Research report

The sensory timecourses associated with conscious visual item memory and source memory

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HIGHLIGHTS

• The timecourse of conscious and nonconscious visual sensory memory effects.
• Visual sensory source memory and item memory effects are temporally distinct.
• The rapid onset of visual sensory item memory effects.

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ABSTRACT

Previous event-related potential (ERP) findings have suggested that during visual item and source memory, nonconscious and conscious sensory (occipital–temporal) activity onsets may be restricted to early (0–800 ms) and late (800–1600 ms) epochs, respectively. In an ERP experiment, we tested this hypothesis by separately assessing whether the onset of conscious sensory activity was restricted to the late epoch during source (location) memory and item (shape) memory. We found that conscious sensory activity had a late (>800 ms) onset during source memory and an early (<200 ms) onset during item memory. In a follow-up fMRI experiment, conscious sensory activity was localized to BA17, BA18, and BA19. Of primary importance, the distinct source memory and item memory ERP onsets contradict the hypothesis that there is a fixed temporal boundary separating nonconscious and conscious processing during all forms of visual conscious retrieval.

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1. Introduction

Memory can be based on explicit (conscious) processing or implicit (nonconscious) processing. Conscious retrieval and nonconscious retrieval are typically investigated using direct or indirect tasks, respectively. During direct tasks, such as old-new recognition, participants respond based on conscious memorial experience. By comparison, during indirect tasks, participants respond based on a non-memorial feature, such as item pleasantness, but behavioral or neural memory effects can still be measured. For instance, repetition priming is reflected by a change in the magnitude of neural activity for repeated versus novel items. Despite the widespread assumptions that direct memory tasks tap into conscious processing and indirect tasks tap into nonconscious processing, it has long been known that both types of tasks can reflect nonconscious and conscious processing (i.e., performance on memory tasks is not process-pure; [1–3]). However, previous studies have successfully isolated conscious and nonconscious memorial processing using a single direct memory task by using the appropriate comparisons [4–11, for a review, see 12]. For instance, it is common to compare memory judgments associated with high retrieval content (e.g., retrieval success, remembering, or true recognition) with memory judgments associated with low retrieval content (e.g., retrieval attempt, knowing, and false recognition) to isolate conscious memory processes. In contrast, memory judgments with no conscious retrieval (e.g., inaccurate memory judgments) have been used to isolate nonconscious memory.

Previous event-related potential (ERP) results have suggested that nonconscious memory activity in visual sensory regions occurs relatively early in time, within 800 ms after stimulus onset [7,13–15, see also, 16], while conscious memory activity in visual sensory regions occurs relatively late in time, within 800 to 1600 ms after stimulus onset [7]. For example, visual object priming effects, which can be assumed to reflect nonconscious memory processing, have been shown to occur before 800 ms [15]. In contrast,
Conscious sensory activity for accurate retrieval has been shown to occur after 800 ms [7]. It should be noted that the latter conscious memory effects that were associated with visual sensory reactivation in occipital–temporal regions are spatially distinct from the conscious memory effects that have been associated with the processes of familiarity and recollection in frontal regions (within 300–500 ms) and parietal regions (within 500–800 ms), respectively (for a review, see [17]).

Of particular relevance to the present investigation, Slotnick and Schacter [7] used ERPs to measure the time at which conscious and nonconscious activity occurred in visual sensory occipital–temporal regions-of-interest (ROIs) during a direct memory task. In that study, as in the present study, abstract shapes were presented to the left or right of fixation during encoding (Fig. 1A). During retrieval, previously presented (old) shapes and new shapes were shown at fixation and, for each shape, participants made a combined item memory and source memory judgment (old and previously on the left, “old-left”, old and previously on the right, “old-right”, or “new”; Fig. 1B).

