Perirhinal cortex tracks degree of recent as well as cumulative lifetime experience with object concepts

Devin Duke, Chris B. Martin, Ben Bowles, Ken McRae and Stefan Köhler

Abstract

Evidence from numerous sources indicates that recognition of the prior occurrence of objects requires computations of perirhinal cortex (PrC) in the medial temporal lobe (MTL). Extant research has primarily probed recognition memory based on item exposure in a recent experimental study episode. Outside the laboratory, however, familiarity for objects typically accrues gradually with learning across many different episodic contexts, which can be distributed over a lifetime of experience. It is currently unknown whether PrC also tracks this cumulative lifetime experience with object concepts. To address this issue, we conducted a functional magnetic resonance imaging (fMRI) experiment in healthy individuals in which we compared judgments of the perceived lifetime familiarity with object concepts, a task that has previously been employed in many normative studies on concept knowledge, with frequency judgments for recent laboratory exposure in a study phase. Guided by neurophysiological data showing that neurons in primate PrC signal prior object exposure at multiple time scales, we predicted that PrC responses would track perceived prior experience in both types of judgments. Left PrC and a number of cortical regions that are often co-activated as part of the default-mode network showed an increase in Blood-Oxygen-Level Dependent (BOLD) response in relation to increases in the perceived cumulative lifetime familiarity of object concepts. These regions included the left hippocampus, left mid-lateral temporal cortex, as well as anterior and posterior cortical midline structures. Critically, left PrC was found to be the only region that showed this response in combination with the typically observed decrease in signal for perceived recent exposure in the experimental study phase. These findings provide, to our knowledge, the first evidence that ties signals in human PrC to variations in cumulative lifetime experience with object concepts. They offer a new link between the role of PrC in recognition memory and its broader role in conceptual processing.

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1. Introduction

The ability to recognize prior occurrences of objects in the environment is critical to many aspects of adaptive behavior. There is a consensus in the neuroscience literature across rodents, non-human primates, and humans that it requires the integrity of perirhinal cortex (PrC) in the medial temporal lobe (MTL) (Brown & Aggleton, 2001; Eichenbaum, Yonelinas, & Ranganath, 2007; Suzuki & Naya, 2014; for exceptions, see Martin, McLean, O’Neil, & Köhler, 2013). A noticeable but less consistent body of research also suggests that the role of PrC in recognition is specific to item-based familiarity assessment (Brown & Aggleton, 2001; Eichenbaum et al., 2007; Montaldi & Mayes, 2010; Ranganath & Ritchey, 2012; but see Wixted & Squire, 2011).

Recognition of prior occurrence is typically probed in humans with recognition-memory tasks that include an initial experimentally controlled study phase for a list of items. Responses are classified as familiarity-based when an item is endorsed as studied, with no evidence of successful recovery of contextual detail about that study encounter. Critically, when meaningful stimuli such as object concepts (i.e., the concrete object that a word or picture refers to; Martin, 2015) are employed, as is the case in the majority of published studies (Kim, 2013), participants make their memory judgment with reference to the recent study episode rather than with respect to their lifetime of experience, which may have involved hundreds or thousands of item encounters in many different episodic contexts. As such, extant research on the role of human PrC in recognition memory for meaningful stimuli has typically examined recent incremental changes rather than absolute levels of familiarity (Mandler, 1980; for further discussion see Bridger, Bader, & Mecklinger, 2014; Mandler, 2008).

Behavioral findings suggest that humans can also judge their cumulative past experience with object concepts accrued outside the laboratory. For example, people can easily judge whether they are more familiar with pliers or scalpels. Indeed, in normative databases on conceptual knowledge (Cree & McRae, 2003; Moreno-Martinez, Montoro & Rodriguez-Rojo, 2014; Schröder, Gemballa, Ruppin, & Wartenburger, 2012), participants are often asked to rate their cumulative familiarity with object concepts over their lifetime (sometimes simply referred to as ‘concept familiarity’). Such judgments display considerable consistency across participants, and are also known to have some external validity, as reflected in significant correlations with objective word frequency (Cree & McRae, 2003; Moreno-Martinez, Montoro & Rodriguez-Rojo, 2014; Schröder et al., 2012). The neural and cognitive mechanisms that support this ability, however, are poorly understood at present. In the present study, we took a first step in addressing this issue with a functional neuroimaging approach. Specifically, we asked whether the medial-temporal lobe structure that has most consistently been implicated in recognition memory in prior research, i.e., PrC, tracks not only recent but also cumulative lifetime experience with object concepts.

