The anatomy of non-conscious recognition memory

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Abstract

Cortical regions as early as primary visual cortex have been implicated in recognition memory. Here, we outline the challenges that this presents for neurobiological accounts of recognition memory. We conclude that understanding the role of early visual cortices in this process will require the use of protocols that mask stimuli from visual awareness.

The relation between recognition memory and (un)awareness

Recognition memory, the ability to explicitly recall previously encountered items and events (e.g., episodes), is widely considered to be a conscious function, and dependent on a network involving the prefrontal cortex, parietal cortex, and medial temporal lobe (MTL) (perirhinal, parahippocampal, entorhinal cortices, and hippocampus). Here, we re-consider the neurobiology of recognition memory in light of recent evidence that stimuli masked from visual awareness (i.e., subliminal) can be used to investigate non-conscious influences in recognition memory [1, 2], and cortical regions as early as primary visual cortex (V1) can mediate recognition memory for both visible (i.e., supraliminal) [3] and subliminal stimuli [2]. These data are likely to raise skepticism in two areas: (i) how can non-conscious influences and (ii) cortical processing in sensory regions as early as V1 underlie the *sine qua non* assay of episodic memory?

No single general experimental protocol has been applied to investigate non-conscious influences in recognition memory. Until recently, protocols employed supraliminal stimuli for memory encoding and retrieval (corresponding to the experimental conditions of "study" and "test"). In this research, manipulations, such as divided attention, have been used to diminish awareness of supraliminal stimuli and thereby induce recognition unaccompanied by the subjective feeling of "familiarity" [4]. One consideration with the use of supraliminal stimuli to investigate non-conscious influences is that, under some conditions, recognition memory and even repetition priming effects (henceforth priming) that stem from (i) briefly presented (~50-500 ms exposure, but unmasked) items or from (ii) the masked priming of visible retrieval cues can both be explained by a single continuous, conscious, memory strength process [5].

Many of the conceptual and methodological issues associated with isolating non-conscious influences in recognition memory can be minimized by ensuring that the stimuli presented at study and as retrieval cues (e.g., words) are subliminal [1, 2] (Fig. 1). Notably, the task structure with this approach – 'old'-'new' discrimination and a post-trial confidence judgment – can remain ostensibly similar to a standard recognition test implemented with supraliminal stimuli [1]. It is, nonetheless,

important not to underestimate the challenges in ensuring adequate masking of stimuli from visual awareness (Box 1).

A key advantage of masking both study and test stimuli from visual awareness is that recognition memory can be investigated without the cascade of 'top-down' neural activity impinging on cortical processing – i.e., related to conscious attention and perceptual selection, cognitive (e.g., memory) control, and updating of conscious representations. Such conditions are particularly relevant when investigating areas such as V1 within early visual cortex (EVC), because early stages of visual processing, originating in V1, are modulated by feed-forward and 'top-down' recurrent neural activity. Another advantage is that non-conscious influences in recognition memory can be studied with little or no impact on memory retrieval of mechanisms that are related to novelty-detection, the reinstatement of episodic information, and operations 'downstream' of retrieval such as attention-to-memory content and perceptual expectations.

V1 and recognition memory for subliminal discontiguous associations

Rapid conjunctive coding of arbitrary associations specified in a spatial context has been previously identified as a basic hippocampal-mediated feature of conscious recollection [6]. More recent neurobiological accounts argue that the hippocampus supports non-conscious as well as conscious memory involving processes such as associative binding [7]. Recent evidence indicates that EVC may also contribute to non-conscious (recognition) memory for complex associations. In particular, evidence from an fMRI study indicated that the learning and recognition of subliminal visual stimuli that needed to be associated across different spatial locations and across time (i.e., the associations were discontiguous) were subtended by an occipital-temporal network that included the hippocampus (Fig. 1) [2]. Notably, only activity in V1 at study and on the later (~20 min delay) test predicted recognition memory for the subliminal sequence. These data extend consideration of non-conscious associative learning and recognition memory mechanisms to include V1.

A role for V1 in the recognition of associations is perhaps less surprising given that V1 can support broader-based cognitive operations, such as perceptual expectation and

learning, which are similar to those mediated by later cortical areas and the hippocampus [8]. Conversely, and unlike the hippocampus, V1 is generally not well suited to rapid perceptual or associative learning, but it can support perceptual learning of supraliminal colour-orientation associations, after 3 days of training [9]. Therefore, the mechanisms by which V1 contributes to associative recognition memory are, as yet, unclear, although, functional coupling of V1 with hippocampal-mediated association mechanisms and neighbouring mnemonic substrates may play a role [2].

