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Conscious and nonconscious memory effects are temporally dissociable

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Abstract

Intentional (explicit) retrieval can reactivate sensory cortex, which is widely assumed to reflect conscious processing. In the present study, we used an explicit visual memory event-related potential paradigm to investigate whether such retrieval related sensory activity could be separated into conscious and nonconscious components. During study, abstract shapes were presented in the left or right visual field. During test, old and new shapes were presented centrally and participants classified each shape as “old-left”, “old-right”, or “new”. Conscious activity was isolated by comparing accurate memory for shape and location (old-hits) with forgotten shapes (old-misses), and nonconscious activity was isolated by comparing old-left-misses with old-right-misses and vice versa. Conscious visual sensory activity had a late temporal onset (after 800 ms) while nonconscious visual sensory activity had an early temporal onset (before 800 ms). These results suggest explicit memory related sensory activity reflects both conscious and nonconscious processes that are temporally dissociable.

Keywords

Retrieval; Priming; ERPs

Memory for objects, sounds, and smells can reactivate visual, auditory, and olfactory sensory cortex, respectively (Slotnick, 2004). Within the visual domain, memory for items presented in the left or right visual field can reactivate right and left hemisphere (contralateral) retinotopic visual regions (Slotnick & Schacter, 2006), which can occur very rapidly (within 100–250 ms after stimulus onset; Slotnick, 2009). While explicit memory paradigms, such as those just described, are designed to tap into conscious processing by requiring participants to retrieve previously studied information, nonconscious neural processes invariably operate as well (Jacoby, 1991; Rugg, Mark, Walla, Schloerscheidt, Birch, & Allan, 1998; Paller, Voss, & Boehm, 2007). For instance, in visual explicit memory paradigms, the same items are presented at study and test, which can produce repetition priming, a form of nonconscious memory that modulates activity in occipital-temporal cortex (Wiggs & Martin, 1998; Slotnick & Schacter, 2006). While conscious versus nonconscious memory processes have been explored to some degree (Rugg et al., 1998; Slotnick & Schacter, 2004), the temporal dynamics of explicit memory related sensory effects are unknown.

The present event-related potential (ERP) study used an explicit visual memory paradigm known to produce robust retinotopic effects in occipital-temporal regions (Slotnick & Schacter,

2006; Slotnick, 2009). We hypothesized that a) nonconscious visual memory effects would have an early temporal onset (0–800 ms after stimulus onset), based on previous object priming effects (Henson, Rylands, Ross, Vuilleumier, & Rugg, 2004; Eddy & Holcomb, in press), and b) conscious visual memory effects would have a late temporal onset (800–1600 ms), corresponding to previous memory effects associated with monitoring the contents of retrieval (Schacter, Curran, Galluccio, Milberg, & Bates, 1996; Curran, Schacter, Johnson, & Spinks, 2001; Hayama, Johnson, & Rugg, 2008). During study, abstract shapes were presented in the left or right visual field (Figure 1A). During test, previously presented (old) and new shapes were presented centrally and participants classified each shape as “old-left”, “old-right”, or “new” (Figure 1B). Conscious effects were isolated by comparing old-hit versus old-miss activity (which tracks subjective experience; Slotnick & Schacter, 2004; Wheeler & Buckner, 2004), while nonconscious effects were isolated by comparing old-miss versus baseline activity (which is independent of subjective experience; Rugg et al., 1998; Slotnick & Schacter, 2004, 2006).

Method

Participants

Twelve undergraduates (five females) with normal or corrected-to-normal vision and complete datasets were included in the analysis. The experimental protocol was approved by the Boston College Institutional Review Board and informed consent was obtained from each participant before the experiment commenced.

