

Impaired familiarity with preserved recollection after anterior temporal-lobe resection that spares the hippocampus

Ben Bowles*, Carina Crupi*, Seyed M. Mirsattari†, Susan E. Pigott†, Andrew G. Parrent†, Jens C. Pruessner‡, Andrew P. Yonelinas[§], and Stefan Köhler*[¶]

*Department of Psychology, University of Western Ontario, London, ON, Canada N6A 5C2; [§]Department of Psychology, University of California, Davis, CA 95616; [†]Clinical Neurological Sciences, University of Western Ontario, London Health Sciences Centre, London, ON, Canada N6A 5A5; and [‡]Department of Psychiatry, McGill University, Montreal, PQ, Canada H4H 1R3

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It is well established that the medial-temporal lobe (MTL) is critical for recognition memory. The MTL is known to be composed of distinct structures that are organized in a hierarchical manner. At present, it remains controversial whether lower structures in this hierarchy, such as perirhinal cortex, support memory functions that are distinct from those of higher structures, in particular the hippocampus. Perirhinal cortex has been proposed to play a specific role in the assessment of familiarity during recognition, which can be distinguished from the selective contributions of the hippocampus to the recollection of episodic detail. Some researchers have argued, however, that the distinction between familiarity and recollection cannot capture functional specialization within the MTL and have proposed single-process accounts. Evidence supporting the dual-process view comes from demonstrations that selective hippocampal damage can produce isolated recollection impairments. It is unclear, however, whether temporal-lobe lesions that spare the hippocampus can produce selective familiarity impairments. Without this demonstration, single-process accounts cannot be ruled out. We examined recognition memory in NB, an individual who underwent surgical resection of left anterior temporal-lobe structures for treatment of intractable epilepsy. Her resection included a large portion of perirhinal cortex but spared the hippocampus. The results of four experiments based on three different experimental procedures (remember-know paradigm, receiver operating characteristics, and response-deadline procedure) indicate that NB exhibits impaired familiarity with preserved recollection. The present findings thus provide a crucial missing piece of support for functional specialization in the MTL.

epilepsy | medial-temporal lobe | perirhinal cortex | recognition memory

Recognition of stimuli encountered in the past can be supported by recollection or familiarity (1). Recollection is a retrieval process that involves remembering specific details from episodic memory regarding a past experienced event. Familiarity, by contrast, is a process that gives rise to recognition without recovery of any contextual episodic detail. Cognitive psychology has not provided a conclusive answer as to whether these two components of recognition reflect two independent processes or different strengths of a single process (1–3). In terms of neural mechanisms, impairments in recognition memory have long been established as a hallmark of anterograde amnesia after medial-temporal lobe (MTL) damage. However, as in the cognitive domain, controversy exists in that it is uncertain whether familiarity and recollection rely on a single shared or multiple distinct MTL mechanisms. Some authors have argued that different MTL structures play independent roles in recognition memory (1, 4), with the hippocampus supporting recollection and perirhinal cortex supporting familiarity; others have suggested that the simple dichotomy between familiarity and recollection does not capture any functional specialization within the temporal lobes (3, 5, 6).

Human lesion research has shown that selective hippocampal damage can produce isolated recognition impairments in recollection that spare familiarity (7–9). Together with findings demonstrating that larger MTL lesions, including the hippocampus and perirhinal cortex, result in impairments in familiarity and recollection (9, 10), such evidence has been taken as support for functional independence and for the idea that there is division of labor within the MTL. However, given that the neuroanatomical connectivity in the MTL is organized hierarchically, with perirhinal cortex providing one of the major sources of input to the hippocampus (11–13), the described pattern of findings must be considered inconclusive with respect to whether the two processes rely on distinct MTL mechanisms. It is possible that perirhinal cortex supports only weak or poorly differentiated memory for the study episode, whereas the hippocampus supports stronger memory representations. Accordingly, hippocampal damage might selectively disrupt the ability to retrieve complex details about the study event, while leaving intact a weaker form of memory supported by perirhinal cortex. To rule out this alternate account and to establish that distinct MTL mechanisms support recollection and familiarity, it needs to be shown that temporal-lobe lesions that spare the hippocampus can produce selective impairments in familiarity.

