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Research report

Dissociation between the neural correlates of recollection and familiarity in the striatum and hippocampus: Across-study convergence

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ABSTRACT

In tests of recognition memory, neural activity in the striatum has consistently been reported to differ according to the study status of the test item. A full understanding of the functional significance of striatal 'retrieval success' effects is impeded by a paucity of evidence concerning whether the effects differ according to the nature of the memory signal supporting the recognition judgment (recollection vs. familiarity). Here, we address this issue through an analysis of retrieval-related striatal activity in three independent fMRI studies (total N = 88). Recollection and familiarity were operationalized in a different way in each study, allowing the identification of test-independent, generic recollection- and familiarity-related effects. While activity in a bilateral dorsal striatal region, mainly encompassing the caudate nucleus, was enhanced equally by recollected and 'familiar only' test items, activity in bilateral ventral striatum and adjacent subgenual frontal cortex was enhanced only in response to items that elicited successful recollection. By contrast, relative to familiar items, activity in anterior hippocampus was enhanced for both recollected and novel test items. Thus, recollection- and familiarity-driven recognition memory judgments are associated with anatomically distinct patterns of retrieval-related striatal activity, and these patterns are at least partially independent of recollection and novelty effects in the hippocampus.

1. Introduction

According to dual-process models of recognition memory [1,2], accurate recognition of a test item can be supported by two different memory signals, which are frequently termed 'recollection' and 'familiarity'. Recollection refers to retrieval of qualitative information about a past episode. This includes information both about whether the test item has been encountered previously, and about the study episode more generally, including spatio-temporal information unique to the episode. By contrast, familiarity supports judgments of prior occurrence in the absence of contextual or other information diagnostic of a specific study episode.

It has been widely argued that recollection and familiarity are functionally dissociable, and that their respective component processes rely on at least partially distinct neural regions and networks (e.g. [3,4]. Consistent with this view, fMRI studies have reported largely non-overlapping patterns of neural activity in association with recollection- and familiarity-based memory judgments (e.g. [5]; see for review [6,7]. When recollection is operationalized by the contrast between correctly recognized memory test items for which recollection either succeeded or failed, enhanced activity is evident in a characteristic brain network (the 'core recollection' network) that includes the hippocampus and medial prefrontal, posterior cingulate, middle temporal and ventral parietal cortex [8,9]. Familiarity (operationalized either by the contrast between recognized but unrecollected items and unstudied items, or by activity that covaries with subjective ratings of familiarity strength) is associated with enhanced activity in a different set of regions, including the intra-parietal sulcus (IPS), precuneus, and dorsal medial, left lateral and left anterior PFC (e.g. [5,7]. Familiarity has also been associated with *reductions* in activity relative to new items. Such 'novelty effects' are especially prominent in perirhinal cortex, where they have been linked with signals supporting familiarity-driven recognition [10], and the anterior hippocampus, where the effects are frequently interpreted as correlates of encoding novel item-context associations [11,12]. [Note that when we refer to 'familiarity' and 'novelty' effects below, we are using these terms simply to define the direction of the respective

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contrasts (familiar > novel, and vice-versa), without any implication that the effects reflect qualitatively distinct mnemonic processes].

Whereas dissociations between recollection- and familiarity-related neural activity in the hippocampus and neocortex are well documented, less attention has been paid to the possibility of analogous dissociations in subcortical regions that have been implicated in mnemonic processing, such as the striatum. Retrieval-related modulation of striatal activity has been noted in reviews and meta-analyses dating back over several years [13,6,7,14], but little research has directly addressed whether the location or magnitude of this activity differs when memory judgments are based on recollection versus familiarity. Instead, recent studies aimed at elucidating the functional significance of retrieval-related striatal activity [15–17] have mainly employed variants of 'yes/no' recognition that did not permit judgments to be segregated according to whether they were recollection- or familiarity-driven. Perhaps as a consequence of this, Han et al. [15] were able to interpret their findings in terms of a single role for the striatum in recognition memory ('goal-satisfaction'). Both Schwarze et al. [16] and Clos et al. [17] argued however that their findings suggested that striatal activity during recognition judgments reflects two distinct sources of 'subjective value'. These are derived from 'perceived oldness' and response confidence respectively.