Behavioral Task and Analysis

There were six abstract shape study-test phases. Each shape was pseudo-randomly constructed from four Bezier curves placed end-to-end on adjacent sides of a 5.5° square and filled with colored oriented lines (Slotnick & Schacter, 2004). During each study phase (Figure 1A), 32 shapes were presented in the left or right visual field 3° from central fixation. Shapes were displayed for 2.5 s followed by a 0.5 s fixation period. During each test phase (Figure 1B), 32 old and 16 new shapes were shown centrally for 2.5 s followed by a 4.5 s fixation period and participants classified each shape as “old-left”, “old-right”, or “new”. Participants were encouraged to respond as accurately as possible (in an effort to maximize accuracy, response time was not stressed as important). Participants were instructed to always maintain fixation. No more than three shapes of a given event type were sequentially presented at study or test, and shapes were counterbalanced using a Latin Square design according to event type at test (old-left, old-right, and new). Analysis was restricted to old-hits (accurate retrieval of shape and location; e.g., responding “old-left” to an item previously on the left), old-misses (completely forgotten items; e.g., responding “new” to an item previously on the left), and correctly rejected new items. Item memory accuracy was the percentage of correctly detected old and new items weighted by the probability of each event type (Macmillan & Creelman, 2005) irrespective of spatial memory accuracy. Spatial memory accuracy was the percentage of correct spatial location identification, contingent on correct old item detection.

Acquisition and Analysis

Data were acquired in a shielded chamber (Global Partners in Shielding, Inc., Passaic, NJ) with a 128-channel NeuroScan system (Quik-Cap with sintered silver/silver chloride electrodes, SynAmps² amplifiers, and SCAN acquisition software; Compumedics USA, Charlotte, NC). The sampling rate was 1 ms and impedances were maintained below 15 kΩ. Preprocessing was conducted using BESA (MEGIS Software GmbH, Gräfelfing, Germany). On a run-by-run basis, blink correction consisted of removing the minimum number of principal components that explained at least 85% of the variance. Trials and electrodes with amplitudes or gradients greater than the default threshold values were excluded from the analysis. A high-pass

(forward) filter was used with a 0.5 Hz cutoff at 6 dB/octave. To minimize temporal shifts in the waveforms, no low-pass filter was used. Event-related averages were computed from -500 to 2000 ms after stimulus onset from a weighted average across runs for each participant.

Regions-of-interest (ROIs; Figure 2C) consisted of electrodes over left and right occipital-temporal scalp previously associated with retinotopic perception and attention effects (Clark, Fan, & Hillyard, 1995; Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002) that evinced robust retinotopic activity during study (Slotnick, 2009). Electrodes were further split into occipital and temporal ROIs as previous studies have reported robust retinotopic memory effects at temporal sites (Gratton, Corballis, & Jain, 1997; Fabiani, Stadler, & Wessels, 2000). The 10-5 electrode naming convention was used (Oostenveld & Praamstra, 2001) where the left hemisphere occipital ROI included electrodes I1, O1, PO1, P1, PO9, PO7, PO5, P3, the left hemisphere temporal ROI included electrodes P9, P7, P5, CPP3, TPP9, TPP7, CPP5, CP5, TTP7h, TP7, and the right hemisphere ROIs consisted of analogous even numbered electrodes.

Hemispheric laterality was assessed from ROI activity at each time point ± 6 ms (based on the predicted 13 ms duration of retrieval related retinotopic effects; Slotnick, 2009). For a given ROI and time point, activity was deemed lateralized if it was significantly greater than zero and significantly greater than activity in occipital and temporal ROIs in the opposite hemisphere. Given that laterality was based on three one-tailed t-tests, the statistical threshold was adjusted (Fisher, 1973) to yield a joint p-value of 0.05. The number of lateralized activations (e.g., contralateral versus ipsilateral) were compared using a binomial test ($p = q = 0.5$). To correct for multiple comparisons, false discovery rate (Benjamini & Hochberg, 1995; Genovese, Lazar, & Nichols, 2002) was computed from the number of false positives, assumed equivalent to ipsilateral activations, divided by the number of true positives, assumed equivalent to contralateral activations, plus the number of false positives (Slotnick, 2009).