Existing evidence from lesion studies in non-human species and from functional neuroimaging in humans also does not yet provide a conclusive answer. Although it is well established that selective perirhinal cortex lesions in rats (14) and non-human primates (15–17) produce robust recognition memory impairments for objects, the evidence available does not allow for the conclusion that this deficit is specific to a familiarity process. Although past functional MRI (fMRI) research in healthy humans has shown promising dissociations in perirhinal and hippocampal signals (18–22) that are in line with the dual-process model, this evidence does not address, because of the correlational nature of fMRI data, whether the recollection process supported by the hippocampus necessitates an intact familiarity signal as its input.

In the present investigation, we had the rare opportunity to test an individual who underwent surgical removal of left

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Abbreviations: MTL, medial-temporal lobe; ROC, receiver operating characteristics; RK, remember-know.

[¶]To whom correspondence should be addressed. E-mail: stefank@uwo.ca.

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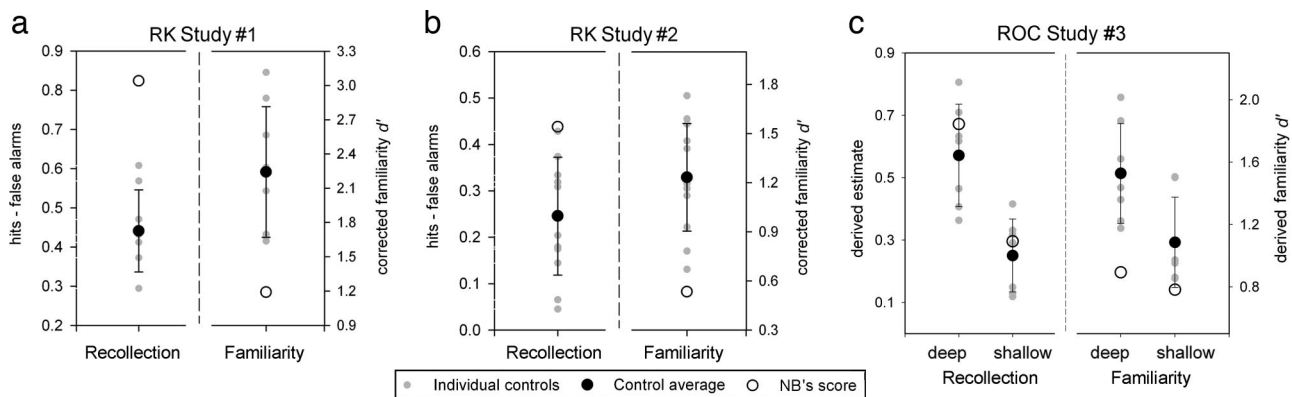


Fig. 2. Estimates for recollection and familiarity accuracy in Experiments 1, 2, and 3. Data are shown for NB as compared with control individuals. Error bars represent standard deviations in controls. Recollection (R) and familiarity (F) scores were calculated in the RK experiments (a and b) by using the independence correction procedure and in the ROC experiment (c) by using the least-squares method. Note that NB exhibited the lowest familiarity score despite an above-average recollection score in all experimental conditions.

was even more striking ($z = -7.02$; $P < 0.0005$) and was specifically apparent in her increased false-alarm rate for know responses ($z = 5.47$; $P < 0.005$).

Given NB's high proportion of remember responses in Experiment 1, one might argue that the observed familiarity impairment reflects the outcome of her above-average recollection abilities. NB reported that she frequently engages in spontaneous efforts to create unique associations for information she aims to remember, a strategy that could explain her high recollection. Thus, we conducted another experiment with the RK procedure that limited any opportunity to engage in idiosyncratic encoding processes beyond those required by the task. During study, participants encountered 200 words in a fast-paced sentence verification paradigm, in which they indicated whether a target word fit meaningfully into a subsequently presented sentence. At test, we also offered "guess" as a response option to minimize any potential contributions of guessing to our familiarity measure (30). The results indicate that NB's deficit is not an artifact of exceedingly high recollection, because we again observed a familiarity impairment (with correction for independence $z = -2.12$, $P < 0.05$; without correction $z = -2.73$; $P < 0.05$), this time in combination with a recollection score in the upper normal range ($z = 1.52$; see Fig. 2b and SI Table 3 for raw data).