Boundary conditions of V1 activity

It is also currently unknown what type of information is represented by the V1 activity associated with recognition memory for subliminal visuospatial associations. Tackling this issue can begin to address the boundary conditions under which V1 involvement in recognition might be predicted. For example, a V1-centred voxel-wise encoding model could be used to decode correctly recognised retrieval cues (hits) and correct rejections (retrieval cues correctly endorsed as new), as a function of recognition memory for subliminal discontiguous associations, simpler adjacent pairs of items (paired associates), and single-items. The results could help reveal whether V1 represents information about specific discontiguous associations rather reflect generalised recognition test-based plasticity, and also whether V1 can represent specific paired associates and feature-specific information about single-items in the context of recognition memory.

It will also be important to determine if the loci and functions that describe mnemonic and perception-related V1 activity are discrete (i.e., domain specific). One approach would be to compare V1 activity during recognition memory and perceptual discrimination tasks under conditions that preclude or curtail visual awareness of stimuli associated with V1 activity. These data would provide an informative counterpart to evidence that a hippocampal subfield region known as CA1 can generate a continuous strength-based signal which tracks the confidence associated with perceptual discriminations, whereas recognition memory generates a thresholded state-based hippocampal CA1 signal [10].

V1 and V1-hippocampal functional connectivity are, however, unlikely to be necessary and sufficient features of non-conscious recognition memory; rather, they are more likely to be evinced under conditions where the experimental protocol is optimised to isolate the role of activity in V1, as a counterpart to studies on domain-specific visual object recognition mediated by the object-sensitive ventral visual-perirhinal-hippocampal stream [11]. One way in which to test this hypothesis is to explore the effect of different types of memory content on neural activity associated with recognition memory without visual awareness (e.g., associative recognition of an item, such as a word or picture, alone or bound with another item, context, or location). Existing neural regions implicated in recognition memory might subtend recognition without visual awareness for conventional stimuli such as single-words and paired word-associates, along similar lines to that seen with recognition memory for supraliminal single-item versus paired-associates subtended by the perirhinal cortex and hippocampus, respectively [11].

Links with other varieties of conscious and non-conscious retrieval experience

A further issue that has, as yet, received no attention is how recognition without visual awareness relates to other varieties of retrieval experience. Multiple lines of evidence indicate that the hippocampus and perirhinal cortex provide qualitatively different contributions to recognition memory for supraliminal stimuli, such that the recovery of contextual information represented in parahippocampal cortex and medial entorhinal area is hippocampal-mediated, whereas the perirhinal cortex supports an acontextual familiarity-mediated feeling of knowing. It is conceivable that, for single-item or simple associative recognition memory of words, the hallmarks of recollection, familiarity, and non-conscious influences will be revealed through differences in dynamic network connectivity between established MTL and neocortical regions implicated in recognition memory. It is less clear how such contrasts will play out with the recognition of complex associations (e.g., discontiguous associations described in Fig. 1) because there appears to be little neural overlap in the networks that underlie the learning of supra- and sub-liminal visuospatial associations [2].

Previous studies have reported that implicit, non-conscious recognition memory based on guess responses and perceptual priming-based retrieval of supraliminal geometric shapes are both associated with a similar negative-going old-new event-related potential [12]. Priming on a wide array of experimental task is associated with activity in later visual areas such as lateral occipital complex that does not predict behavior [13]. It is unknown, however, if similar profiles of visual cortex activity mediate both recognition without visual awareness and priming effects, under conditions where comparable masking of stimuli from visual awareness is employed with both types of test of non-conscious memory. Overlap would provide insight into whether seemingly diverse non-conscious mnemonic operations share a similar neural substrate. Such an outcome is unlikely, however, given that priming can involve multiple and dissociable behavioral processes and neural signals [13].

Commonalities and differences in the functional properties and neural correlates of non-conscious influences in recognition and priming can also be examined by applying experimental manipulations the dissociate recognition memory from priming, such as dual-task attention, speeded responding, and delay between study and test (i.e., as a proxy of mechanisms related to memory consolidation). For example, evidence that encoding of subliminal studied items under dual-task conditions does not selectively affect recognition memory compared perceptual identification priming would suggest a common cognitive basis for non-conscious influences.

