies Inc). The photographs depicted items from a range of categories including foods, tools, vehicles, animals and furniture. All stimuli were presented in the centre of the screen on a grey rectangle with a black border measuring 260×196 pixels. Photographs were randomly divided into three lists of 150 forming remote study, recent study and new items. Lists were rotated to create three different stimulus sets (counterbalanced between participants) such that each item appeared once as a remote item, once as a recent item and once as a new item within these sets.

1.2.3. Procedure/design

Participants attended two experimental sessions separated by an interval of 1 week. The first session involved a study phase where photographic stimuli were encoded to form the remote memory set. The second session involved an additional study phase to form the recent memory set and was followed by a recognition test.

During each study episode, photographs were presented in random order for 2500 ms with a self-paced break roughly every 30 items. To aid subsequent memory, participants completed a different semantic encoding task at each delay. They were either required to rate each item in terms of whether it represented something encountered frequently or infrequently (frequency task) or they rated each photograph in terms of whether it depicted something pleasant or unpleasant (pleasantness task). The assignment of each task to either the recent or remote study phase was counterbalanced between participants. The rationale behind using different tasks at each delay was that it would potentially provide a contextual detail that would inform remember responding and would also help maintain motivation at the second session. A short practice run preceded each study phase using additional photographs depicting distinctive people. Practice items were chosen to minimise overlap with the critical stimuli.

At session two only, following encoding, participants were presented with written instructions for the remember/know procedure. Instructions were adapted from Dudukovic and Knowlton (2006) and included a number of examples to clarify the difference between recollection and familiarity. Participants were asked to explain in their own words how they would distinguish between these types of memory before completing a practice run. Following the practice, participants were again asked how they had made remember and know responses and to provide examples. Further clarification regarding the instructions was given where necessary before the test phase commenced.