Results

Item and spatial memory accuracy were $63.0 \pm 1.8\%$ and $66.5 \pm 2.3\%$, respectively (mean \pm s.e.m.; chance was 50%). Reaction times for old-hits, old-misses, and new-correct rejections were 1827 ± 88 ms, 1912 ± 109 ms, and 1854 ± 100 ms, respectively. We first compared ERP activity associated with accurate memory for old items in the left visual field (old-left-hit) versus right visual field (old-right-hit) and vice versa. These comparisons subtracted out non-retinotopic activity and thus can be assumed to reflect relatively isolated retinotopic memory effects (Slotnick, 2009). Figure 2A illustrates the old-left-hit - old-right hit and old-right-hit - old-left-hit ERP activation timecourses in occipital and temporal ROIs (pre-stimulus activity can be attributed to anticipation effects; Sylvester, Shulman, Jack, & Corbetta, 2007; McMains, Fehd, Emmanouil, & Kastner, 2007). Mirroring perceptual retinotopic effects, memory for stimuli in the left visual field (Figure 2A, top) produced significant lateralized activations that were almost completely restricted to right occipital and temporal ROIs, and memory for stimuli in the right visual field (Figure 2A, bottom) produced significant lateralized activations that were completely restricted to the left occipital and temporal ROIs. Retinotopic activity occurred across the entire time period, as manifested by a greater number of contralateral than ipsilateral activations. To more clearly illustrate retinotopic effects, Figure 2B shows the same significant lateralized activations in occipital and temporal ROIs separated by hemisphere (i.e., Figure 2B, top, contralateral activations are to the right and ipsilateral activations are to the left; Figure 2B, bottom, contralateral activations are to the left and ipsilateral activations are to the right). Figure 2C illustrates retinotopic voltage topographies that occurred early in time. The number of lateralized activations collapsed over region and hemisphere produced a significant retinotopic effect (28 contralateral, 1 ipsilateral, $p < 0.001$). There was no significant difference in retinotopic effect by region (occipital versus temporal, $p > 0.20$) or time (early

versus late, $p = 0.13$). Critically, these retinotopic effects were corrected for multiple comparisons (false discovery rate $p < 0.05$). As mentioned above, the preceding results can be assumed to reflect both conscious and nonconscious activity.

Figure 3A shows lateralized activations associated with conscious retrieval corresponding to accurate (i.e., old-hit) versus inaccurate (i.e., old-miss) memory for old items in the left visual field (old-left-hit – old-left-miss) and right visual field (old-right-hit – old-right-miss). The number of lateralized activations collapsed over region and hemisphere produced a significant retinotopic effect (21 contralateral, 7 ipsilateral, $p < 0.01$). There was a significant difference in retinotopic effect by region ($p < 0.001$), with no significant retinotopic effect in occipital ROIs (4 contralateral, 3 ipsilateral, $p > 0.20$) but a significant retinotopic effect in temporal ROIs (17 contralateral, 4 ipsilateral, $p < 0.01$). There was also a significant difference in retinotopic effect by time ($p < 0.001$), with no significant early retinotopic effect (0–800 ms, 5 contralateral, 3 ipsilateral, $p > 0.20$) but a significant late retinotopic effect (800–1600 ms, 16 contralateral, 4 ipsilateral, $P < 0.01$). Post hoc analysis (in 200 ms increments) revealed the conscious temporal retinotopic effects reached significance between 1200–1400 ms after stimulus onset ($p < 0.05$).

Figure 3B shows the lateralized activations associated with nonconscious retrieval corresponding to forgotten old items in the left versus right visual field (old-left-miss – old-right-miss) and right versus left visual field (old-right-miss – old-left-miss; which subtracted out common non-retinotopic activity; Slotnick, 2009). The number of lateralized activations collapsed over region and hemisphere produced a significant retinotopic effect (11 contralateral, 3 ipsilateral, $p < 0.05$). There was no significant difference in retinotopic effect by region or time (both $ps > 0.20$). Critically, there was a conscious (Figure 3A) by nonconscious (Figure 3B) retinotopic effect by region ($p < 0.001$) and time ($p < 0.001$).

Figure 4A shows lateralized activations associated with conscious and nonconscious retrieval corresponding to accurate memory for old items in the left visual field versus new-correct rejections (old-left-hit – new-correct rejection) and accurate memory for old items in the right visual field versus new-correct rejections (old-right-hit – new correct rejection). The number of lateralized activations collapsed over region and hemisphere produced a significant retinotopic effect (27 contralateral, 10 ipsilateral, $p < 0.01$). There was no significant difference in retinotopic effect by region ($p > 0.20$) or time ($p = 0.13$).