Conscious memory activity was isolated by taking the difference in activity between accurate item memory and source memory (old item memory-hits and source memory-hits, referred to as old-hit-hits) and completely forgotten items (inaccurate item memory and source memory, old-miss-misses), given that these events track memorial experience (“old” versus “new”) with item type (old items) held constant [6,18]. Nonconscious memory activity was isolated by taking the difference in activity between inaccurate item memory and source memory and correctly rejected new items (old-miss-misses — new-correct rejections), given that these events differ as a function of item type (old versus new) with memorial experience (reflected by “new” responses) held constant [4–6,10, see also, 19]. Slotnick and Schacter [7] reported that the onset of nonconscious memory activity occurred in the early (0–800 ms) epoch, while the onset of conscious memory activity occurred in the late (800–1600 ms) epoch.

As the previous study collapsed across both conscious (i.e., accurate) item and source memory (old-hit-hits + old-miss-misses), it is possible that the previously described temporal dissociation in visual sensory regions exists during all forms of conscious retrieval (i.e., item memory and source memory), which predicts that there is a fixed temporal boundary (at 800 ms) between the onset of nonconscious processing and the onset of conscious processing. Alternatively, such a temporal dissociation may only exist during certain types of conscious retrieval, which predicts the onsets of nonconscious and conscious processing will not be restricted to particular epochs. In the first experiment of the present study, we used ERPs to distinguish between these hypotheses by separately measuring the onset of conscious sensory activity during source memory and item memory, two forms of conscious retrieval. Conscious source memory was isolated by taking the difference in activity between old-hit-hits and old-hit-misses. Conscious item memory was isolated by taking the difference in activity between old-hit-misses and old-miss-misses. As source memory and item memory performance can be assumed to be based on both conscious processing and nonconscious processing, we also isolated and subtracted out nonconscious processing for each type of memory. A follow-up fMRI experiment that employed the same paradigm was also conducted. To anticipate the present ERP results, the onset of conscious processing differed during source memory and item memory, which indicates there is no fixed temporal boundary separating nonconscious and conscious processing during all forms of conscious retrieval in visual sensory regions.

2. Experiment 1

2.1. Materials and methods

2.1.1. ERP participants

Twelve right-handed participants (5 females, aged 18.9–21.8) with normal or corrected-to-normal vision completed the experiment. The protocol was approved by the Boston College Institutional Review Board, and informed consent was obtained from each participant. Although the current experiments utilize datasets analyzed by Slotnick [21] and Slotnick and Schacter [6,7], the results presented in the current manuscript have not been reported previously.

2.1.2. ERP stimuli and task

In each of 6 runs at encoding, 32 abstract shapes filled with colored oriented lines [6] were each presented for 2.5 s followed by a 0.5 s fixation period (Fig. 1A). Each shape spanned 5.5° of visual angle with the nearest edge 3° of visual angle to the left or right of fixation. Participants were instructed to maintain fixation and encode each shape and its spatial location. During retrieval, the 32 old shapes from encoding and 16 new shapes were randomized and presented at fixation for 4 s followed by a 2 s fixation period (Fig. 1B). The time delay between encoding and retrieval was 10 s, which included an 8 s instruction screen followed by a 2 s fixation screen. Participants classified each shape as old and previously on the left, “old-left”, old and previously on the right, “old-right”, or “new”. Item types (old-left, old-right, and new) were counterbalanced using a Latin square design. Participants responded via a button box in their left hand. During encoding and retrieval, no more than 3 shapes of a given type were repeated.
Event types included accurate item memory and source memory (old-hit-hits, e.g., “old-left” responses to old-left shapes), accurate item memory and inaccurate source memory (old-hit-misses, e.g., “old-left” responses to old-right shapes), and inaccurate item memory and source memory (old-miss-misses, “new” responses to old shapes). Item memory accuracy was the weighted percentage of correctly identified old and new shapes: $p(\text{old}) \times \text{old-hit rate} + p(\text{new}) \times \text{new-correct rejection rate}$, with $p(\text{old}) = 66.7$% and $p(\text{new}) = 33.3$% [20]. Source memory accuracy was the percentage of correctly identified old-left and old-right shapes contingent on correct old item identification: old-hit-hits/(old-hit-hits + old-hit-misses). Chance performance for both item memory and source memory was 50% correct.