Unlike in the three studies just mentioned, Elward et al. [18] employed a source memory procedure rather than a test of item (recognition) memory. Subjects were informed that accurate retrieval of one of two study contexts (sources) would result in high monetary reward ($2), while correct retrieval of the other context would lead to low reward (2c). They were also informed that inaccurate judgments would lead to corresponding losses. Regardless of the value of the associated reward, accurate source judgments (assumed to be supported by recollection) elicited greater activity in ventral and lateral striatum than did inaccurate judgments (when recollection was assumed to be weak or absent), replicating prior findings [13,14]. Additionally, adjacent ventral striatal regions demonstrated enhanced activity for judgments associated with high versus low reward, irrespective of the accuracy of the source judgment, while no regions were identified where the factors of recollection success and reward value interacted. These findings suggest that retrieval-related activity in the striatum is sensitive not only to 'retrieval success' in tests of item recognition, but also to whether recollection of the study context of a recognized item succeeds or fails (see also [14]. The findings further suggest that this recollection-related activity can be dissociated from striatal responses linked to the prospect of reward ('goal satisfaction' in the terminology of [15]). Elward et al. [18] did not, however, examine striatal activity during familiarity-based recognition.

Here we take advantage of three independent data sets (described originally in [18–21]) to examine whether memory judgments based on recollection or familiarity are associated with dissociable patterns of striatal activity. The three studies employed memory tests that differed markedly in their operationalization of recollection and familiarity (see Table 1 and Methods) and used diverse experimental materials. We assume that fMRI effects shared across the three studies reflect general, rather than material- or test-specific, effects that provide insight into the neural regions and networks linked to different classes of memory process (see [9], for an analogous approach). To anticipate the results, we find compelling evidence that previously reported dissociations between recollection- and familiarity-driven neural responses extend to the striatum and closely adjacent regions. The findings constrain proposals about the role or roles of the striatum in memory retrieval.

Table 1
Summary of the three experiments contributing data to the present analyses.

	Retrieval Test	N	Critical trials
Expt. 1	Remember/Know	24	Remember, Know, New
Expt. 2	Associative Recognition	36	Intact judged intact, Intact judged rearranged, New judged new
Expt. 3	Source Memory	28	Source correct, source incorrect but item correct, New

Table 2
Mean (SD) RTs (ms) for recollected (R), familiar (F) and new (N) items in each experiment.

	R	F	N
Expt. 1	2140 (769)	3060 (1083)	2920 (994)
Expt. 2	1855 (388)	2274 (468)	2075 (464)
Expt. 3	1573 (276)	1741 (389)	1122 (147)

2. Results

2.1. Behavioral findings

Accuracy data for each of the three experiments have been fully described previously [18–21], see also [9]. In each case estimates of recollection and familiarity were robustly above chance. Reaction time (RT) data were however not fully reported in Wang et al. [21] and de Chastelaine et al. [19]. Accordingly, we report these data here (Table 2). For each experiment, the RT data were subjected to one-way repeated measures ANOVA (Geisser-Greenhouse corrected for non-sphericity). The ANOVAs revealed main effects of trial type ($F1.92,44.1 = 26.00$, $F1.88,65.8 = 46.69$, $F1.4,26.2 = 59.85$ for experiments 1, 2 and 3 respectively, min $p < 0.001$). Post-hoc contrasts (Bonferonni corrected) indicated that in each experiment RTs for recollected and new items were reliably shorter than those for familiar items. However, whereas in experiments 1 and 2 RTs for new items were longer than those for recollected items, this difference was reversed in experiment 3.

2.2. fMRI findings

For the reasons outlined in the Introduction, we focus here on results for each of the contrasts of interest (recollection, familiarity and novelty) that were common to the three experiments. Common effects were defined as those that survived our conjoint height and cluster extent thresholds for the main effect across experiments (see Methods), as well as inclusive masking with the simple effect in each experiment, thresholded at $p < 0.05$ uncorrected. The masking procedure was employed to limit the results to voxels where effects were shared across the experiments. Along with the outcome of the masked across-experiment ANOVA, the key finding (the dissociation between memory effects in the dorsal and ventral striatum) is illustrated in Fig. 1a–c for each experiment separately.

Striatal familiarity and recollection effects are illustrated in Fig. 1 and, along with novelty effects, are documented in Table 3. As is evident from the figure, relative to new items, familiar test items elicited enhanced activity in dorsal (caudate) and, to a more limited extent, ventral striatum. By contrast, relative to familiar items, successfully recollected items did not elicit any additional activity in the caudate, but instead elicited enhanced activity in the most ventral aspects of the striatum and the adjacent subgenual frontal cortex (corresponding mainly to Brodmann's Area 25; [22]). For each subject, the parameter estimates representing the magnitude of the responses elicited by recollected, familiar, and novel items were extracted from the voxels in the left and right striatum where familiarity or recollection effects were maximal ('peak' parameter estimates; see Table 3 for their MNI co-ordinates). The across-subjects means of these estimates are plotted in Fig. 2d and e. The novelty contrast (N > F) identified an effect in the posterior aspect of the right putamen (not illustrated).

We employed exclusive masking to further assess the independence