Figure 4B shows the lateralized activations associated with nonconscious retrieval corresponding to old forgotten items in the left visual field versus new-correct rejections (old-left-miss – new-correct rejection) and right visual field versus new-correct rejections (old-right-miss – new-correct rejection). The number of lateralized activations collapsed over region and hemisphere did not produce a significant retinotopic effect (13 contralateral, 9 ipsilateral, $p = 0.12$), which was not surprising given that this comparison did not subtract out non-retinotopic activity (Slotnick, 2009), and there was no significant difference in retinotopic effect by region or time (both $ps > 0.20$). Of importance, there was a conscious (Figure 3A) by nonconscious (Figure 4B) retinotopic effect by region ($p < 0.001$) and time ($p < 0.001$).

Discussion

The present results suggest that nonconscious visual sensory memory effects occur relatively early in time (0–800 ms), while conscious visual sensory memory effects occur relatively late in time (800–1600 ms). These occipital-temporal memory effects complement previous conscious versus nonconscious memory results in frontal and parietal regions (Paller et al., 2007; Rugg & Curran, 2007). Of particular relevance, conscious retrieval of specific details has been associated with a 400–800 ms parietal effect (Rugg & Curran, 2007). The relative

timing of activity suggests that conscious memory related processing begins in the parietal cortex and then feeds back to occipital-temporal regions later in the retrieval process. A more detailed picture emerges when also considering the 0–800 ms visual sensory priming effects (Henson, Rylands, Ross, Vuillemeir, & Rugg, 2004; Eddy & Holcomb, in press) and the 800–1600 ms retrieval monitoring effects discussed previously (Schacter, Curran, Galluccio, Milberg, & Bates, 1996; Curran, Schacter, Johnson, & Spinks, 2001; Hayama, Johnson, & Rugg, 2008). Specifically, the present and previous results suggest that early visual sensory memory effects are nonconscious, reflecting priming or an automatic pattern completion process, while later visual sensory memory effects are conscious, corresponding to frontal-parietal monitoring or attentional amplification of the occipital-temporal contents of retrieval.

It is important to consider whether old-misses might have reflected some degree of conscious processing. For instance, a significant proportion of old-misses might have been just sub-threshold of the “old” response criterion. We addressed this issue in a previous functional magnetic resonance imaging that used the identical protocol except participants also made a “sure”-“unsure” judgment following each response at retrieval (Slotnick & Schacter, 2004). If a proportion of old-misses did reflect conscious processing, activity associated with “unsure” responses should be relatively greater in magnitude (as this activity can be assumed to be close to the “old” response criterion), while activity associated with “sure” responses should be relatively smaller in magnitude (as this activity can be assumed to be far from the “old” response criterion). In fact, the magnitude of old-miss-sure and old-miss-unsure visual sensory activity did not significantly differ, which suggests that all old-misses (regardless of confidence) reflect nonconscious activity. The present results provide additional evidence that old-misses reflected nonconscious retrieval. If old-misses reflected conscious processing, this analysis would have yielded a similar pattern of conscious and nonconscious retrieval results. However, conscious and nonconscious effects were qualitatively different, indicating old-misses reflected nonconscious processing.

The present retinotopic memory effects associated with conscious retrieval appeared to be greatest in right hemisphere ROIs (Figure 3A), as indicated by a significant difference in retinotopic effect by hemisphere ($p < 0.05$), with no significant left hemisphere retinotopic effect (7 contralateral, 3 ipsilateral, $p = 0.12$) but a significant right hemisphere retinotopic effect (14 contralateral, 4 ipsilateral, $P < 0.05$). By comparison, for nonconscious retrieval (Figure 3B) there was no significant difference in retinotopic effect by hemisphere ($p > 0.20$). The hemispheric differences observed may have stemmed from preferential categorical visual spatial processing in the left hemisphere and preferential coordinate visual spatial processing in the right hemisphere (Kosslyn, 1987; Kosslyn, Thompson, Gitelman, & Alpert, 1998; Slotnick, Moo, Tesoro, & Hart, 2001). This model of hemispheric visual spatial processing has been supported by evidence indicating that the right hemisphere is preferentially associated with memory for specific details (Koutstaal, Wagner, Rotte, Maril, Buckner, & Schacter, 2001; Simons, Koutstaal, Prince, Wagner, & Schacter, 2003; Garoff, Slotnick, & Schacter, 2005; Slotnick & Moo, 2006). In the present study, conscious retrieval of spatial location presumably involved visualization of the shape relative to fixation, arguably a coordinate based process, and thus the greatest retinotopic effects might be expected to occur in the right hemisphere.