The RK paradigm has been criticized because of its reliance on introspective report of familiarity and recollection and potential interindividual variability in interpreting the difference between remembering and knowing (32). Therefore, we sought to confirm NB's familiarity impairment with a paradigm that does not require participants to distinguish between these two different types of recognition awareness. Examining receiver operating characteristics (ROC) based on the distribution of confidence responses across old and new items provides another method to assess familiarity and recollection. This method has revealed selective recollection deficits associated with hippocampal lesions in past research (8, 9, 33). In Experiment 3, we obtained ROC estimates of recollection and familiarity at two different memory strengths, induced by semantic or nonsemantic orienting tasks at encoding. At test, participants were required to distinguish between six different levels of confidence for their recognition responses. We used the least-squares approach, an ROC modeling technique that assumes recollection and familiarity reflect independent processes, to estimate these processes (1). We confirmed NB's familiarity impairment at the higher memory strength ($z = -1.98$, $P = 0.056$; see Fig. 2c). At the lower strength, after nonsemantic encoding, NB exhibited familiarity performance in the low-normal range ($z = -1.05$), with a score

lower than that of any control participant. That her impairment was more pronounced after semantic encoding is consistent with previous findings showing less memory benefit from conceptual processing in left-lateralized temporal-lobe epilepsy (34).

Further examination of the distribution of NB's responses also revealed an unwillingness to endorse responses in the low-confidence range (responses "3" and "4") as compared with controls ($z = -2.53$; $P < 0.05$; see Fig. 3b). This observation is consistent with anecdotal evidence from our second RK study, in which NB considered the low-confidence guess responses of limited use. In addition, linearity and quadratic analyses were used to assess whether the shape of NB's ROC data in probability space (see Fig. 3a and SI Fig. 9 for graphical depiction) and z space (see SI Fig. 10) differed systematically from that of controls. If NB exhibited a selective deficit in familiarity with disproportionately high contributions from recollection, then the ROC should be more linear in probability space and more U-shaped in z space than those of the control subjects (35). Consistent with these predictions, we found that the linearity of NB's ROC ($R^2 = 0.88$, $z = 1.34$; see SI Fig. 11) and the quadratic component of her ROC in z space ($b = 0.08$, $z = 2.27$, $P < 0.05$ for semantic) were higher than those of any controls. This evidence supports the conclusion that NB's pattern of recognition performance is the result of impaired familiarity.

Although examining familiarity and recollection with an ROC procedure does not require the distinction between two different types of recognition awareness, it still demands metamemory judgments. In Experiment 4, we aimed to demonstrate that NB's familiarity impairment does not reflect any abnormality in making metamemory judgments. For this purpose, we focused on the temporal dynamics of her recognition decisions. Building on previous work showing that familiarity is available earlier than recollection (36–38), we tested whether NB's recognition accuracy would be disproportionately reduced when decisions were required quickly. We used two yes–no recognition tests that differed only in the time allowed to make a recognition response (2,000 vs. 400 ms). When comparing the detrimental effect of shortening the response deadline between NB and controls using a difference score measure (39), NB's accuracy was found to be disproportionately affected ($P < 0.05$; see Fig. 4 and SI Table 4 for raw data). To the extent that performance depends more on familiarity under the shorter deadline, this finding indicates that NB's familiarity impairment becomes apparent even when there is no requirement for her to judge the quality of her recognition experience.

shape of her ROC curve as an outcome of reduced familiarity contributions. Notably, her ROC results cannot be accounted for by assuming that she was simply biased to make more high-confidence responses than the controls. Shifts in response bias of this type would result in shifting of the ROC points along the same ROC function and would not change the shape of the ROC. Similarly, in the RK data, the specific criteria used by the subject should not affect the discriminability measure (d').

NB's familiarity impairment contrasts with her overall normal recognition memory performance in our experimental tasks as well as on clinical neuropsychological tests. In fact, there was no evidence for any episodic memory impairments in her neuropsychological examination; the only hint of a deficit after surgery was a reduced score in semantic fluency. This task can be used to assess semantic memory ability and has also been suggested to depend on perirhinal cortex function (43). Inasmuch as the assessment of familiarity is considered an expression of semantic memory (44), whereas recollection emerges from episodic memory, this finding provides further support for the selectivity and specificity of her impairment.