Flexibility of recognition memory without visual awareness

Another key limitation in current understanding is how recognition memory relates to visual awareness when there is mismatch between retrieval cues and previously studied items, namely, whether and how the capacity to generalize from studied items to mismatch retrieval cues (i.e., exhibit representational flexibility) depends on awareness. This is an important question given that priming effects associated with early visual areas are often associated with specificity [13], and flexibility is considered as a defining feature of episodic memory. Inchoate evidence indicates that perceptual changes to word orthography or the visual mask between study and test do not affect the recognition of subliminal words [1]. Neurocomputational models of

recognition have extensively explored effects of partial (sparse) cueing - e.g., where there is mismatch in perceptual overlap between study and test - on the reinstatement of a previously encountered item, and implicate a pattern completion based computation within a hippocampal subfield (CA3). Of particular note is recent evidence that has linked pattern completion with reinstating predictive perceptual (de)coding in V1 [8]. Speculatively, these operations might align with the hippocampal-V1 functional coupling observed with recognition memory for subliminal discontinuous serial associations [2], such that V1 can draw upon general-purpose associative learning mechanisms in the MTL.

An ideal framework to test generalisation in non-conscious recognition would be to examine the effect of changes in mismatch between study and test on pattern completion and separation (i.e., discrimination) based computations in hippocampal subfields and neocortical reinstatement, conducted as a function of different states of visual awareness, familiarity, and recollection based retrieval. Such studies would test, for example, whether successful discrimination between old and highly similar (but novel) retrieval cues (known as lures), typically associated with recollection rather than familiarity, can be accomplished by non-conscious influences in recognition memory.

In summary, we have outlined the merits of visual masking during encoding and later retrieval to study the impact of non-conscious influences on recognition memory without visual awareness, and have presented future directions for research to explain how recognition memory is implemented in cortical areas as early as V1 across states of visual (un)awareness. It will be important to determine how these data fit into existing theoretical accounts that explain the signals underlying visual recognition memory in terms of a summated continuous strength based process [14], independent contributions [15], or, interactions.

Text Box

Box 1. Measuring non-conscious recognition memory with subliminal stimuli (recognition memory without visual awareness)

Equivocal conclusions about evidence for recognition memory without visual awareness can be minimised if observers exhibit no perceptual awareness for stimuli – as assessed, for example, on independent pre- and post-experimental psychophysical based measures of the efficacy of visual masking – whereas measures of mnemonic sensitivity based on signal detection theory demonstrate above chance performance (i.e., significant d' or receiver-operating characteristic curves plotting the hit rate and false alarm rate as a function of post-trial confidence judgments). Neural evidence of non-conscious recognition may be found on the basis of established contrasts that are, for example, based on the study status of retrieval cues (old<new), retrieval success (hits>correct rejections), and subsequent memory effects at encoding (hits>misses (old item endorsed as new)). Notably, the link between old-new discriminations and confidence judgments is not straightforward. Each cannot be assumed to depend on the same underlying source of information because non-conscious recognition can occur with null perceptual and mnemonic sensitivity to the retrieval cues (i.e., perceptual and mnemonic d'=chance), but be evinced by significant meta-d' [2], a recently developed measure of the signal available to perform metacognitive discrimination (i.e., how well observer's confidence ratings distinguish between correct and incorrect memory and perceptual judgments) [16].

Glossary

Recognition memory – the capacity to recall whether items have been presented before. For example, in a recognition test, old (studied) items are presented in a list also comprised of new (non-studied) items, and observers' decide whether or not each item on the list was presented at study.

Episodic memory – the conscious encoding, storage, and retrieval of personally experienced past episodes, comprised of integrated sensory, conceptual, emotional, what, when, and where content. Episodic memory can support the simulation of episodes in either the past or the future, and subtends our sense of a coherent identity that across time.

Repetition priming – the faster or more accurate production, identification, or classification of a previously presented stimulus or related stimulus on a memory test that does not make reference to the prior presentation. Priming can support memory

effects that last minutes or longer and for different materials (e.g., words or faces), and operate without awareness of memory retrieval and has thus been considered an expression of non-conscious or implicit memory. Subtypes have been described with respect to whether perceptual, meaning (conceptual), or both types of information processing operate on the stimuli.

