



Finding meaning in novel geometric shapes influences electrophysiological correlates of repetition and dissociates perceptual and conceptual priming

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ABSTRACT

Repeatedly viewing an object can engender fluency-related implicit memory for perceptual and conceptual attributes, as indexed in tests of perceptual and conceptual priming, respectively. Stimuli with minimal pre-experimental meaning allow direct comparisons between these two types of priming and explorations of whether corresponding neural mechanisms differ. We therefore examined electrophysiological correlates of perceptual and conceptual priming for minimalist geometric shapes (squiggles). Response time measures of conceptual priming were evident for squiggles rated by individual subjects as most meaningful, but not for those rated least meaningful. Conceptual-priming magnitude was proportional across individuals to the amplitude of FN400 brain potentials, but only for meaningful squiggles. Perceptual priming was evident for squiggles irrespective of meaningfulness, and perceptual-priming magnitude was proportional to the amplitude of frontal P170 potentials. These findings therefore show that a single exposure to a novel stimulus can lead to neural processing accompanying conceptual priming that is distinct from that accompanying perceptual priming (FN400 potentials vs. P170 potentials, respectively). Overall, this evidence is also relevant to the current debate over the neural correlates of familiarity-based recognition, and runs counter to the prominent supposition that familiarity can be generically indexed by FN400 potentials.

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Introduction

A stimulus is perceived. Later, it is perceived again. What differs between these two events? One way to address this question is to identify changes in how subjects and neurons respond to stimuli that repeat during memory tests. *Priming* refers to a change in the speed, accuracy, or other aspect of a behavioral response to a stimulus based on prior exposure to the same stimulus or to a related stimulus (Schacter, 1987; Richardson-Klavehn and Bjork, 1988; Roediger, 1990). Priming tests are implicit measures of memory in that subjects are not required to indicate overtly that stimuli are repeating, as they would in a recall or recognition test, though they may incidentally realize this (Richardson-Klavehn and Bjork, 1988).

Perceptual priming and conceptual priming are behaviorally distinct expressions of priming defined based on the nature of the information processing steps responsible for the repetition effects. Priming for repeated, physical features of stimuli is considered to underlie perceptual priming, whereas priming for stimulus meaning, independent from physical properties, underlies conceptual priming. Stimuli such as words and nameable pictures can engender both types

of priming: perceptual priming for the visual word form and conceptual priming for word meaning, for instance. Changing the physical form of a stimulus from one presentation to the next (e.g., a word first read, then heard) should preferentially reduce perceptual priming, and manipulations such as format-switching are frequently used to dissociate behavioral and neural correlates of perceptual and conceptual priming (Henson, 2003; Schacter et al., 2004).

Perceptual and conceptual priming have been associated with changes in neural processing at distinct loci of the ventral visual-processing stream (Henson, 2003; Schacter et al., 2007), with conceptual priming involving neural repetition effects that are more anterior than those for perceptual priming. However, both forms of priming have been studied primarily using categories of well-learned and conceptually rich stimuli, such as words and nameable pictures. Indeed, some investigators have failed to find neural repetition effects for stimuli without pre-experimental familiarity (Rugg and Doyle, 1994; Crites et al., 2000; Schendan and Maher, 2009). Here we sought to determine the extent to which perceptual and conceptual priming can occur for novel geometric shapes and whether these different memory expressions occur in conjunction with characteristic neural repetition effects.

We measured event-related brain potential (ERP) correlates of perceptual and conceptual priming to obtain millisecond-by-millisecond observations of the neural activity associated with each memory

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expression. This level of temporal resolution is important because perceptual processing is thought to precede conceptual processing; perceptual processing steps (as in contour detection, figure-ground segregation, and perceptual grouping) are considered prerequisites for object categorization and retrieval of associated conceptual information (Biederman, 1987; Schendan and Kutas, 2002), although pre-experimental knowledge about meaningful stimuli can also influence perceptual processing (e.g., Peterson and Enns, 2005). The notion that perceptual and conceptual priming are distinct neural processes that potentially operate on distinct memory representations is generally consistent with theories of multiple memory systems (Tulving, 1972; Tulving and Schacter, 1990; Squire and Zola-Morgan, 1991), whereas some grounded-cognition theories of knowledge (Barsalou, 2008) would allow for similar neural operations underlying perceptual and conceptual processing.

We measured perceptual and conceptual processing using two implicit memory tests. Perceptual priming was measured during a perceptual task, loop detection, and conceptual priming was measured during a conceptual task involving meaning ratings. For both tasks, the study phase involved a meaning rating task. This design provided behavioral correlates of perceptual and conceptual priming that allowed their ERP correlates to be compared. Furthermore, we used minimalist geometric shapes, which we refer to as “squiggles,” to gain leverage on dissociating perceptual and conceptual processing, as described below.

Based on previous results obtained using the same stimulus set (Voss and Paller, 2007), we predicted that conceptual priming would occur selectively for the shapes given the highest meaningfulness ratings, and that conceptual priming of meaningful shapes would occur in conjunction with repetition effects on FN400 brain potentials. The FN400 is a negative ERP deflection between approximately 300 and 500 ms that is largest at frontocentral scalp locations and is reduced (i.e., more positive) for repeated relative to new items. In our previous study, we found evidence that conceptual priming occurred only for the most meaningful squiggles, although ERPs were recorded during a recognition test, not during an implicit memory test. FN400 potentials during recognition were reduced for meaningful squiggles, which were also able to support conceptual priming; squiggles that carried less meaning did not appear to support conceptual priming and did not exhibit FN400 repetition effects during the recognition test. These predictions are at odds with the dominant interpretation of FN400 potentials as generic markers of familiarity during episodic memory tests (reviewed in Rugg and Curran, 2007), but are consistent with recent results linking FN400 potentials to conceptual processing (Voss and Paller, 2006, 2007, 2009; Danker et al., 2008; Voss et al., *in press*).