2.1.3. ERP acquisition and analysis

The ERP acquisition and analysis methodology has been detailed and employed previously [7,21,22]. ERPs were recorded in a shielded chamber (Global Partners in Shielding, Inc., Passaic, NJ), measured with 128 sintered silver/silver chloride electrodes embedded in a Quik-Cap, amplified using NeuroScan SynAmps2, and acquired at a 1 ms sampling rate using SCAN software (Compumedics USA, Charlotte, NC). Electrode impedances were maintained below 15 kΩ. Data preprocessing was conducted for each run using BESA (MEGIS Software GmbH, Graefelfing, Germany) and included removing 1–2 blink topography principal components that accounted for at least 85% of the variance, excluding trials and electrodes with amplitudes above 120 μV or gradients above 75 μV/sample, and high-pass forward filtering (0.5 Hz cutoff at 6 dB/octave; low-pass filtering was not conducted [7,21,22]). It is important to note that this high-pass filter threshold eliminated waveforms with periods of greater than 2 s, which more than spans the time window of interest (0–1600 ms; i.e., this was similar to filtering out linear drift). That is, such low frequency activity might have produced a single peak of activation within the analysis epoch. Critically, the absence of a single activation (a null result) would not have affected the pattern of results observed, which was based on numerous significant activations (see Section 2.2.2). Baseline correction was not conducted as the high-pass filter removed low frequency activity (including DC offset) such that baseline activity was close to 0. For each participant, event-related averages were computed for each event type at retrieval from −500 to 2000 ms after stimulus onset. Each event-related average was weighted by the number of trials in each run to ensure that runs with a lower number of trials were not equally weighted as runs with a higher number of trials.

Left and right hemisphere temporal and occipital electrodes were grouped into 4 ROIs based on the scalp distribution of previously reported visual sensory encoding/perception ERP effects (Fig. 2A; [21; see also, 23–25]). The left occipital ROI consisted of electrodes 11, O1, P1, P3, P5, P7, and P9 (labeled according to the 10–20 system; [26]). Right hemisphere ROIs consisted of analogous even numbered electrodes. Following previous visual perception and memory studies, Cz was used as the reference electrode [7,9,21,22,27,28]. Statistical analysis was conducted using the mean activity within each ROI.

For each participant, the ERP difference between the two conditions of interest was averaged for each timepoint ±6 ms. Visual activity at retrieval that overlapped with visual activity at encoding was of primary interest, as this can be assumed to reflect recapitulation of the previous visual experience. Therefore, the 13 ms epoch was independently computed based on the known durations of retrieval and encoding related fMRI and ERP activity in visual sensory regions [21]. For each 13 ms epoch, a within-participants t-test was used to assess whether the magnitude of activity was greater than 0 across participants. To illustrate, Fig. 2A shows the voltage topography at 1368 ms after stimulus onset associated with old-right-hit-hits – old-right-hit-misses (which corresponds to accurate source memory for items previously presented in the right visual field), and Fig. 2B shows the activation timecourse associated with each ROI (asterisks mark time points at which the magnitude of activity is significantly greater than 0).

Items in each visual field were first analyzed separately to allow for hemispheric processing differences [29–31]. In order to maximize sensitivity, periods of significant activity at retrieval were collapsed across the visual field location at encoding. A binomial test was used to evaluate whether the number of activations in the late (800–1600 ms) epoch was greater than the number of activations in the early (0–800 ms) epoch. Activations that were closer than 12 ms were counted as a single activation to ensure statistical independence (i.e., activity at a particular timepoint never entered into the analysis more than once). Of importance, due to multiple comparisons, it is necessary to ensure our results are not due to type I error. Critically, if type I error was appreciable, this would have produced null findings. As a significantly greater number of activations were observed in the late versus early epochs for both source memory and item memory (see Section 2.2.2), this indicates that type I error was not a major concern (i.e., if our results were due to noise, the distribution of significant activations would have been randomly distributed across both earlier and later time epochs, and there would not have been any significant differences across time).