The current findings directly confirm predictions made by dual-process models of MTL organization that propose a mapping of familiarity and recollection onto perirhinal and hippocampal functions, respectively. Past functional MRI research in healthy individuals has shown that activity in human perirhinal cortex is correlated with gradual changes in perceived familiarity (18, 20, 21). The outcome of the present study extends this evidence by suggesting that an intact familiarity signal is not required by the hippocampus to mediate normal recollection. This point is of particular importance with respect to the hierarchical and reciprocal organization of MTL connectivity, because the primate perirhinal cortex provides one of the major sources of input via entorhinal cortex to the hippocampus (12, 45, 46). That the hippocampal recollection processes can proceed normally in the context of damage to perirhinal and entorhinal cortex supports models of MTL organization that propose some independent functioning for the different components within an overall hierarchical system (4, 11, 13). That NB exhibits a familiarity impairment as a result of removal of MTL structures that feed into the hippocampus corroborates the notion that these structures give rise to memory processes that go beyond relaying information between sensory association cortices and the hippocampus (11). It is important to note, however, that NB's lesion in perirhinal and entorhinal cortex is only partial, and that her impairment does not reflect the total absence of familiarity. Therefore, the present findings do not rule out that a more extensive perirhinal or entorhinal lesion would also have a negative impact on hippocampal functioning.

NB's impaired familiarity in the context of normal recollection and normal overall recognition ability is even more striking considering we also found her left hippocampus to be reduced in volume. Previous studies in epilepsy patients who underwent left temporal lobe resections that included the hippocampus as well as perirhinal cortex have shown consistent impairments in recognition memory for verbal materials of the type used in our investigation (27, 29). When specifically examined, these impairments have been found to affect familiarity as well as recollection (9). The pattern of performance observed in NB is likely different because her volume reduction in the hippocampus was not a result of the surgical resection performed.

Although NB's impairment is most strongly predicted by models of memory that posit a role for perirhinal cortex in familiarity, it is important to consider the possibility that other structures removed in the surgical treatment, including entorhinal cortex, caused her impairment. Given that selective lesions to entorhinal cortex can mildly impair recognition performance in rhesus monkeys (15), partial removal of this structure may have contributed to the observed deficit. However, our conclu-

sions regarding the functional independence of the neural substrates of familiarity in the temporal lobe hold regardless of whether damage to perirhinal cortex or entorhinal cortex underlies NB's unique recognition profile.

Another structure to consider is temporopolar cortex. This structure is thought to be involved not in recognition of prior occurrence but rather in the naming and identification of unique entities, such as famous individuals or landmarks (47, 48). Finally, the primary structure targeted by the resection was the left amygdala. Past patient (49) and imaging work (50) indicates that the role of the amygdala in memory processing is limited to emotionally arousing information and even then, specifically to the recollection of this information (50). By contrast, the stimulus material we used was emotionally neutral. This makes it unlikely that the resection of NB's left amygdala contributed to her familiarity deficit.

In sum, the results of the current study demonstrate that focal temporal-lobe damage that includes perirhinal cortex can selectively impair the familiarity process of recognition memory. Together with past findings showing that hippocampal lesions can result in selective recollection deficits, our findings indicate that familiarity has a neural substrate in the human temporal lobe that is distinct from the one that supports recollection.

Methods

Subjects. Case NB was recruited in collaboration with health professionals at the epilepsy unit of the London Health Science Center. Our investigation was motivated by our knowledge of her lesion profile, not by her neuropsychological profile or any subjectively perceived memory abnormalities. All control subjects (Experiment 1, $n = 8$; Experiment 2, $n = 12$; Experiment 3, $n = 7$; and Experiment 4, $n = 10$) were recruited at the university and matched to NB for age (± 3 years) and education. To determine whether NB's behavioral performance could be classified as statistically abnormal, we used tests specifically developed to reveal the statistical abnormality of a patient's score relative to a small sample (51). We considered any value associated with $P < 0.05$ to be significant. Raw z scores for NB are also reported for descriptive purposes.