The current results have important implications for interpreting explicit memory studies, in that they help both to reveal and characterize nonconscious influences that can impact performance on nominally explicit tasks. Moreover, the nonconscious-conscious temporal dissociation observed here may extend to other cognitive domains, such as attention or language, that employ explicit tasks where sensory modulation has commonly been assumed to reflect conscious processing.

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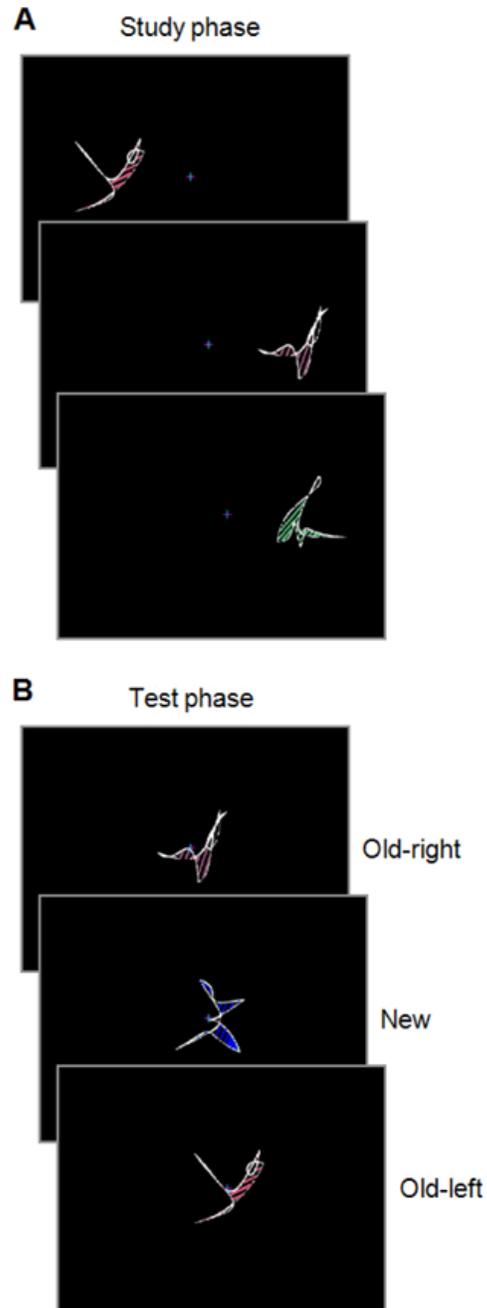


Figure 1. (A) Study phase. (B) Test phase (accurate labels shown to the right).