For source memory, unconscious activation increases were isolated by taking the difference in activity between old-left-miss-misses and old-right-miss-misses and vice versa. A previous fMRI study that employed the same paradigm as the present study found that these comparisons produced increases in retinotopic early visual areas that likely reflected spatial location repetition priming, a form of unconscious memory [32; for other instances of priming related sensory activation increases associated with unfamiliar visual stimuli, see 33,34]. For item memory, unconscious activation increases were isolated by taking the difference in activity between old-miss-misses and new-correct rejections, as has been done previously [4–8,10,14,35]. This comparison isolates unconscious activity associated with item type (old versus new, with response, “new”, constant). Of importance, a previous study showed that old-miss-misses not only reflect spatial location priming (see above) but also, item priming [32]. Thus, to isolate unconscious item memory, we then subtracted the number of unconscious source memory activations identified by the previous difference (old-left-miss-misses – old-right-miss-misses and vice versa; if the difference was less than 0, it was assumed to be 0).

It is important to mention that the current experiment focused on ERP memory effects in visual sensory regions that are not commonly investigated or reported in the memory literature (as compared to the frontal 300–500 ms FN400 or the parietal 500–800 old-new recognition effect; for a review, see [17]). The presence or absence of these effects is unrelated to the current experimental aim; that is, to assess whether conscious item and source memory effects assumed to reflect visual sensory reactivation are temporally dissociable.

2.2. Results

2.2.1. Behavioral ERP results

Source memory accuracy was 64.5 ± 1.9% and item memory accuracy was 62.3 ± 1.7% (mean ± standard error). The rates of old-hit-hits, old-hit-misses, old-miss-misses, and new-correct rejections were 44.2 ± 2.5%, 24.2 ± 1.4%, 31.6 ± 2.9%, and 50.2 ± 3.8%, with ranges (minimum–maximum) of 33–106, 14–62, 32–72, and 24–59, respectively. The reaction times for old-hit-hits, old-hit-misses, old-miss-misses, and new correct rejections were...
1816 ± 84, 2004 ± 113, 1917 ± 110, and 1850 ± 101 ms (which are beyond the analysis window).

2.2.2. ERP results

ERP activation timecourses associated with old-hit-hits, old-hit-misses, old-miss-misses, and new-correct rejections are depicted in Fig. 3. These waveforms illustrate a robust initial positivity (which likely corresponds to the visual sensory P100) followed by a negativity, but otherwise do not largely deviate from 0.

Fig. 4 shows the significant activations across time associated with conscious source memory (isolated by taking the difference in activity between old-hit-hits and old-hit-misses) and conscious item memory (isolated by taking the difference in activity between old-hit-misses and old-miss-misses). During conscious source memory (Fig. 4A) in occipital ROIs, a significantly greater number of activations occurred within the late epoch as compared to the early epoch (4 versus 0, p < 0.05), while in temporal ROIs the number of late versus early activations did not significantly differ (4 versus 2, p > 0.05). During conscious item memory (Fig. 4B) in occipital ROIs, the number of late versus early activations did not significantly differ (13 versus 13, p > 0.05), while in temporal ROIs a significantly greater number of late versus early activations occurred (13 versus 8, p < 0.05). These results are consistent with the findings of Slotnick and Schacter [7] in that conscious sensory activity occurred relatively late in time. However, there was a significant interaction between information type (source memory, item memory) and epoch (early, late) in occipital ROIs (p < 0.05), which provides some evidence against a fixed temporal boundary separating nonconscious and conscious processing for all forms of conscious retrieval (the information type by epoch interaction was not significant in temporal ROIs, p > 0.05, but a null finding does not constitute compelling evidence).