Perceptual priming of visual shapes, typically nameable objects, has been associated with ERP repetition effects that onset earlier than FN400 potentials and index posterior cortical processing associated with visual perception (e.g., Allison et al., 1999). For example, frontocentral P150 potentials are larger for repeated than new objects between 120 and 200 ms (Schendan and Kutas, 2003) and are thought to index perceptual categorization processes (Schendan et al., 1998). Furthermore, lateral occipitotemporal P200 potentials between 190 and 270 ms are larger for new than repeated fragmented line drawings and are thought to index perceptual grouping processes (Schendan and Kutas, 2007a). We therefore predicted that ERP perceptual priming effects would occur earlier than FN400 effects associated with conceptual priming, which typically occur between 300 and 500 ms. However, neural correlates of perceptual priming might differ for squiggles versus highly familiar nameable objects.

We also predicted that incidental retrieval of episodic information from the study phase would occur during the priming tests despite the fact that the tests were indirect (Richardson-Klavehn and Bjork, 1988). Furthermore, this incidental retrieval would be associated with late-onset positive potentials with a posterior distribution, termed

late positive complex or LPC potentials (Friedman and Johnson, 2000; Rugg and Curran, 2007; Voss and Paller, 2008). Indeed, explicit memory for study-phase episodes for squiggle stimuli is highly correlated with LPC potentials (Voss and Paller, 2007).

Methods

Subjects

Behavioral and electrophysiological data were collected from 15 Northwestern University students after informed consent was obtained. Five subjects were male, and all were right-handed, native English speakers between 18 and 24 years of age with normal or corrected-to-normal vision.

Materials

Visual stimuli were 300 minimalist visual shapes known as “squiggles” (Fig. 1). Squiggles were created by random hand-deformation of a square, circle, or triangle (Groh-Bordin et al., 2006), and were presented on a computer monitor in black on a white background. Stimulus onset times were synchronized to the monitor refresh (100 Hz). Each squiggle was sized to fit a square subtending approximately 5° of visual angle.

Behavioral paradigm

All 300 squiggles were presented during the course of 10 study-test blocks. Five of these blocks included a perceptual priming test and five included a conceptual priming test, with type of block in randomized order. Subjects were made aware of the study-test format of the experiment prior to the first block, but the total number of blocks of each type was not divulged to subjects in order to prevent anticipation of the test format during the prior study phase or during the 45-s break between study and test. During this break, subjects counted backwards aloud by threes from a designated integer for 30 s and then were read test-phase instructions. Prior to the first block, subjects practiced each behavioral task using an additional set of stimuli.

In each study phase, subjects viewed 20 squiggles that they had not viewed before. Each squiggle was presented a single time for 2000 ms with randomized interstimulus intervals (ISI) lasting 1500–3000 ms, during which a fixation cross appeared. All stimuli appeared at the center of the screen and subjects were instructed to maintain central fixation and avoid blinking. Subjects rated each squiggle using a 4-point meaningfulness scale with 1 corresponding to “high meaningfulness,” and 4 to “no meaningfulness.” Subjects were instructed to make a rating of 1 if the squiggle “looks like a nameable object, face, or animal” and 2 if the squiggle “looks like a more abstract nameable object, face, or animal.” A rating of 3 indicated that the squiggle “does not look like anything nameable, but is in some way meaningful.” A rating of 4 corresponded to “a random collection of lines that is in no way meaningful.” Ratings were to be distributed across the four levels, such that the most meaningful stimuli could be segregated from the least meaningful stimuli for each subject. As in our prior study (Voss and Paller, 2007), we operationally defined squiggles given meaningfulness ratings of 1 or 2 as “high-meaning” and squiggles given ratings of 3 or 4 as “low-meaning.” Responses were made using the right hand, with two assignments of meaningfulness rating to response finger varied such that adjacent fingers corresponded to adjacent ratings either with 1 for the index finger (eight subjects) or 1 for the little finger (seven subjects).

A perceptual priming test followed the study phase for five of the study-test blocks. In each test, the same 20 squiggles presented during the previous study phase (old) were presented along with 10 entirely novel squiggles (new). Each squiggle was presented in randomized

