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Research article

The neural mechanism underlying recollection is sensitive to the quality of episodic memory: Event related potentials reveal a some-or-none threshold

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ABSTRACT

Although much is known about the underlying neural systems that support recollection, exactly how recollection operates remains unclear. One possibility is that recollection reflects the operation of a continuous retrieval process, whereby test cues always elicit some information from memory. Alternatively, recollection may reflect the operation of a thresholded process that allows for retrieval failure, whereby test cues sometimes elicit no information from memory at all. Here we demonstrate that recollection is thresholded by measuring a commonly reported electrophysiological correlate of episodic retrieval – known as the Left Parietal old/new effect. We use a novel source task designed to directly measure the accuracy of retrieval success, finding that the neural correlate of retrieval was sensitive to the precision of responses when recollection succeeded, but was absent when recollection failed. The results clarify the nature of the neural mechanism underlying episodic memory, providing novel evidence in support of some-or-none threshold models of recollection.

Introduction

Episodic recollection is one of the defining features of human declarative memory, allowing events such as the birth of one's child to be vividly remembered years later, while details of yesterday's finance meeting are simply forgotten. Although recollection can be clearly dissociated from other retrieval processes (see Yonelinas, 2002 for a review), and much is known about the neural systems supporting episodic recollection (Brown and Aggleton, 2001; Rugg et al., 2002; Squire, 2004; Vilberg and Rugg, 2008), questions remain about the way recollection operates (Parks and Yonelinas, 2009; Slotnick and Dodson, 2005; Wixted, 2007). Here we investigate one key characteristic: does the neural activity underlying recollection operate in a thresholded or continuous fashion? Whilst threshold versus continuous accounts of recollection have been extensively debated within the behavioral literature (Mickes et al., 2009; Slotnick, 2013; Yonelinas et al., 2010), to date relatively little progress has been made in characterizing the mechanism supporting recollection at a neural level of analysis. To be clear, although much is known about *which* structures support recollection, exactly *how* the neural mechanisms underlying recollection operate remains unknown. Below we outline a novel source memory task that allows us to directly assess the accuracy of episodic recollection responses whilst recording brain activity, revealing that the electrophysiological correlate of recollection operates as a some-or-none thresholded process.

Behaviourally, attempts to characterize recollection as either thresholded or continuous have focused heavily on the interpretation of memory-related confidence ratings (using Receiver Operating Characteristics, or ROC curves). ROCs are formed by plotting Hits and False Alarms as a function of confidence [typically ranging from 1 (sure new) to 6 (sure old)]. ROCs have received particular attention because the shape of the ROC has been taken to reflect the contribution of specific retrieval processes. For example, Yonelinas (1997) argued that recollection produces relatively linear ROCs (consistent with a threshold process that either succeeds or fails, such that information is only available from memory on some occasions), whereas familiarity leads to more curvilinear and symmetrical ROC curves (consistent with a continuous process that always provides some information from memory). Recent analysis of ROCs during source memory tasks (in which recollection is believed to be the primary means of retrieval) have, however, revealed nonlinear ROC curves – leading some authors to reject the threshold account of recollection in favour of a continuous model (Slotnick, 2013; Wixted, 2007). In contrast to thresholded accounts of recollection, continuous accounts (e.g., the Unequal Signal Detection model: Mickes et al., 2009; Green and Swets, 1966) predict that recollection attempts always return some information from memory, but the information varies in strength (leading to curvilinear confidence-based ROC curves equivalent to those seen for familiarity).

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Within the behavioral memory literature the thresholded versus continuous model question remains hotly debated (e.g., Parks and Yonelinas, 2007; Wixted, 2007), with confidence ratings being used to support claims made by both sides (e.g., Mickes et al., 2009; Yonelinas and Parks, 2007). Ultimately, however, our view is that confidence ratings are not an ideal measure for characterising the underlying nature of retrieval processes. First, ROC curves reflect metacognitive judgements about memory rather than memory *per se*, and as such can be influenced by a number of non-mnemonic factors (such as mood, or task instructions) (e.g., Bröder and Schütz, 2009; Grasha, 1970; Malmberg, 2002). Second, the interpretation of ROCs is highly model specific, in that the same data fitted to a different model will result in vastly different conclusions. For example, curvilinear ROCs observed during source tasks can be interpreted as either a continuous recollection signal (as in single process accounts) or as the added contribution of familiarity under encoding conditions that promote unitization (i.e., encoding individual item information as a single holistic unit: as in dual process accounts – see Diana et al., 2008; Yonelinas et al., 2010). Third, the conclusion drawn from ROCs is highly sensitive to the sensitivity of the response scale employed – whilst studies typically employ a 6-point confidence scale, had 20 or 100 point scales been used then quite different conclusions may have been drawn (for an illustrative example see Fig. 4 from Harlow and Donaldson, 2013). In essence, confidence ratings cannot unambiguously discriminate between threshold and continuous accounts of recollection and therefore alternative methods must be employed.