Of relevance to the interpretation of the present findings, Slotnick and Schacter [7] found that the number of late versus early activations did not significantly differ during nonconscious retrieval, which suggests that nonconscious processing is relatively constant across time. Furthermore, in that study (as in the present study), a significantly greater number of late versus early sensory activations were observed during conscious retrieval, which was taken to suggest that conscious processing occurs relatively late in time. However, the large number of activations that occurred during the early epoch in the present study, particularly during item memory (Fig. 4B), suggests that conscious memory activations may not be restricted to the late epoch. As such, we next quantified the degree to which nonconscious memory activations occurred during the early epoch that then served as a baseline measure to estimate whether rapid conscious activations did in fact occur (note, this analysis was not conducted by Slotnick and Schacter [7]).

Fig. 5 shows the significant activations across time associated with nonconscious source memory (isolated by taking the difference in activity between old-left-miss-misses and old-right-miss-misses and vice versa) and nonconscious item memory (isolated by taking the difference in activity between old-miss-misses and new-correct rejections). During source memory within the early epoch, the number of conscious versus nonconscious activations in occipital ROIs and temporal ROIs did not significantly differ (0 versus 2 and 2 versus 3, respectively, both ps > 0.05; the number of conscious activations was not significantly greater than 0 in occipital or temporal ROIs, both ps > 0.05, Fisher’s exact test). Of importance, the total number of nonconscious activations during source memory (5) was significantly greater than 0 (p < 0.05, Fisher’s exact test), which confirmed that our paradigm produced detectable nonconscious memory effects. During item memory within the early epoch, a significantly greater number of conscious than nonconscious activations occurred in occipital ROIs.
Fig. 3. ERP activation timecourses. (A) Old-hit-hits, (B) Old-hit-misses, (C) Old-miss-misses, (D) New-correct rejections. Vertical dotted lines at 0 ms and 800 ms demarcate event onset and separate early and late epochs (key to the upper right).

(13 versus 0, p < 0.05; the number of conscious activations was significantly greater than 0, p < 0.05, Fisher’s exact test) and temporal ROIs (8 versus 0, p < 0.05; the number of conscious activations was significantly greater than 0, p < 0.05, Fisher’s exact test). These differential results were confirmed by a significant interaction between information type (source memory, item memory) and processing type (conscious, nonconscious) in occipital ROIs (p < 0.05) and temporal ROIs (p < 0.05). Thus, during item memory, but not source memory, visual sensory activations within the early epoch can be attributed to conscious processing.

To more precisely determine when item memory effects were initiated, we next compared the number of conscious versus nonconscious activations in successive 200 ms epochs. Within the 0–200 ms epoch, a significantly greater number of conscious than nonconscious activations occurred (5 versus 0, p < 0.05; the number conscious activations was significantly greater than 0, p < 0.05,

Fig. 4. Conscious memory ERP results. (A) Conscious source memory occipital ROI and temporal ROI ERP activations were identified by taking the difference in activity between old-hit-hits and old-hit-misses (significant activations are shown in green; vertical dotted lines at 0 ms and 800 ms demarcate event onset and separate early and late epochs). (B) Conscious item memory occipital ROI and temporal ROI ERP activations were identified by taking the difference in activity between old-hit-misses and old-miss-misses (significant activations are shown in red). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)
Fisher’s exact test, demonstrating that conscious item memory activity begins very early in time. Note that this occipital–temporal effect onset is earlier than the frontal FN400 effect, which is commonly attributed to conscious memory/familiarity [17, but see 36].