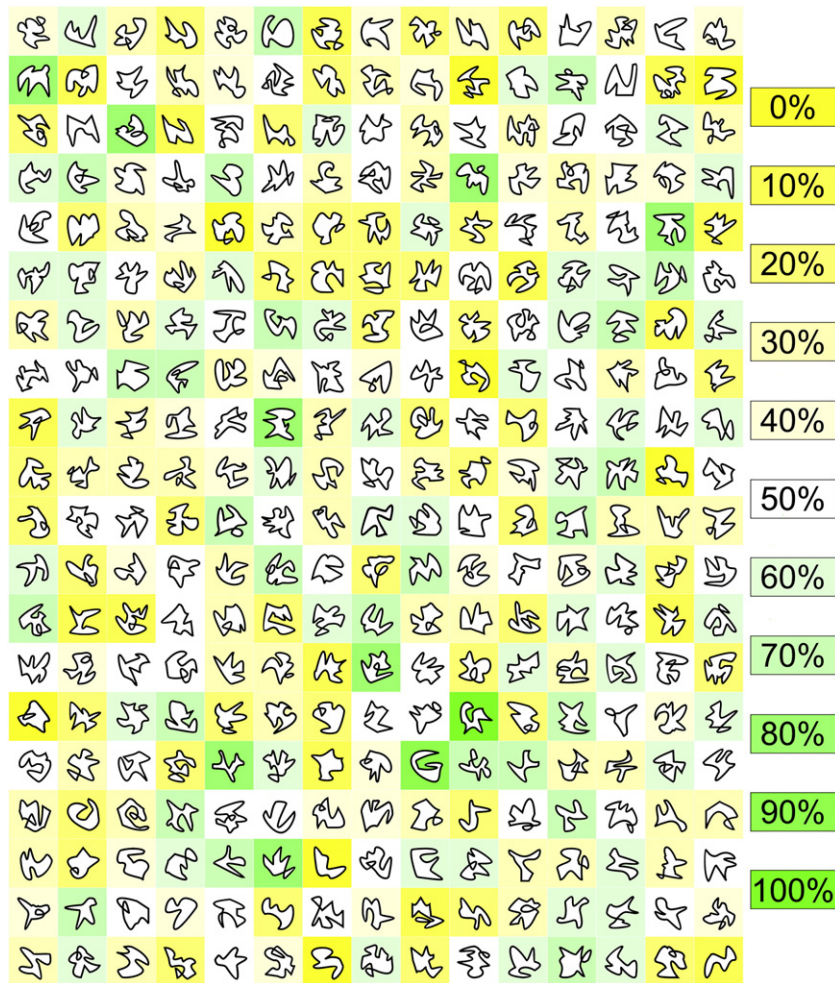


Fig. 1. Meaningfulness rating variability. For each of the 300 squiggle stimuli, background color indicates the degree to which meaningfulness ratings were inconsistent across individuals. Squiggles assigned to the high-meaning category by 50% of the subjects and to the low-meaning category by 50% of the subjects are presented on a white background. Increasingly saturated yellows indicate increasing assignment to the low-meaning category, whereas increasingly saturated greens indicate increasing assignment to the high-meaning category. Note that the majority of squiggles are presented on fairly unsaturated yellow and green backgrounds, indicating approximately matched assignment to high-meaning versus low-meaning categories across subjects.

order a single time for 1000 ms with randomized ISI lasting 1000–2000 ms, during which a fixation cross appeared. Subjects were instructed to indicate if each squiggle contained a loop by pressing one button for “loop” and another button for “no loop.” A loop was present in 50% of the squiggles (see Fig. 1). Responses were made using the right hand, with assignment of loop decision to response finger (index or middle) alternated across subjects. Response speed was strongly emphasized. Subjects were instructed to disregard the fact that some of the squiggles might have been seen before, and that focusing on repetition could potentially retard responses. “Loop” and “no loop” responses were collapsed for analysis to emphasize effects due to priming rather than the response decision. Both response types were approximately equally prevalent in each collapsed condition, given that meaningfulness ratings did not differ for items with versus without loops (see below).

A conceptual priming test followed the study phase in the other five study-test blocks. All parameters were identical to those in the perceptual priming test except for behavioral response requirements. Subjects rated the meaningfulness of each squiggle using the 4-point scale described above and the same response-finger assignments as in the study phase. Response speed was strongly emphasized. Subjects were instructed to disregard the fact that some of the squiggles might have been seen before, and that they were not required to provide the same rating as in the study phase. Subjects were told that focusing on

repetition or trying to make the same rating could potentially retard responses.

Squiggles were counterbalanced across subjects to minimize any stimulus-specific effects. Three separate stimulus sets, each with 100 squiggles randomly selected with the requirement that 50% contained a loop, were thus rotated across old and new conditions. In addition, old and new squiggles were randomly assigned to each experimental block such that 50% contained a loop.

ERP procedures

Stimulus-locked ERPs were extracted from continuous electroencephalographic recordings made during study and test phases. Recordings were made from 59 scalp locations using tin electrodes evenly spaced in an elastic cap. Electrode placement corresponded approximately to 10–20 system locations; locations are referred to using an italicized letter to indicate locations slightly *anterior*, *posterior*, *inferior*, *superior*, or *medial* to the corresponding 10–20 position. Five additional recording locations included the left mastoid and four locations for monitoring eye movements in horizontal (lateral to each canthus) and vertical (inferior to each eye) directions. Recordings were referenced to right mastoid, and rereferenced offline to average mastoids. Electrode impedance was ≤ 5 k Ω . Signals were amplified with a band pass of 0.05 to 200 Hz and sampled at 1000 Hz

with 16-bit precision. Stimulus-locked activity was extracted for 1100-ms epochs, beginning 100 ms prior to stimulus onset. Baseline correction was performed for each epoch by subtracting the prestimulus mean amplitude from all data points. Epochs contaminated by artifacts were discarded. Study-phase high-meaning and low-meaning ERPs comprised a mean of 85 ($SE=5.2$) and 94.5 ($SE=5.6$) trials per subject, respectively. The high-meaning, low-meaning, and new ERPs for the perceptual priming test comprised a mean of 36 ($SE=2.2$), 44 ($SE=3.3$), and 40 ($SE=1.0$) trials per subject, respectively. ERPs for the same three conditions in the conceptual priming test comprised a mean of 39 ($SE=2.5$), 45 ($SE=2.2$), and 43 ($SE=1.1$) trials per subject, respectively. Waveforms were smoothed with a 40-Hz zero-phase-shift Butterworth filter for presentation purposes only. Topographic maps (2D and 3D) were created using EEGLAB (Delorme and Makeig, 2004). Statistical comparisons were made using repeated-measures ANOVA for ERP amplitudes averaged over latency intervals and electrode clusters, with Geisser–Greenhouse corrections when necessary. The alpha level was 0.05, and p -values less than 0.10 are reported.