Two sources of evidence hint at a potential role of PrC in signaling cumulative levels of prior object exposure over the long-term. First, neurophysiological recordings in non-human primates have shown that some PrC neurons track the degree of exposure to objects that accumulates through hundreds of presentations over the course of weeks (Höscher, Rolls, & Xiang, 2003; Rolls, Franco, & Stringer, 2005). This cumulative increase in responding contrasts with the decrease that is typically observed in relation to repetition within experimental sessions, a phenomenon that has been coined repetition suppression (Fahy, Riches, & Brown, 1993; Li, Miller, & Desimone, 1993; Miller, Li, & Desimone, 1991; Xiang & Brown, 1998). A second source of evidence comes from a neuropsychological case study from our laboratory, which recently showed that an individual (NB) with a rare left anterior temporal lobe lesion that includes PrC but spares the hippocampus exhibits noticeable abnormalities in judging cumulative lifetime familiarity for object concepts (Bowles, Duke, Rosenbaum, McRae, & Köhler, 2016). This individual was also impaired in making frequency judgments for graded exposure to concept names in a recent experimental study phase (Bowles et al., 2016), and in making familiarity-based memory judgments in other experimental paradigms that required reference to such a study phase (Bowles et al., 2007; Martin, Bowles, Mirsattari, & Köhler, 2011). Our findings in NB suggest that left anterior temporal structures play a necessary role in assessing the cumulative lifetime familiarity of object concepts. However, NB’s lesion, which resulted from surgical resection, was not restricted to PrC but included anterior-lateral and temporo-polar cortex as well. Thus, these neuropsychological findings do not specifically point to PrC. Given that neighboring anterior temporal structures in the left hemisphere have also been implicated in conceptual processing (e.g., Jackson, Hoffman, Pobric & Lambon-Ralph, 2016; Skipper, Ross, & Olson, 2011; Wright, Randall, Clarke, & Tyler, 2015), it is important to seek evidence that directly links variations in lifetime experience with objects concepts to PrC.

In the present study, we employed functional magnetic resonance imaging (fMRI) in healthy individuals to examine whether PrC tracks participants’ responses when they judge their cumulative lifetime familiarity with object concepts. For the purpose of comparison, we also included frequency judgments that required assessment of the degree of recent item exposure in an experimental study phase. We provide evidence that left PrC and several other cortical structures respond to perceived higher lifetime familiarity for object concepts with an increase in Blood-Oxygen-Level Dependent (BOLD) signal. We also report that PrC is the only structure that shows this pattern in combination with a signal change in opposite direction for perceived recent item exposure.

2. Materials and methods

2.1. Participants

Twenty healthy young adults (mean age = 25.6, SD = 3.9, 10 females) participated in the experiment. Participants were pre-screened to rule out the presence of neurological disorders. This research was approved by the Health Sciences Research Ethics Board at Western University.
2.2. Materials

Two hundred verbal labels for basic-level object concepts were drawn from the normative database on object concepts published by Cree and McRae (2003) (see also McRae, Cree, Seidenberg, & McNorgan, 2005). Two sets of 100 words were used, and were matched on word frequency, word length, number of syllables, and the range and mean of normative concept familiarity ratings (i.e., normative ratings of lifetime concept experience; Cree & McRae, 2003). Assignment of sets to tasks was counterbalanced across participants. Creation of subsets of items with different familiarity values was based on normative ratings; we selected five subsets of 20 items with progressively increasing levels of normative lifetime familiarity, with items in each set matched on word length and number of syllables. For frequency judgments of recent exposure, five subsets of 20 object concepts, matched for mean normative lifetime familiarity, were assigned to one of the five repetition conditions during the initial study phase. For the lexical-decision task at study, forty pronounceable non-words were also employed as fillers. Presentation order at study was constrained such that any stimulus repetition was separated by at least three trials.