3. Experiment 2

Experiment 2 employed the same paradigm, unless otherwise noted, and had 3 aims. First, as the ERP results of Experiment 1 have limited spatial resolution, Experiment 2 was conducted to more accurately localize the regions associated with conscious processing during source memory and item memory. Second, although the Experiment 1 analysis assumed that old-miss-misses reflected nonconscious processing, such activity might have reflected conscious processing to some degree (i.e., below an “old” response threshold). This possibility was empirically evaluated in Experiment 2 based on an additional confidence rating response (“sure” or “unsure”) at retrieval. Specifically, if old-miss-misses did reflect some degree of conscious processing, old-miss-unsure responses should produce greater visual sensory activity than old-miss-miss-sure responses, as “unsure” responses can be assumed to reflect a greater degree of conscious memorial experience (i.e., the corresponding activation/memory strength should be closer to the “old” response criterion, see [6]). Third, in Experiment 1 we assumed that differences in accuracy during source memory and item memory (i.e., hits > misses) isolated conscious processing. However, accurate performance can also be driven by guess responses that are not associated with conscious memory (for a review, see [37]). We evaluated this possibility by comparing the magnitude of visual sensory activity associated with old-hit-sure responses, which can be assumed to reflect conscious memory, and old-hit-unsure responses, which can be assumed to reflect guesses.

3.1. Materials and methods

3.1.1. fMRI participants

Twelve different right-handed participants (7 females, aged 18.4–25.9) with normal or corrected-to-normal vision completed the experiment. The protocol was approved by the Massachusetts General Hospital Institutional Review Board, and informed consent was obtained from each participant.

3.1.2. fMRI stimuli and task

Unless otherwise stated, the paradigm was identical to Experiment 1. During the retrieval phase of each run, each shape was presented for 2.5 s followed by a 1.5–9.5 s fixation period. Participants also made a “sure” or “unsure” confidence rating response following each of the responses. Participants responded via a button box in their left hand.

3.1.3. fMRI acquisition and analysis

A 3T Siemens Allegra scanner was used for data acquisition. Functional images were acquired using an echo-planar imaging sequence (TR = 2 s, TE = 30 ms, acquisition matrix = 64 x 64, 30 slices, 4.5 mm resolution). Anatomical images were acquired using a magnetization rapidly acquired gradient echo sequence (1.33 mm x 1 mm x 1 mm resolution).

A random-effect general linear model analysis was conducted using BrainVoyager QX (Brain Innovation B.V., Maastricht, The Netherlands). Functional data preprocessing included slice-time correction, motion correction, and temporal filtering by removal of linear components and frequency components below 3 cycles per run. Runs with greater than 3 mm of motion in the x, y, or z dimension were excluded. All images were transformed into Talairach space. For each participant, events were modeled based on the corresponding stimulus onsets and behavioral response duration or, if no response was made, stimulus offset. Event types included encoding of shapes and locations, all retrieval event types described in Experiment 1, and new false alarms, separated as a function of confidence rating, failures to respond, and a constant.

For all contrasts, an individual voxel threshold of p < 0.001 was enforced, corrected for multiple comparisons to p < 0.05 by requiring a cluster extent threshold of at least 7 resampled voxels. This extent was computed using a Monte Carlo simulation with 10,000 iterations with an estimated spatial correlation of 4.5 mm (across all contrasts, the minimum spatial correlation was selected to avoid inflation by real/noise activations). Note that the contrasts used to isolate nonconscious processing were different for Experiment 1 (ERP) and Experiment 2 (fMRI) given that the fMRI data was not amenable to the more complex temporal analysis conducted with ERPs.

To ensure memory related activity reflected visual sensory recapitulation and to focus on the regions corresponding to occipital–temporal ERP activity in Experiment 1, only occipital–temporal activations that were active during both encoding and retrieval were considered (encoding activity was identified by contrasting encoding-left > encoding-right and vice versa; see, [21]). Group activity was projected onto a cortical surface of a representative participant (for details, see [38]). Event-related fMRI timecourses were extracted from all voxels within a given activation from ~2 to 14 s after stimulus onset (and baseline corrected from 0 to 2 s before stimulus onset). As there is a high degree of temporal autocorrelation in fMRI activation timecourses, analysis was restricted to the timepoint of maximum average activity across the relevant event types to ensure statistical independence.