Results

Encoding

Results were collapsed across the 10 blocks for analyses because at the time of encoding subjects were unaware of the subsequent test format. The proportion of squiggles garnering meaningfulness ratings of *high*, *medium*, *low*, and *none* was 0.17 ($SE=0.02$), 0.27 ($SE=0.01$), 0.33 ($SE=0.02$), and 0.23 ($SE=0.02$), respectively. The high-meaning category (ratings *high* and *medium* together) comprised 44% ($SE=3\%$) of squiggles and the low-meaning category (ratings *low* and *none* together) comprised 56% ($SE=3\%$) of squiggles. Mean response times (RTs) were similar for high-meaning and low-meaning squiggles (2611 and 2581 ms, respectively; $t(14)=0.6$, ns).

An item analysis revealed that meaningfulness ratings for each individual squiggle were highly variable across subjects (Fig. 1). The standard deviation of the rating was computed across subjects for each squiggle, and the average of this value for all squiggles was 0.95 on the 4-point scale. As in our prior research, this variability made it necessary to use ratings from each individual subject in order to accurately track meaningfulness. The high degree of rating variability led to an approximate counterbalancing of squiggles to the high-meaning and low-meaning categories. On average, an individual squiggle stimulus was assigned to the high-meaning category by approximately 45% of subjects ($SE=1.4\%$ across stimuli) and to the low-meaning category by the remaining subjects. Indeed, 74% of stimuli were assigned to the high-meaning category by between 40% and 60% of subjects, and to the low-meaning category by the remaining subjects. ERPs during encoding differed minimally as a function of meaningfulness until approximately 600 ms following stimulus onset, when high-meaning ERPs were significantly more positive than low-meaning ERPs (Supplemental Fig. 1).

Perceptual priming

As shown in Fig. 2A, RTs to correct decisions in the perceptual priming test differed for high-meaning-old, low-meaning-old, and new items [$F(2,28)=6.6$, $p=0.005$]. Loop judgments were faster for old items compared to new items [high-meaning-old vs. new, $t(14)=6.1$, $p<0.001$, and low-meaning-old vs. new, $t(14)=3.0$, $p=0.01$, respectively]. RTs were similar for old items in the two meaningfulness categories [$t(14)=0.43$, ns]. Accuracy was near ceiling levels and was similar for high-meaning-old, low-meaning-old, and new items [average hit rate=0.95, 0.95, and 0.96, respectively, $F(2,28)=0.1$, ns]. RT effects did not change over the five test blocks, as indicated by a nonsignificant interaction in a

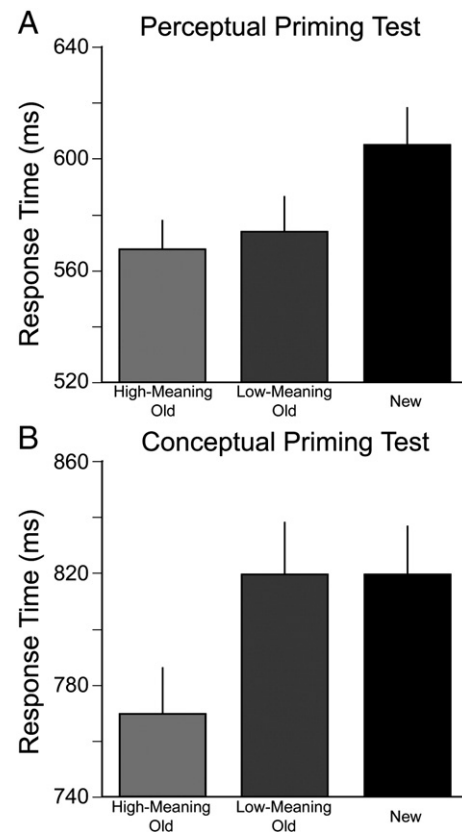


Fig. 2. Response-time measures of perceptual priming and conceptual priming. Average response times for high-meaning-old, low-meaning-old, and new squiggles are shown for the perceptual priming test (A) and the conceptual priming test (B). Error bars indicate SE after correcting for between-subject variability in mean values over all conditions, and therefore correspond to error terms used to assess statistical significant differences between conditions.

condition-by-block ANOVA [$F(8,112)=0.9$, ns]. In short, perceptual implicit memory was indicated by response speeding, but there was no evidence for differential speeding as a function of subjective meaningfulness.

ERPs elicited by high-meaning-old, low-meaning-old, and new items during the perceptual priming test appear in Fig. 3A. Visual inspection indicated that ERPs differed most strikingly in two ways: (1) old items elicited ERPs that were more negative than those to new items from approximately 150–180 ms at frontal locations, corresponding to a positive peak at 170 ms, and (2) old items elicited ERPs that were more positive than those to new items from approximately 450–1000 ms with maximal differences at parietal/occipital electrodes. Differences between high-meaning-old and low-meaning-old conditions were minimal, paralleling the behavioral measures of priming.