Imaging. NB's postsurgical structural MRI scan was obtained with a 4-T Siemens/Varian (Erlangen, Germany) MR whole-body scanner, using a T1-weighted sagittally oriented MRI sequence [repetition time (TR) = 9.0 ms, echo time (TE) = 5.0 ms, inversion time (TI) = 600.0 ms, flip angle = 15° , spatial resolution = $1 \times 1 \times 1$ mm]. For the volumetric analyses, we followed a previously published integrated protocol for the assessment of MTL structures with proven validity and reliability (25, 26). Volumetric measurements of 12 age-matched female control participants were derived from the normative data set used to validate this protocol (see *SI Text* for further detail).

Experiment 1, RK Recognition. At encoding, subjects saw 50 words for 5 s each (500-ms interstimulus interval) and were asked to make a subjective judgment as to whether a word referred to something pleasant, unpleasant, or neutral. After a delay of ≈ 1 hour, they were given the recognition test, which included the visual presentation of 50 previously studied (old) and 50 new words in intermixed order. Subjects first made an old–new decision; for items considered “old,” they were subsequently required to provide an additional RK response. Recollection scores were calculated by using hits minus false alarms for “remember” responses. Familiarity scores were calculated based on the “know” responses, using d' with and without correcting for the proportion of remember responses provided, i.e., with and without correction for independence (1). To allow for calculation of d' measures in instances where no false alarms

were given, we used a correction recommended by Snodgrass and Corwin (52).

Experiment 2, RK Recognition. At encoding, subjects completed a sentence verification task for 200 words. In each trial, a word first appeared in the top half of a computer screen for 500 ms. It was followed by a sentence, with one word missing, presented for 2,500 ms closer to the bottom of the screen. The subjects' task was to decide whether the word fit meaningfully into the sentence. After a 5-min distractor task, subjects made old–new recognition decisions for 300 test words (200 old). For words considered “old,” subjects indicated the basis of their decision by providing a “remember,” “know,” or “guess” response (30). To ensure that subjects followed instructions, they were required to indicate, for each “remember” response they provided within the first 25 trials, what it was they recollected about encountering the word at study. As is typical for experiments that allow for a separate guessing option, participants were encouraged to use “know” and “remember” responses only when they were confident that the word was presented previously (i.e., to use a stringent response criterion). Recollection scores and familiarity scores were calculated as in Experiment 1.

Experiment 3, ROC Recognition. We used a previously published protocol (8), which involved two sessions completed \approx 3 weeks apart (with different stimuli and orders of encoding conditions). In the deep-encoding condition, subjects heard 80 words and were required to indicate for each stimulus whether it was abstract or concrete. In the shallow-encoding condition, they were required to indicate for a different set of 80 words how many syllables each of them contained. After encoding, subjects were given a recognition memory test in which they heard a list of 160 studied words and 80 new lures. Subjects were required

to indicate their recognition response in combination with a confidence rating, using a six-point scale (6 = sure the word was studied to 1 = sure it was not studied). Familiarity and recollection scores were calculated separately for each encoding condition (deep and shallow) using the least-squares method (1).

Experiment 4, Response Deadline Procedure. For each subject, we compared performance on two recognition tests, which differed in the amount of time allowed before a recognition decision was required. The two tests involved the use of two different stimulus lists and were administered sequentially. In each test, at encoding, subjects made abstract/concrete judgments on 30 words that were presented visually for 2 s each, with an interstimulus interval of 1 s. During recognition, 30 old and 30 new items were included in each test. A test trial began with a fixation period of 3,000 ms, which was followed by the critical word presented for either 400 ms (first test) or 2,000 ms (second test). Subjects were instructed to provide their old–new response immediately after this limited presentation, when the stimulus became underlined and bolded for another 400 ms. If a response was provided outside of this 400-ms response window, subjects were informed about their diversion with a “beep,” and the trial was discarded from analysis. To facilitate sustained attention, subjects were given a break every 10 trials. To maximize the number of valid responses during the response window, participants obtained extensive training with the response-deadline procedure before administration of the two tests. Recognition scores were calculated as hits minus false alarms.

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