3.2. Results

3.2.1. Behavioral fMRI results

Source memory accuracy was 70.0 ± 2.0% and item memory accuracy was 67.2 ± 1.6% (mean ± standard error). Source memory reaction times were 2324 ± 153 and item memory reaction times were 2502 ± 143 ms.
3.2. fMRI results

Source memory (isolated by the contrast old-hit-hits > old-hit-misses) produced activity in occipital–temporal regions BA17, BA18, BA19, and BA37 (Fig. 6A). Item memory (isolated by the contrast old-hit-misses > old-miss-misses) also produced activity in BA17, BA18, and BA19 (Fig. 6B). It is notable that each item memory activation partially overlapped with a source memory activation. These fMRI findings are consistent with the occipital–temporal ERP activations observed in Experiment 1.

To assess whether old-miss-misses reflected nonconscious processing, we conducted a whole-brain general linear model analysis. The contrast old-miss-miss-unsure > old-miss-miss-sure did not produce any visual sensory activity, even after relaxing the threshold to \( p < 0.01 \). These results are consistent with our previous assumption (in Experiment 1) that old-miss-misses reflect nonconscious processing. However, such a null finding does not rule out the possibility that there might be sub-threshold old-miss-miss-unsure versus old-miss-miss-sure activity. As such, we conducted an ROI analysis. Nonconscious memory activity was first isolated by the contrast old-miss-misses > new-correct rejections (\( p < 0.01 \), uncorrected), which revealed two visual area activations in BA18 and BA19 (Fig. 7A). Then, activity associated with old-miss-miss-unsure responses and old-miss-miss-sure responses was extracted (Fig. 7B). In both regions, the magnitude of activity associated with old-miss-miss-sure responses was greater than old-miss-miss-unsure responses. Moreover, in the BA19 activation a post-hoc significance test revealed that the magnitude of activity associated with old-miss-miss-sure responses was significantly greater than that associated with old-miss-miss-unsure responses (\( t(11) = 2.27, p < 0.05 \)). The pattern of results in both regions is in direct opposition to the possibility that old-miss-misses reflect some degree of conscious processing and, of primary importance, indicates that old-miss-misses in Experiment 1 did reflect nonconscious processing.

To assess whether our conscious memory effects in Experiment 1 might have been due to guessing, we compared activity associated with “sure” and “unsure” responses during accurate source memory. For source memory, the contrast old-hit-miss-sure > old-hit-unsure produced activity in occipital–temporal regions BA17, BA18, BA19, and BA37. For item memory, the contrast old-hit-miss-sure > old-hit-unsure produced activity in occipital–temporal regions BA18, BA19, and BA37 (at \( p < 0.001 \), uncorrected). These results indicate that our source memory and item memory effects reflected conscious processing.

4. Discussion

In the present study, Experiment 1 showed that sensory ERP activity associated with conscious processing had a late (800–1600 ms) onset during source memory but had an early (0–800 ms) onset during item memory. That item memory produced sensory activity more rapidly than source memory could be taken to support the dual-process model of memory, which stipulates that non-detailed familiarity is a faster process than detailed recollection (for a review, see [39]). Such an interpretation rests on the assumption that source memory and item memory are largely mediated by the processes of recollection and familiarity, respectively. However, this assumption is tenuous given that item memory often involves detailed retrieval [cf., [40]], which is illustrated by the substantial rate of “remember” responses commonly observed in remember-know item memory studies. Moreover, empirical evidence directly opposes the conjecture that familiarity-based responses are faster than recollection-based responses. Specifically, in the present study source memory reaction times were faster than item memory reaction times, which replicate previous findings [41–43]. Furthermore, “remember” response times have been shown to be faster than familiarity-based response times [44–46]. It could be argued that familiarity-based responses might take longer to reach the response criterion (e.g., due to relatively less detailed retrieval); however, this possibility only underscores that the sub-processes associated with recollection and familiarity are uncertain. Thus, for both theoretical and empirical reasons, the present results should not be taken to support the dual-process model of memory.