Across-condition amplitude differences at 150–180 ms varied significantly across anterior, middle, and posterior regions [condition-by-region interaction, $F(1.9,27.7)=4.8$, $p=0.02$]. Only the anterior differences were reliable [$F(1.6,23.1)=4.4$, $p=0.03$; middle region, $F(2,28)=0.3$, ns ; posterior region, $F(2,28)=1.2$, ns]. For the anterior region, amplitudes for high-meaning-old and low-meaning-old squiggles did not differ reliably ($p=0.58$), and were both reliably more negative than for new squiggles ($p=0.01$ and 0.02 , respectively).

Based on *a priori* hypotheses regarding LPC, we tested the significance of amplitude differences at 500–700 ms, the same latency range we used previously (Voss and Paller, 2007). ERPs were more positive for high-meaning-old and low-meaning-old squiggles than for new squiggles at anterior, middle, and posterior regions [$F(1.7,23.4)=4.6$, $p=0.03$], with a marginal condition-by-

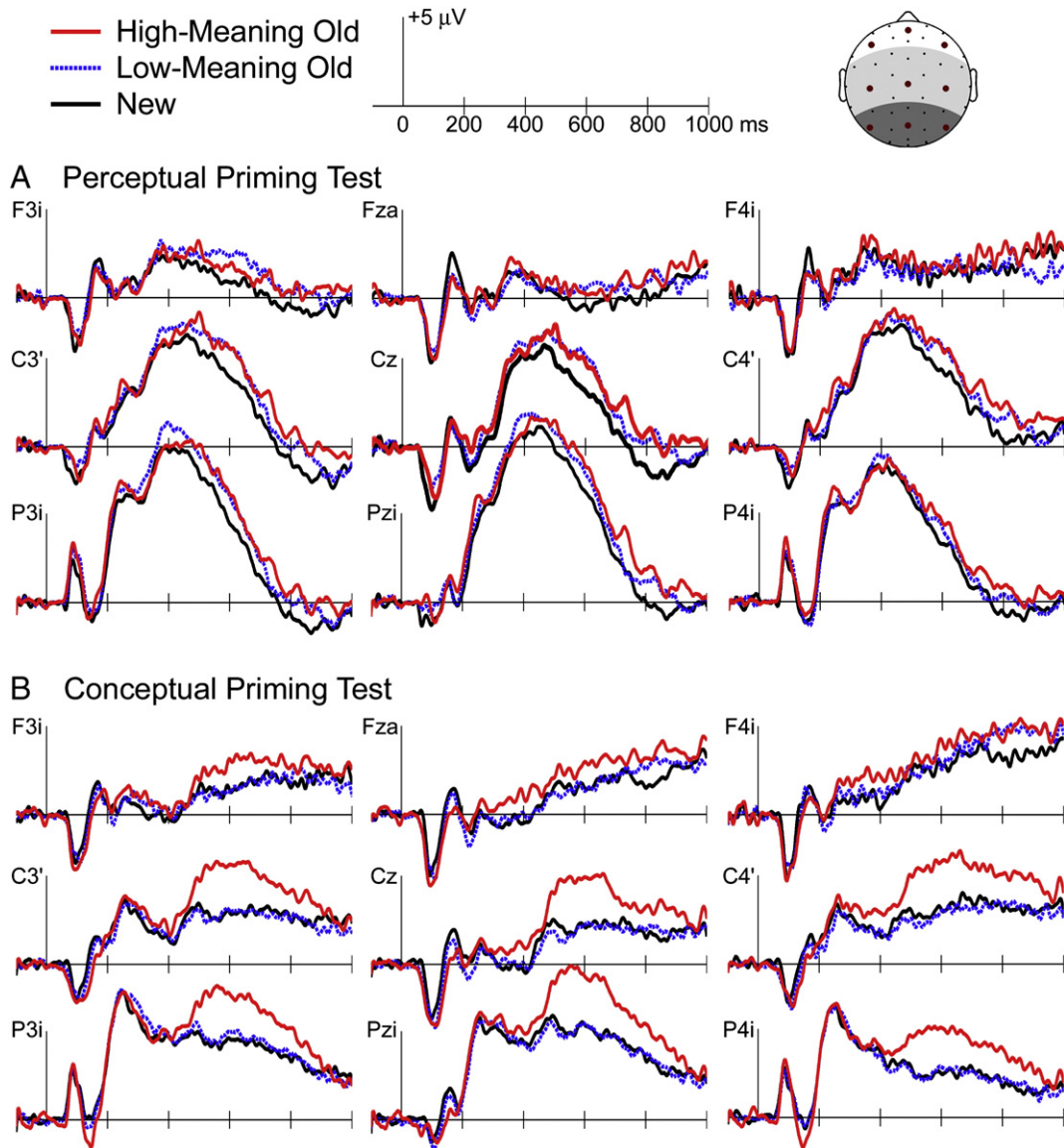


Fig. 3. ERP correlates of perceptual priming, conceptual priming, and familiarity-based recognition. ERP waveforms are presented for the high-meaning-old, low-meaning-old, and new conditions for each of nine electrode locations. The schematic view of the head from above, with the nose toward the top, shows the locations of these nine electrode locations (circles) as well as all other electrodes locations (small dots). The center electrode is the vertex (Cz). The gray shading indicates the three scalp regions used in statistical analyses. (A) ERP waveforms for the perceptual priming test. (B) ERP waveforms for the conceptual priming test.

region interaction [$F(1.8,25.1) = 3.2, p = 0.06$], reflecting reliable differences for middle and posterior regions but not the anterior region (anterior high-meaning-old versus new and low-meaning-old versus new $p = 0.22$ and 0.27 , respectively, middle $p < 0.01$ and < 0.01 , and posterior $p < 0.01$ and < 0.01). Amplitudes for high-meaning and low-meaning old did not differ reliably for any region (p 's > 0.36).