2.3. Procedure

During an initial study phase, participants were exposed to the set of 100 object concepts later to be probed in the frequency-judgment task, in combination with the non-word filler items (see Fig. 1). Each item was presented for 1000 msec with a 500 msec inter-stimulus interval (ISI). Participants made lexical-decision judgments and were asked to respond as quickly as possible. They were also informed that some stimuli would be repeated, but no reference was made to any subsequent memory test. The five subsets of object concepts were presented 1, 2, 4, 7, or 12 times, respectively. The subsequent test phase provided the fMRI data of interest and object concepts were presented 1, 2, 4, 7, or 12 times, respectively. The lifetime familiarity ratings of different participants correlated highly with each other (mean r = .53, SD = .06 across 100 items). We also observed a significant positive relationship between participants' ratings and the five levels (i.e., bins) of normative concept familiarity (Cree & McRae, 2003) that were used to generate our lists (mean r = .66, SD = .07, p < .001; see Fig. 2a). For the frequency task probing recent exposure, ratings of relative frequency of experimental stimuli (e.g., Daselaar, Fleck, & Cabeza, 2006; Henson, Cansino, Herron, Robb, & Rugg, 2003; Kim, 2013; but see Martin, Cowell, Gribble, Wright, & Köhler, 2016; for findings with other acquisition sequence (repetition time (TR) 2500 msec; echo time (TE) 25 msec; slice thickness 3 mm; in-plane resolution 3 × 3 mm; field of view (FOV) 192 × 192 mm; flip angle, 70°). To optimize Magnetic Resonance (MR) signal in the most inferior and anterior aspects of the temporal lobe, we used an oblique transverse slice orientation. Each of the 171 functional volumes included 42 contiguous slices collected in an interleaved manner that covered the entire brain volume except for the most superior aspects (<10 mm) of frontal and parietal cortex. T1-weighted anatomical images were obtained using an Magnetization-Prepared Rapid Acquisition with Gradient Echo (MPRAGE) sequence (192 slices; TR 2300 msec; TE 4.25 msec; flip angle 9°; FOV 256 × 256 mm; 1 mm isotropic voxels). Data were preprocessed using BrainVoyager QX version 2.6 (Brain Innovation). Functional images were slice-scan time corrected, motion corrected, and high-pass filtered. Functional images were subsequently co-registered with the anatomical images in Talairach space, and smoothed using a three-dimensional Gaussian kernel with a full-width at half-maximum of 8 mm.

A canonical hemodynamic response function was used for analyzing event-related responses (Friston et al., 1998). The BOLD response to each event type was modeled by convolving a series of delta functions corresponding to the onset of each event with canonical hemodynamic response function. For each participant, all response outcomes (lifetime 1–5 and frequency 1–5) were modeled as separate conditions. A whole-volume voxel-wise approach was used to identify linear trends in BOLD signal that tracked participants' ratings in each task. These trends were probed in a conjunction analysis (Nichols, Brett, Andersson, Wager, & Poline, 2005). Statistical significance was established using control for false discovery rate (FDR) (p < .05).

3. Results

3.1. Behavioral results

The lifetime familiarity ratings of different participants correlated highly with each other (mean r = .53, SD = .06 across 100 items). We also observed a significant positive relationship between participants' ratings and the five levels (i.e., bins) of normative concept familiarity (Cree & McRae, 2003) that were used to generate our lists (mean r = .66, SD = .07, p < .001; see Fig. 2a). For the frequency task probing recent exposure, ratings of relative frequency of experimental exposure showed a significant positive relationship with the five levels of repetition frequency used in the study phase (mean r = .40, SD = .13, p < .001; see Fig. 2a), revealing sensitivity to our frequency manipulation at study, and by extension, some validity of the judgments provided.