A recent ERP study has provided convergent evidence for an early onset of conscious activity during item memory [47]. Kaleidoscope images were presented at the center of a screen and participants encoded these shapes under either full attention or divided attention. During a recognition test, participants classified old and new images as “old” or “new”, and for “old” items, made a “remember”, “know”, or “guess” response. During the 180–220 ms epoch, the magnitude of visual sensory activity
associated with “remember” responses was greater than that associated with “know” responses.

The present fMRI results are relevant to a hypothesis that there is a functional-anatomic boundary separating nonconscious memory processing in earlier visual regions BA17 and BA18 from conscious memory processing in later visual regions BA19 and BA37 [6,32; see also, 48]. In Experiment 2, source memory and item memory activity was observed in BA19 (and BA37 during source memory), but also occurred in BA17 and BA18. Similarly, in a recent study, activity associated with conscious processing was observed in earlier visual regions (BA17/18) and later visual regions (BA19/37) during retrieval of spatial information and during specific retrieval orientation [35]. That is, the present and recent results are inconsistent with the hypothesis that there is a fixed anatomic boundary separating nonconscious and conscious processing in visual sensory regions, and rather suggest that BA17 and BA18 can mediate conscious processing.

It is reasonable to assume that the visual regions localized with fMRI associated with conscious source memory and item memory are those that contributed to the corresponding visual sensory ERP effects (cf., [21]). Still, there were differences across the current ERP and fMRI experiments that are worth noting. Specifically, item memory effects were more robust for the ERP experiment than the fMRI experiment and spatial memory effects were more robust for the fMRI experiment than the ERP experiment. Although these differences are notable, the relationship between fMRI activity and ERP activity is inherently uncertain. For instance, more ventral temporal cortical activity might produce a weak ERP response in occipital–temporal ROIs with a strong fMRI response, while more posterior occipital cortical activity might produce a strong ERP response in occipital–temporal ROIs with a weak fMRI response. Moreover, the electromagnetic fields produced by cortical activity on opposite faces of a sulcus can cancel out, producing little or no ERP response with a robust fMRI response. Of most importance, the cognitive events of interest (i.e., source memory and item memory) were conserved across the ERP experiment and the fMRI experiment, and the overall pattern of ERP activity and fMRI activity were consistent. Therefore, although there were differences in the magnitude of activity across experiments, such differences do not impact the conclusions of the present investigation.

Of relevance to the primary aim of the present study, previous ERP findings have suggested a fixed temporal boundary separating conscious and nonconscious processing during conscious retrieval [7], which predicts a late onset for sensory activity associated with both source memory and item memory. By contrast, Experiment 1 revealed differential conscious activity onsets during source memory (which onset after 800 ms) and item memory (which onset within 200 ms). As these activations were relatively dispersed in time, they likely reflect multiple visual sensory processes. It will be important for future research to determine the nature of these processes (e.g., detail how the memory representation is constructed over time; see, [21]). It is perhaps not surprising that conscious processing can occur very rapidly, which is consistent with rapid recurrent neural processing models [49]. We note,
however, that the current results cannot speak to whether the ERP effects associated with conscious item and source memory reflect feedback or feed-forward processing. It will be important for future research to disambiguate these possibilities. Based on the present findings, one possibility that can be envisaged is that the initial feed-forward sensory signal is devoid of source information, as exemplified by our early 200 ms item memory effect. However, later in time, through either feedback or additional feed-forward processing, source information is accrued.

Considering the present and previous findings, the onset of conscious processing and the anatomic regions mediating conscious processing do not appear to be fixed, but rather seem to depend on other factors such as the type of information retrieved. Future work will be needed to assess the degree to which conscious and unconscious processing can be temporally and anatomically dissociated by identifying and testing other memorial factors (such as retrieval orientation, the quantity of details retrieved, and the subjective experience associated with retrieval).

References

[40] Slotnick SD. Does the hippocampus mediate objective binding or subjective remembering. Neuroimage 2010;49:1769–76.