We tested for amplitude differences at 300–500 ms based on *a priori* hypotheses regarding FN400 potentials (Voss and Paller, 2007) and on prior evidence that priming for meaningful shapes is related to repetition effects on FN400-like potentials between 300 and 500 ms (Ganis and Kutas, 2003; Schendan and Maher, 2009). However, the three conditions did not differ significantly for any electrode region during this latency interval [condition main effect: $F(2,28) = 0.9, ns$; condition-by-region interaction: $F(4,56) = 1.9, ns$].

The anterior repetition effects from 150 to 180 ms may have co-occurred with polarity-inverted, ERP effects at posterior scalp locations. A single set of neural generators in posterior ventral visual cortex can produce an electrical dipole that results in opposite-polarity effects at frontal and occipitotemporal locations (Joyce and

Rossion, 2005). Although a positive repetition effect was not observed at 150–180 ms for the bilateral posterior electrode cluster, collapsing across multiple locations may have lessened sensitivity, given that such effects typically have a relatively focal distribution and given the proximity of the reference location. To explore this possibility, we analyzed results where between-condition differences were maximal, namely, a frontopolar cluster and a left occipitotemporal cluster (Fig. 4A). Average values for high-meaning-old minus new and low-meaning-old minus new differed significantly from zero for each condition and electrode cluster, as indicated in Fig. 4A. In sum, negative repetition effects on frontal potentials from 150 to 180 ms coincided with opposite-polarity repetition effects on left occipitotemporal potentials during the same latency interval.

As is characteristic for such potentials, implementing an average scalp EEG reference can enhance the apparent occipitotemporal effect (Joyce and Rossion, 2005). Accordingly, when left occipitotemporal ERPs were assessed at 150–180 ms using an average scalp reference (Fig. 4B), a clear difference was apparent for high-meaning-old and low-meaning-old compared to new items.

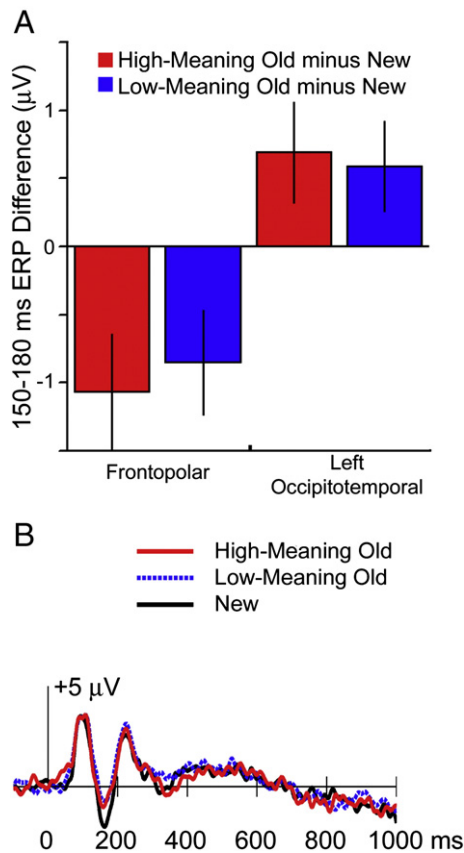


Fig. 4. Focal analysis of frontopolar/occipitotemporal ERP correlates of perceptual priming. (A) Mean amplitudes for the high-meaning-old vs. new and low-meaning-old vs. new ERP differences were computed for a frontopolar electrode cluster (Fza, Fzp, Fp1m, and Fp2m) and an occipitotemporal electrode cluster (TI1, TO1, and O11) for the 150–180 ms latency interval. Error bars indicate \pm SE. (B) ERP waveforms computed with an average scalp reference are presented for the high-meaning-old, low-meaning-old, and new conditions during the perceptual priming test, averaged across a set of left-hemisphere occipitotemporal electrodes where between-condition differences were maximal (TI1, TO1, O1, O11, and I1).

Conceptual priming

As shown in Fig. 2B, RTs in the conceptual priming test differed among high-meaning-old, low-meaning-old, and new items [$F(2,28) = 11.5, p = 0.0002$]. RTs were collapsed across meaningfulness rating levels for new items because they did not differ significantly for high-meaning (825 ms on average) compared to low-meaning (816 ms on average) categories [$t(14) = 0.2, ns$]. Meaningfulness ratings were significantly faster for high-meaning-old items compared to both new items [$t(14) = 4.2, p < 0.001$] and low-meaning-old items [$t(14) = 3.4, p = 0.004$]. RTs for low-meaning-old items and new items did not differ significantly [$t(14) < 0.1, ns$]. RT effects did not change over the five blocks, as indicated by a nonsignificant interaction in a condition-by-block ANOVA [$F(8,112) = 0.3, ns$]. The same pattern of RT effects was obtained when new items were subdivided by meaningfulness rating levels [high-meaning old versus high-meaning new $t(14) = 4.5, p < 0.001$; low-meaning old versus low-meaning new $t(14) = 0.6, ns$]. RTs thus provided evidence for conceptual implicit memory for meaningful items.