3.2. Neuroimaging results

In the fMRI literature on recognition-memory, a decrease in PrC signal is the most commonly reported response that is associated with judged recent exposure to meaningful verbal stimuli (e.g., Daselaar, Fleck, & Cabeza, 2006; Henson, Cansino, Herron, Robb, & Rugg, 2003; Kim, 2013; but see Martin, Cowell, Gribble, Wright, & Köhler, 2016; for findings with other
stimulus types). Accordingly, we predicted that the judged frequency of recent laboratory exposures would be negatively correlated with BOLD signals in PrC. For cumulative lifetime experience, directional predictions are more difficult to make based on published data. However, neurophysiological recordings in non-human primates have revealed PrC neurons that exhibit a gradual increase in responding over the course of weeks of testing, with hundreds of stimulus repetitions, when animals perform recognition memory tasks (Holscher et al., 2003; Rolls et al., 2005). While the mapping of repetition effects in single-cell recordings onto fMRI BOLD signals remains incompletely understood (see Grill-Spector, 2006), we note that evidence from local field potentials, i.e., physiological signals that have been closely linked to fMRI BOLD responses (Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001), also suggests that long-term familiarity of objects, accumulated over many sessions, is reflected in a response increase in monkey inferotemporal cortex (Anderson, Mruczek, Kawasaki, & Sheinberg, 2008). In line with this notion, prior fMRI research has revealed increases in PrC activity during processing of familiar meaningful as compared to unfamiliar abstract objects (Barense, Henson, & Graham, 2011). Accordingly, we predicted that the perceived cumulative lifetime experience with object concepts would be positively correlated with BOLD signals in PrC, effectively leading to opposite directions of change in signal for both types of memory judgments.

A whole-volume voxel-wise analysis that tested for a significant conjunction of these two linear trends (i.e., with logical operator ‘and’; Nichols et al., 2005) offered a powerful way to examine our predictions in a single test across all experimental conditions (i.e., all response options across both tasks). The only brain region that showed the typical decrease in signal for perceived recent exposure in combination with an increase in response for increases in lifetime experience was a portion of left PrC in the anterior collateral sulcus. Activity in this region survived statistical control for FDR ($p < .05$) and remained the only region showing a significant effect even when a lenient criterion of $p < .05$ (uncorrected) was applied for the conjunction (see Fig. 2b, c). Fig. 3 illustrates the close
correspondence between this activation focus and the anterior portion of left PrC that was resected in patient NB. As previously noted, this individual showed abnormalities in making judgments in both tasks in our prior neuropsychological research (Bowles et al., 2016).

Notably, when the linear contrasts for each task were examined in isolation, there were no additional clusters in PrC, nor within neighboring antero-lateral temporal or temporo-polar cortex (see Binney, Embleton, Jefferies, Parker, & Ralph, 2010; Skipper et al., 2011; Wright et al., 2015, for potential role of these structures in conceptual processing) that showed a linear trend in either direction. The linear task contrast for judgments of lifetime familiarity did, however, reveal regions outside the anterior temporal lobe that showed an increase in signal with perceived increases in lifetime experience with object concepts. These regions included several structures that have previously been found to be co-activated as part of the default mode network and in autobiographical memory tasks (Andrews-Hanna, Smallwood, & Spreng, 2014), including the hippocampus, mid-lateral temporal cortex, as well as medial prefrontal and medial parietal cortex (see Fig. 4).

4. Discussion

The present fMRI experiment revealed that PrC tracks both the perceived frequency of recent laboratory exposure as well as the perceived cumulative lifetime familiarity with object concepts. We found that activity in several cortical regions increased with perceived cumulative lifetime experience. However, left PrC was the only structure that showed this signal change in combination with a decrease in responding for perceived recent laboratory exposure. While a critical role of human PrC in signaling recent occurrence is well established in the neuroscience literature, the current study provides, to our knowledge, the first evidence that also links signals in this structure to variations in cumulative lifetime familiarity with object concepts.