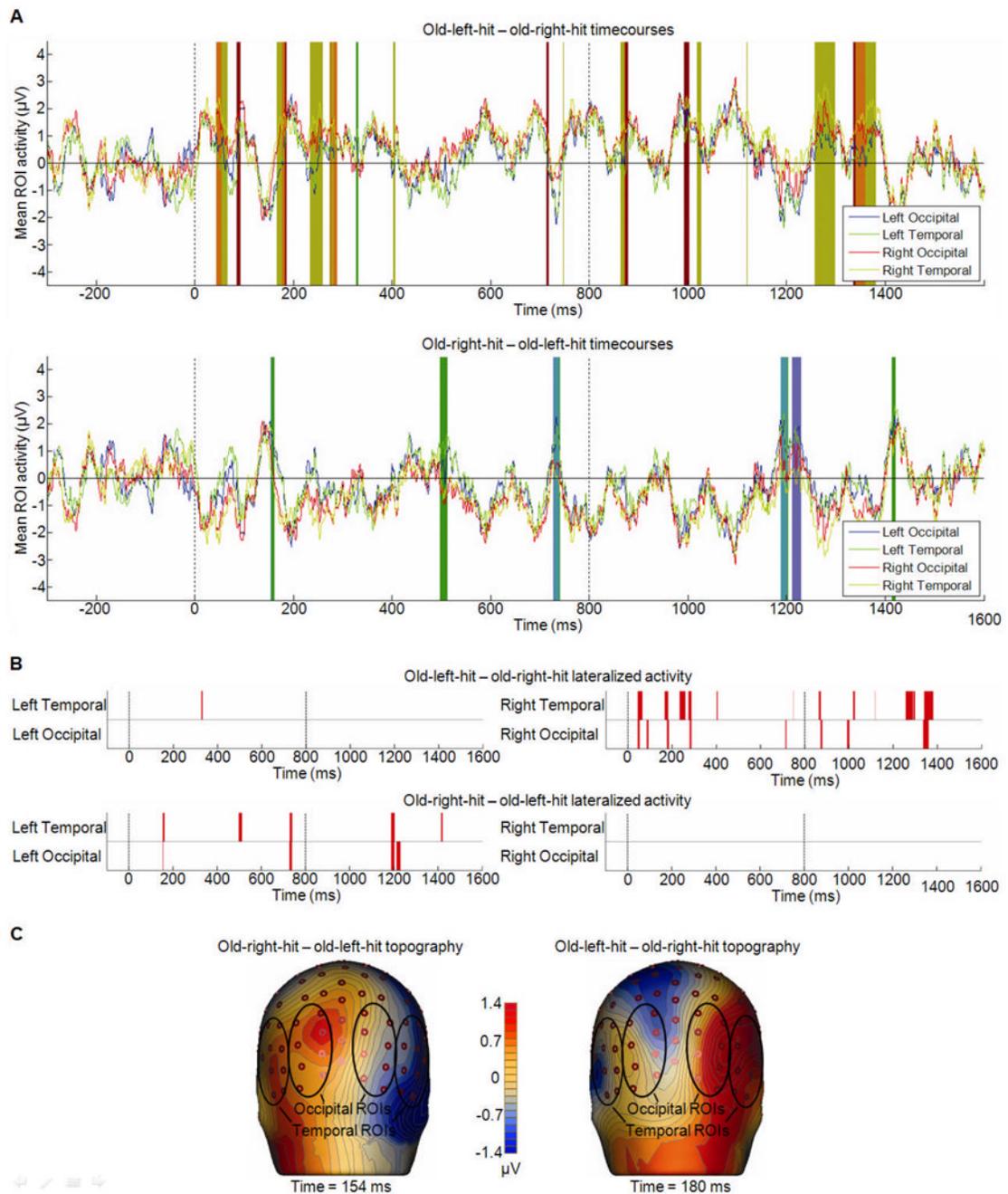


Figure 2. (A) Old-left-hit – old-right-hit (top panel) and old-right-hit – old-left-hit (bottom panel) activation timecourses in left occipital, left temporal, right occipital, and right temporal regions-of-interest (ROIs; color key to right). Significant lateralized activity in right occipital and right temporal ROIs is shown by red and yellow (overlap in orange) vertical bars, respectively, while significant lateralized activity in left occipital and left temporal ROIs is shown in blue and green (overlap in cyan) vertical bars, respectively. (B) Old-left-hit – old-right-hit (top panels) and old-right-hit – old-left-hit (bottom panels) lateralized activity in occipital and temporal regions-of-interest (ROIs). (C) Voltage topographies at early time points

illustrating retinotopic/contralateral activity (posterior view, color scale at center; ovals demarcate ROIs).