A small number of squiggles were not assigned to the high-meaning category at both encoding and retrieval or to the low-meaning category at both encoding and retrieval (4% on average, $SE = 1.8\%$). These inconsistently rated items were excluded from behavioral analyses for conceptual priming and from ERP analyses; thus, high meaning at study indicates high meaning at test, and similarly for low meaning. An analysis of all items (i.e., either consistent or inconsistent

from study to test) indicated that repetition was not associated with an overall increase or decrease in rated meaningfulness, as the small change in mean rating from study to test was unreliable [2.63 to 2.54, $t(14) = 0.9$].

We also tested the hypothesis that the behavioral effects attributed to conceptual implicit memory were instead due to learning of new stimulus–decision mappings (Horner and Henson, 2008). In other words, high-meaning-old items could have garnered faster ratings due to selective facilitation of the association between the stimulus and the button response or meaningfulness decision, rather than due to conceptual fluency *per se*. This analysis relied on a subset of squiggles assigned to the high-meaning category but not given the same rating at encoding and retrieval—either a 1 rating during encoding and a 2 rating during retrieval, or *vice versa* (9% on average, $SE = 3.1\%$). Test-phase RTs did not differ significantly for these items compared to high-meaning items that were given the same rating during encoding and retrieval [means of 774 and 765 ms, respectively, $t(14) = 0.7, ns$]. Given that stimulus repetition produced an RT facilitation for the subset of high-meaning items rated inconsistently [$t(14) = 2.4, p = 0.03$], and that this facilitation was nearly the same magnitude as for high-meaning items rated consistently [40 and 49 ms, respectively, $t(14) = 0.3, ns$], the speed-up can best be attributed to conceptual priming.

ERPs elicited by high-meaning-old, low-meaning-old, and new items during the conceptual priming test appear in Fig. 3B. As in the RT analysis for this test, ERPs elicited by new items were collapsed for items given high-meaning and low-meaning ratings because differences were negligible for all recording sites (Supplemental Fig. 2). Accordingly, the same statistical pattern for old versus new ERP results reported below was obtained when old/new effects were calculated for high-meaning old versus high-meaning new and for low-meaning old versus low-meaning new (see below). Visual inspection indicated that ERPs for high-meaning-old, low-meaning-old, and new items differed most strikingly in three ways and, in all cases, neural repetition effects were evident only for high-meaning old items: (1) greater negativity for high-meaning-old items than for both low-meaning-old and new items from approximately 150 to 180 ms across most scalp locations, (2) greater positivity for high-meaning-old items than for both low-meaning-old items and new items from approximately 250 to 450 ms at frontal and fronto-central locations of the FN400, and (3) greater positivity for high-meaning-old items than for both low-meaning-old items and new items from approximately 500 to 1000 ms maximal at parieto-occipital locations. ERPs were highly similar for low-meaning-old items and new items.

Amplitude comparisons were made for the 150–180, 300–500, and 500–700 ms intervals and for anterior, middle, and posterior electrode regions, as in the analysis of perceptual priming effects. The selectively greater negativity for high-meaning-old items from 150 to 180 ms was reliable for all regions [$F(1.9,26.4) = 4.3, p = 0.03$] and did not differ significantly across regions [condition-by-region interaction: $F(4,56) = 0.5$]. The selectively greater positivity for high-meaning-old items from 300 to 500 ms differed across regions [condition-by-region interaction: $F(1.6,22.7) = 4.9, p = 0.02$], and was reliable for the anterior [$F(1.2,17.1) = 19.1, p < 0.001$] and middle regions [$F(1.3,18.0) = 17.8, p < 0.001$] but not the posterior region [$F(2,28) = 0.8$]. The selectively greater positivity for high-meaning-old items from 500 to 700 ms differed across regions [condition-by-region interaction $F(2.3,32.4) = 5.2, p = 0.01$], with greatest differences for the middle [$F(1.9,26.9) = 12.9, p < 0.001$] and posterior regions [$F(1.7,23.7) = 15.0, p < 0.001$], and lesser differences for the anterior region [$F(1.7,23.4) = 3.9, p = 0.04$]. For all three intervals and regions, except the posterior region from 300 to 500 ms, ERPs differed reliably for high-meaning-old and new squiggles (all p 's < 0.06 ; posterior 300–500 ms $p = 0.16$). Low-meaning-old and new ERPs did not differ reliably for any interval or region (all p 's > 0.19). The same statistical pattern was identified by comparing high-meaning-old

to high-meaning-new (posterior 300–500 ms $p=0.24$, all other p 's < 0.08) and low-meaning-old to low-meaning-new (all p 's > 0.23).

An additional analysis was conducted to determine if the 150–180 ms old/new difference for high-meaning items in the conceptual priming test consisted of a frontopolar negativity accompanied by a left occipitotemporal positivity, as was the case in the perceptual priming test (Fig. 4A). For the same frontopolar and occipitotemporal electrode clusters scrutinized in Fig. 4A, the main effect of condition for high-meaning-old versus new reached significance [$F(1.9,26.1)=4.1$, $p=0.03$], but the condition-by-cluster interaction did not [$F(2,28)=0.7$, *ns*], indicating that the frontopolar effect and the occipitotemporal effect were of the same polarity, unlike the pattern identified for perceptual priming.