Past fMRI research on the role of PrC in recognition memory has typically built on paradigms that require memory decisions with respect to a recent item encounter in an experimentally controlled study phase, which took place minutes, hours, or days prior to memory testing. Findings from this research have linked item-based recognition to differential PrC responses for previously studied as compared to novel items (see Diana, Yonelinas, & Ranganath, 2007; Eichenbaum et al., 2007; Kim, 2013 for reviews). Several studies have reported a negative relationship between the PrC BOLD response and degree of confidence in the perceived ‘oldness’ of test items, a behavioral marker that is often assumed to reflect recent changes in item-based familiarity (see Daselaar et al., 2006; Gonsalves, Kahn, Curran, Norman, & Wagner, 2005; Montaldi, Spencer, Roberts, & Mayes, 2006; Wang, Ranganath, & Yonelinas, 2014; Yonelinas, 2002). In the present study, we observed a strikingly similar negative relationship between the BOLD response in left PrC and the perceived frequency of recent laboratory exposure. Like recognition-memory decisions, frequency judgments have been proposed to depend on both assessments of item-based familiarity (see Daselaar et al., 2006; Gonsalves, Kahn, Curran, Norman, & Wagner, 2005; Montaldi, Spencer, Roberts, & Mayes, 2006; Wang, Ranganath, & Yonelinas, 2014; Yonelinas, 2002). In the present study, we observed a strikingly similar negative relationship between the BOLD response in left PrC and the perceived frequency of recent laboratory exposure. Like recognition-memory decisions, frequency judgments have been proposed to depend on both assessments of item-based familiarity as well as recollection (Hintzman & Curran, 1994; Hintzman, 2004). Evidence from computational modeling and behavioral research on retrieval dynamics suggests, however, that under many experimental conditions, familiarity is the primary basis for accurate frequency judgments (Hintzman & Curran, 1994; see also Dobkins, Simons, & Schacter, 2004). In the present experiment, the exposure to items at study was manipulated in small increments over a substantial range of presentations and, at test, we included no items without any prior study exposure.
(i.e., no novel lures). With this arrangement, we minimized the likelihood that any reliable source of contextual information would allow for differentiation of the frequency of recent exposures, maximizing the need to rely on graded signals that code for recent incremental changes in familiarity. Evidence in support of the success of our manipulation comes from patient-based research with this paradigm. We have previously reported that a focal anterior temporal-lobe lesion that includes left PrC, but spares the hippocampus, produced impairments in making frequency judgments on this task in an individual with documented preserved recollection abilities (Bowles et al., 2016). Thus, although the present results do not establish that the graded PrC response we observed specifically reflects an item-based memory signal, rather than recollection, such a conclusion is supported by prior behavioral work on frequency judgments, as well as by prior lesion-based research. Moreover, it is consistent with prominent accounts of graded PrC activity that has been observed in relations to confidence-based recognition-memory judgments in prior fMRI research.

Critically, our study identified a region in left PrC that did not only track perceived frequency of recent laboratory exposure but also perceived cumulative lifetime experience with object concepts. This finding dovetails with evidence from neurophysiological recordings in non-human primates, which has shown that some PrC neurons track prior exposure of objects over extended time periods. In one study, a gradual increase in firing rates was observed as visual stimuli became increasingly more familiar over the course of weeks of testing with hundreds of stimulus repetitions (Hölscher et al., 2003). Xiang and Brown (1998) noted that PrC neurons differ in their sensitivity to effects of recent versus long term exposure when monkeys perform recognition memory tasks. They reported that some PrC neurons (termed ‘recency neurons’) respond to repetition of a recent (i.e., within-session) stimulus encounter; this response was observed regardless of whether the stimulus in question had previously been seen in many other sessions distributed over multiple days (see also Fahy et al., 1993; Li et al., 1993; Miller et al., 1991; but see; Thome, Erickson, Lipa, & Barnes, 2012). Other PrC neurons identified by Xiang and Brown (1998) responded to whether stimuli had been encountered frequently on prior days, regardless of whether they were seen for the first or the second time in the current session (‘familiarity neurons’).

It is worth noting that in prior neurophysiological work examining responses to frequent exposure over extended time periods, response changes in PrC were observed in the absence of any behavioral requirement to judge the degree of prior exposure across multiple sessions (Hölscher et al., 2003; Xiang & Brown, 1998). In the current fMRI study, by contrast, participants made explicit judgments of cumulative lifetime experience with object concepts during scanning, allowing us to link the graded PrC signals to observed behavior. This behavioral relevance was revealed by performing a parametric examination of the relationship between the BOLD response and judgment outcome.