Single-item recognition memory – recognition memory for individual items, such as a word or a picture, in an episode.

Associative recognition memory – the relation between two items, such as a pairwise association between an object and context or a pair of words (word-word), which either co-occur or are presented contiguously at study and are tested by instructing observers to discriminate studied from new pairs. Associative recognition memory is generally regarded to be mediated by recollection when the pairs are previously unrelated (non-unitized) but can be supported familiarity-based processes.

Familiarity – the subjective conscious experience of recognising an item, object or event, without the retrieval of specific contextual details about the original episode in which it was encountered. Notably, there is ongoing controversy regarding whether recognition memory is driven by recollection and familiarity or independent contributions from recollection and familiarity signals.

Recognition of complex associations – recognition memory can result from new associations formed within an experiment. These tasks measure recognition as the ability to retrieve either discontiguous associations within domains or associations across stimulus domains or sensory modalities.

Perceptual identification priming - items are presented briefly and priming is demonstrated if a greater proportion of old (previously studied) items are identified relative to new (non-studied) items. Perceptual identification and recognition can be measured using the same psychophysical response metric, d'.

Figure 1. Example experimental setup used to investigate recognition memory without visual awareness. (A) Visual masking implemented using a technique based on dichoptic presentation of the visuospatial sequence. (B)(i) Study

phase. Observers viewed a repeating event sequence presented at four fixed monocular locations (1-4), but only perceived two locations (left, right), thereby masking monocular information from visual awareness: stimuli at locations 1 [left eye input] and 3 [right eye input] were perceived within the left placeholder location (L), whereas stimuli at locations 2 [left eye-of-origin] and 4 [right eye-of-origin] were perceived within a right placeholder location (R). (ii) Axial view depicts V1, hippocampus, and basal ganglia based network supporting learning of the subliminal sequence. Sagittal view of this network depicts cluster (in green) within V1. (C) (i) Test phase - recognition memory test without visual awareness. Observers were presented with old (e.g., 341243) and new (e.g., 143241) retrieval cues that differed only in terms of the monocular target sequence and study status, whereas the perceived serial order associated with the old and new retrieval cues was the same (i.e., LRLRRL). Recognition memory was evident when contrast old versus new confidence rating scores on the post-trial confidence judgments rather than in the ability to correctly endorse the retrieval cues as old and new – d'=0, i.e., no greater than chance, suggesting an absence of perceptual awareness and conscious recognition memory, and recognition memory that cannot be attributed to a primed link between the studied stimuli and the response or decision made about the stimuli at test (Box 1). (ii) fMRI results. 3-D render of the whole-brain shows activity in V1, lateral occipital cortex and hippocampus for the contrast between old<new sequences. Sagittal view depicts functional coupling between the hippocampus and V1 (indicated in yellow) as a function of whether the retrieval cue was old or new (occipital mask in blue shading).

Acknowledgements

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Figure 1

(B) Study Phase i. behavioural procedure

ii. fMRI results

Learning a visuospatial sequence masked from visual awareness

Single repeating 12-event second-order conditional sequence
[34124314 2132 - specified in monocular (non-conscious) screen locations]

4 trials of 12-element sequence (e.g., 3412/LRLR)
Perceived (L, R) sequence due to dichoptic presentation
[L R L R R L L R R L L R]

(A) Masking of the visuospatial
sequence from visual awareness
using dichoptic presentation.

Four masked monocular (screen) locations
and mapping to two perceived locations

LEFT EYE | RIGHT EYE
1 2   3 4

PERCEIVED LOCATIONS

L R

Prism-based spectacle lenses

(C) Test Phase i. behavioural procedure

ii. fMRI results

Recognition memory without visual awareness (3-steps on each trial)

(1) Dichoptic presentation of a 6-event
'old' or 'new' non-conscious retrieval cue

(2) Old-New
recognition

Example "OLD" ≠ Example "NEW"
[3 4 1 2 4 3]   [1 4 3 2 4 1]

OLD = NEW
[L R L R R L]

LEFT EYE | RIGHT EYE

LEFT EYE | RIGHT EYE

PERCEIVED

"Old" or
"New"?

six
targets/trial   1 2 3 4   1 2 3 4   L R

(3) Confidence
rating

1
2
3
4
5
6

Rate
confidence