Recently, Harlow and Donaldson (2013) have attempted to move away from binary tests of retrieval (i.e., old/new, Source Correct/Source Incorrect) in favour of a novel continuous measure based on the objective measurement of response accuracy – providing evidence in favour of the thresholded account of recollection. A source memory task was employed in which participants were asked to remember a series of locations marked around a circle – each paired with a single word (illustrated in Fig. 1a). At test, participants were presented with each previously studied word and asked to recollect the paired location (Fig. 1b), allowing the precision (defined as the distance between target location and response) of source memory responses to be measured (Fig. 1c). Critically, because the experiment employed a distractor-free test (i.e., with no unstudied new items) and no old/new decision was required, in this paradigm participants could not respond to the source task on the basis of other retrieval processes (such as familiarity or implicit memory). To be clear, because only studied words are presented at test, participants can only perform the task successfully if they recollect contextual information about locations presented at study.

Threshold and continuous models of recollection make entirely different predictions about performance in this context. Continuous models predict that retrieval always produces some information from memory, with a greater frequency of responding closer to the target: responding should decrease rapidly away from the target, with very few responses far from the target (as illustrated in Fig. 2a). By contrast, threshold models predict that successful recollection responses will cluster close to the target, mixed with a separate set of sub-thresholded guesses. In this case, guesses are made in the absence of any retrieval signal and responses will therefore be randomly distributed relative to the target, producing a raised plateau of responses far from the target (as illustrated in Fig. 2b). According to the continuous model guesses are based on weak below-criteria retrieval signals (and therefore non-random), whereas according to threshold models guesses are based on the genuine absence of any retrieval signal (and therefore randomly distributed).

As is illustrated in Fig. 2c, the behavioural data observed by Harlow and Donaldson (2013) demonstrated that participants were very precise at recollecting the target on some trials (producing a large peak of very precise responses), but on other trials could not remember any information from the study episode and were forced to guess (producing a raised plateau of very imprecise responses). A likelihood ratio test revealed that the threshold model (i.e., a Cauchy plus Guessing model: see Fig. 2b inset) provided a significantly better fit to the observed data compared to a continuous model (i.e., a Gaussian model: see Fig. 2a inset). In essence, the threshold model was better able to account for the high proportion of very precise and imprecise trials (compare Fig. 2b and c), providing strong evidence that recollection is thresholded at a behavioural level.

One important nuance of the Harlow and Donaldson (2013) results lies in the distinction between two broad classes of threshold model: all-or-none versus some-or-none. In the former case recollection is considered to be binary, with memory cues either leading to no output, or triggering a discrete (fixed) output from memory. By contrast, some-or-none models allow the output to vary when retrieval is successful (e.g., in the amount of information recovered, or the precision of the information remembered). Whilst some early models of recollection characterized the threshold as reflecting an all-or-none process (e.g., Yonelinas, 1994), more recent models tend to characterise recollection as some-or-none (e.g., Parks and Yonelinas, 2009). The results from Harlow and Donaldson (2013; see also Harlow & Yonelinas, 2014) clearly supported a some-or-none account; correct recollection responses varied in precision and when memory was tested after a longer study-test delay both the rate and precision of recollection decreased. As Harlow and Donaldson highlighted, behavioral models that treat recollection as thresholded but not variable will underestimate the contribution of recollection to performance. Thus, recollection

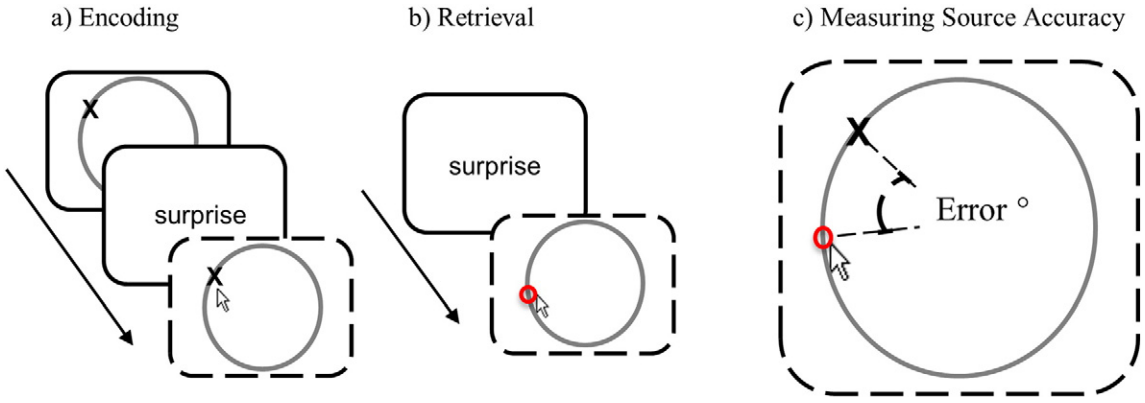

Fig. 1. The source memory task. a) During encoding, participants were instructed to memorize words paired with locations, indicating the location after each trial to confirm attention. b) During retrieval, participants were shown previously presented words and were asked to recall the position using the mouse. c) Source accuracy was measured by calculating arc length (in degrees) between actual and responded locations.