An important question to consider is whether the response pattern in PrC we observed could also reflect differential engagement of episodic encoding processes during lifetime familiarity judgments. There is substantial evidence in the fMRI literature showing that PrC is not only involved in retrieval but also in the encoding (i.e., memory formation) of information about specific object encounters (see Kim, 2013; Diana et al., 2007 for review). Past fMRI research has revealed, for example, that PrC tracks the amount of item-related details that is successfully encoded when visually presented objects are encountered in a study phase, as reflected in performance on a subsequent memory test for these encounters (Staresina & Davachi, 2010). Also, neuroimaging research has shown that trial-specific activity in MTL structures during recognition-memory decisions predict behavioral performance on a subsequent second memory test (Stark & Okado, 2003). Finally, behavioral findings obtained with the current task suggest that increases in lifetime familiarity of object concepts are...
associated with increases in perceived pertinent knowledge. In light of this evidence, it is possible that the graded PrC response we observed also reflects encoding of varying amounts of semantic feature knowledge that is brought online as the outcome of varying degrees of lifetime experience.

To explore a potential link between assessment of lifetime familiarity and episodic encoding, we conducted a supplementary behavioral experiment in which we examined whether degree of perceived lifetime familiarity modulates successful encoding during lifetime-familiarity judgements, such that performance on a subsequent recognition-memory test would be better for items with higher lifetime familiarity ratings (see Supplementary materials). The results of our behavioral experiment did indeed reveal such a pattern of performance. We found that object concepts with high as compared to low lifetime familiarity ratings received a subsequent increase in endorsement as previously studied items. Specifically, we observed an increase in subsequent ‘remember’ responses and a decrease in ‘know’ responses in a test paradigm that emphasized successful access to episodic contextual information as the critical difference between both response types (see Martin et al., 2011; McCabe & Geraci, 2009; for further rationale). To the extent that PrC has most consistently been implicated in encoding of information that supports item-based familiarity, rather than recollection of episodic context (e.g., Ranganath et al., 2004; Staresina & Davachi, 2008; for review see; Diana et al., 2007), the pattern of behavior observed can be seen as providing only limited support for an interpretation of the present fMRI findings in terms of encoding processes. However, the evidence currently available clearly does not rule out such an interpretation. First, Remember-Know paradigms rely on a subjective assessment as to whether a recognition judgment is based on item- or episodic-contextual information, and these subjective assessments do not always converge with the outcome of objective probing (see Diana & Ranganath, 2011; Phelps & Sharot, 2008; Wixted, 2009; for discussion). Moreover, they do not offer any direct measure of the amount of feature information available in item-based memory decisions. Second, firm conclusions require research that goes beyond behavioral experiments, including studies based on functional neuroimaging. Future fMRI research could examine, for example, whether activity differences in PrC for object concepts with different degrees of lifetime familiarity predict subsequent performance on memory tests for item information encountered during scanning. Regardless of the outcome of this future research, we note that a role for PrC in assessment of lifetime experience and in the encoding of specific object encounters is not mutually exclusive. Indeed, there is considerable evidence in the cognitive neuroscience literature that ties episodic encoding to retrieval of conceptual information from semantic memory (see Greenberg & Verfaellie, 2010; Prince, Tsukiura, & Cabeza, 2007; Tulving, 2002). As such, a demonstrated role of PrC in episodic encoding during lifetime-familiarity judgements would not be incompatible with the conclusions drawn in our prior neuropsychological research concerning a critical role of this structure in the assessment of lifetime familiarity.

The current study primarily focused on PrC due to the prominent role this structure has played in prior neuroscience research on recognition memory in human and non-human animals (see Ranganath & Ritchey, 2012; Suzuki & Naya, 2014 for recent reviews). Critically, we found a response profile that was unique to left PrC in a conjunction contrast that probed for the typically observed decrease in BOLD signal based on recent exposure in combination with an increase in BOLD signal with increasing lifetime familiarity. However, when we examined the latter contrast in isolation, we also identified several other cortical regions whose BOLD response showed a positive relationship to the perceived cumulative lifetime familiarity of object concepts. These regions included the left hippocampus, left mid-lateral temporal cortex, and medial prefrontal and posterior cingulate cortices. Notably, these regions are part of the default-mode network, which has been proposed to support self-projection and internally directed thought that is often characterized by an autobiographical attentional focus (Andrews-Hanna et al., 2014; Buckner & Carroll, 2007). Arguably, such a functional characterization also captures judgments of the lifetime familiarity of object concepts.