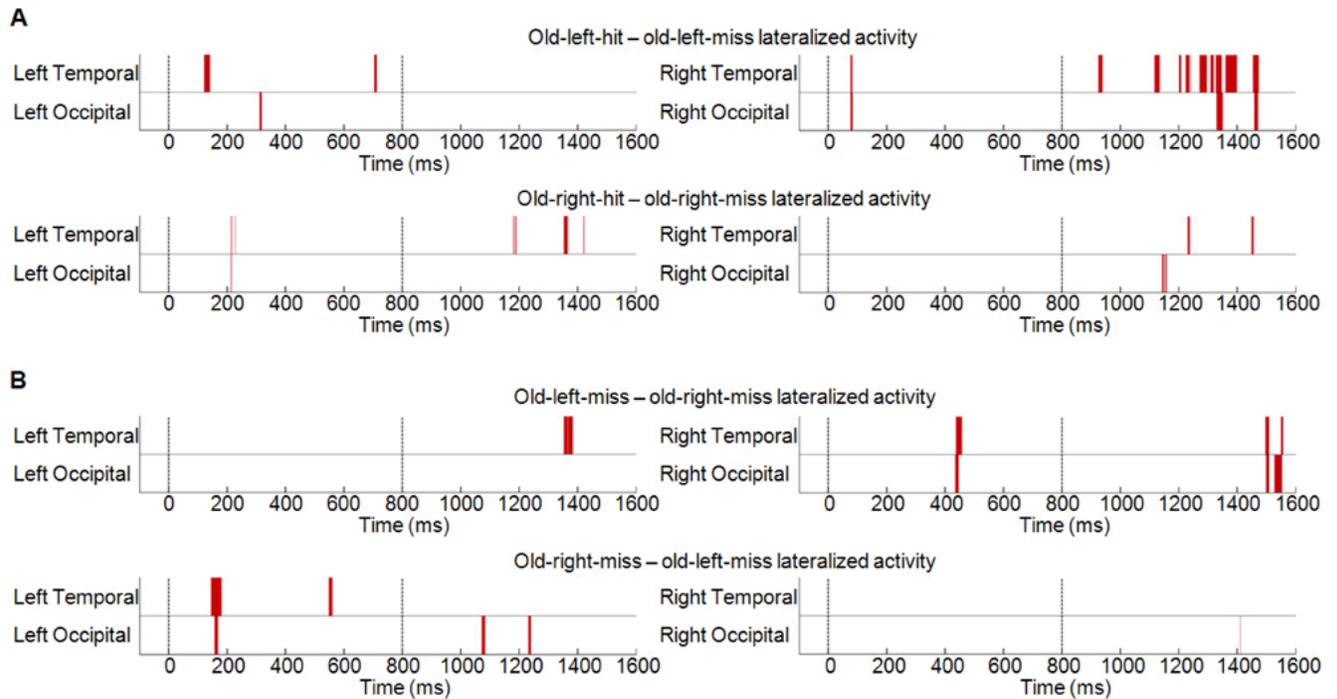


Figure 3. (A) Old-left-hit – old-left-miss (top panels) and old-right-hit – old-right-miss (bottom panels) lateralized conscious activity. (B) Old-left-miss – old-right-miss (top panels) and old-right-miss – old-left-miss (bottom panels) lateralized nonconscious activity.

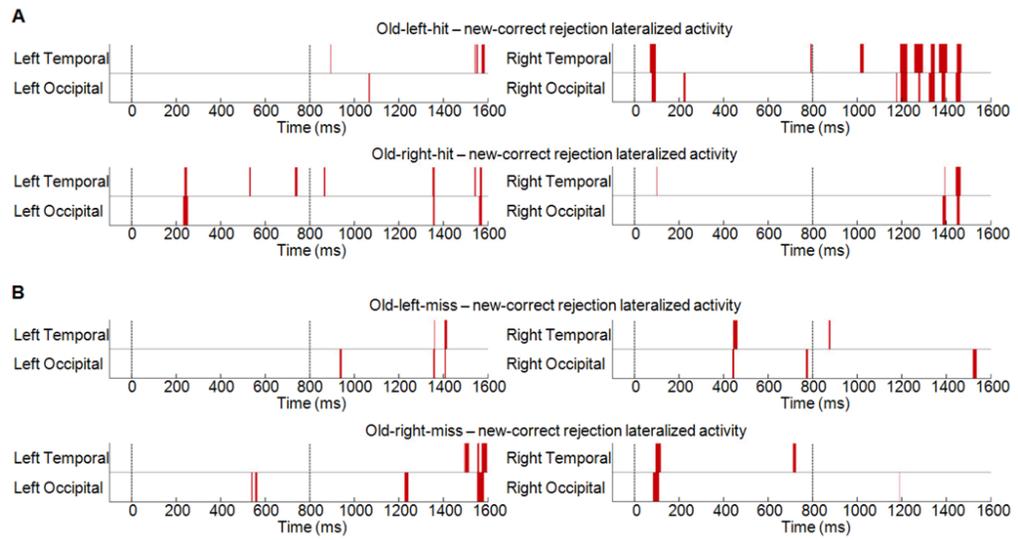


Figure 4. (A) Old-left-hit – new-correct rejection (top panels) and old-right-hit – new-correct rejection (bottom panels) lateralized activity in occipital and temporal ROIs. (B) Old-left-miss – new-correct rejection (top panels) and old-right-miss – new-correct rejection (bottom panels) lateralized nonconscious activity.