A number of fMRI studies have shown that a subset of structures in the default-mode network, centered on the hippocampus, are frequently conjointly activated during episodic recollection in laboratory-based and in autobiographical memory tasks (see Kim et al., 2016; Spreng, Mar, & Kim, 2009; for reviews). Against this background it is interesting to consider whether episodic recollection may have played a role in the task we employed to probe cumulative lifetime familiarity in the current study. This could be the case even though our task had no explicit requirement to make reference to specific past object encounters (see Sheldon & Moscovitch, 2012; for related discussion). For example, while making their judgments, participants may have relied on monitoring the ease with which a pertinent episodic encounter came to mind. Although the available evidence that speaks to this issue is sparse, we note that recent neuropsychological findings argue against a critical (i.e., necessary) role for recollection in assessing cumulative lifetime familiarity. Specifically, we have found that an amnesic individual with well documented impairments in autobiographical recollection (patient HC), due to a lesion in the extended hippocampal system that spared PrC, displays no abnormalities in making judgments about lifetime familiarity (Bowles et al., 2016; Kwan, Carson, Addis and Rosenbaum, 2010). Considered in combination with the reported abnormal performance in patient NB, this neuropsychological evidence suggests a double dissociation between the recollection of particular autobiographical instances of object encounters, and the assessment of cumulative experience with such objects that has accrued over hundreds or thousands of different episodic contexts. Moreover, it suggests that the integrity of the hippocampus may not be necessary for making cumulative lifetime familiarity judgments. Future fMRI research can build on these neuropsychological findings and

\footnote{We conducted a behavioral experiment in a separate group of healthy young participants (n = 31), in which we asked participants to judge not only lifetime familiarity but also the amount of knowledge they have for specific object concepts (again using items taken from McRae et al., 2005). The two types of ratings were obtained in separate blocks of the experiment. Analyses of the resulting data revealed a strong positive correlation (across items \( r = .54, p < .05 \), averaged across participants) between perceived lifetime familiarity and estimated knowledge for object concepts.}
directly compare MTL signals for judgments of cumulative lifetime familiarity with judgments that require recollection of specific autobiographical experiences in response to the same cues.

Returning to PrC, the present findings add to a growing body of evidence that links this structure to the processing of object concepts in task contexts other than memory judgments for recent experimental study encounters. Several prior fMRI studies have employed priming paradigms in which repeated exposure to object concepts led to changes in PrC signals in semantic tasks that made no reference to these repetitions (Dew & Cabeza, 2011; Heusser et al., 2012; O’Kane, Insler, & Wagner, 2005; Voss, Hauner, & Paller, 2009; Wang, Lazzara, Ranganath, Knight, & Yonelinas, 2010, Wang et al., 2014). Past fMRI research has also implicated human PrC in processing of object concepts in tasks that did not involve any manipulation of item repetition, including object naming and judging the presence of specific semantic features (Bruffaerts et al., 2013; Clarke & Tyler, 2014; Liuzzi et al., 2015). In the latter set of studies, it has been shown that PrC carries information that is of particular relevance for making fine-grained distinctions among similar object concepts with high degrees of feature overlap. This evidence has been taken as support for models of PrC functioning that emphasize a broader role in feature integration that is not only critical for memory judgments but also for the representation of objects in perceptual and semantic tasks (Clark & Tyler, 2014; Cowell, Bussey, & Saksida, 2010; Graham, Barense, & Lee, 2010; Murray & Bussey, 1999; O’Neil, Protzner, McCormick, McLean, Poppenk and Cate and Köhler, 2012). An important topic for future research is to examine how the sensitivity of PrC to recent incremental changes and the perceived lifetime familiarity of object concepts we report here is related to computations that are critical for feature integration.

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Supplementary data

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