The possibility that priming effects on ERPs were due to learning of stimulus–decision mappings was tested by computing ERPs for the small number of items rated inconsistently from study to test, as in the aforementioned behavioral test for contributions from response learning. A very small number of trials were available (high-meaning average = 4, $SE=1.5$, and low-meaning average = 5, $SE=1.1$), and data from five subjects were excluded due to excessive noise (average amplitude values for the anterior and posterior electrode clusters for 300–500 and 500–700 ms were over two SD from the mean for at least two clusters, latency intervals, and conditions). For the remaining 10 subjects, a similar pattern of ERP effects were identified as in the main analysis: Low-meaning items did not differ significantly from new items, whereas high-meaning items were more positive than new items for anterior FN400 electrodes from approximately 300 to 500 ms and for posterior LPC electrodes from approximately 500 to 900 ms (Supplemental Fig. 3). The evidence thus weighs against the possibility that stimulus–decision learning was responsible for FN400 correlates of conceptual priming, and such learning clearly cannot be the sole factor in these results. Moreover, we identified similar FN400 potentials during a recognition test when priming of repeated stimulus–decision mappings was not operative (Voss and Paller, 2007).

Perceptual versus conceptual priming

Although anterior old/new effects at 300–500 ms were not observed in the perceptual priming test, it is important to determine whether these old/new effects differed reliably as a function of type of test (perceptual priming versus conceptual priming). Accordingly, the high-meaning-old versus new ERP difference from 300 to 500 ms for the anterior region was shown to be significantly greater in the conceptual priming test than the high-meaning-old versus new and low-meaning-old versus new ERP differences for the same latency interval and region in the perceptual priming test (p 's < 0.05).

Associations between ERPs and behavior

Fig. 5 juxtaposes the ERP correlates of perceptual priming and conceptual priming. For each memory test, correlations between ERPs and memory were assessed as follows. Each subject contributed two behavioral measures for each test type: the RT differences between high-meaning-old items and new items and between low-meaning-old items and new items. Each subject also contributed ERP difference measures averaged over each of the three analysis intervals (150–180, 300–500, and 500–700 ms) for each of the three scalp regions. ERP differences were computed between high-meaning-old and new items and between low-meaning-old items and new items. To account for individual variation in the locus of ERP effects, differences for each region were quantified at the electrode exhibiting the maximum difference between conditions for that region and latency interval in each subject. Although this individualized procedure could function to artifactually enhance ERP effects due to idiosyncratic noise at particular regions and intervals for a particular subject, this procedure would not lead to spurious correlations because any such

individual noise would be expected to degrade correlational results. Across-subject correlations were thus computed between each behavioral measure of memory, separately for high-meaning and low-meaning items, and nine corresponding ERP difference measures (3 regions \times 3 latency intervals).

For perceptual priming, a significant relationship was found between magnitude of priming and magnitude of frontal potentials at 150–180 ms. As indicated in the right column of Fig. 5A, greater priming was associated with greater ERP differences, for both high-meaning and low-meaning items [$r(13)=0.60$, $p=0.01$ and $r(12)=0.58$, $p=0.02$, respectively, with one outlier value (greater than three SD from the mean ERP value) removed from the low-meaning assessment]. No other correlations reached statistical significance for the perceptual priming test [maximum $r(12)=0.35$], indicating that FN400 and LPC effects were not correlated with perceptual priming.

For conceptual priming, a significant relationship was found between magnitude of priming and magnitude of frontal potentials at 300–500 ms. As indicated in the right column of Fig. 5B, greater priming was associated with greater ERP differences for high-meaning items only [$r(13)=0.71$, $p=0.003$]. No other correlations reached statistical significance for the conceptual priming test [maximum $r(13)=0.23$]. In sum, the two potentials that were linked in the primary ERP analyses to perceptual and conceptual priming—P170 and FN400, respectively—also showed correlations with RT priming restricted either to the perceptual priming test (for the P170) or to the conceptual priming test (for the FN400).

Topographic comparisons

Visual inspection of ERP topographies (Fig. 5) indicated distinct patterns for the two ERP old/new effects associated with priming—P170 and FN400—and that these topographies could be identified in more than one memory test. A relative negativity at 150–180 ms was identified for old compared to new items during perceptual priming (Fig. 5A) and for high-meaning-old compared to new items during conceptual priming (Fig. 5B). In addition, 500–700 ms positive differences for old compared to new items were identified in both tests (Figs. 5A, B). We thus performed topographical comparisons on vector-scaled ERP values (McCarthy and Wood, 1985; but see Urbach and Kutas, 2002) to determine if scalp distributions varied across test types.

The first topographic comparison between the perceptual and conceptual priming tests was made for the difference wave of high-meaning-old versus new from 150 to 180 ms (Figs. 5A, B). The electrode-by-test interaction was marginal [$F(5.2,72.3)=2.1$, $p=0.07$], consistent with the observation that the anterior distributions of the effects were partially overlapping, extending to more posterior sites during conceptual priming but reversing polarity occipitotemporally during perceptual priming.

The second comparison concerned positive old/new differences at 500–700 ms (LPC effects). This analysis aimed to determine if LPC topographies differed as a function of meaningfulness in the perceptual priming test or between the conceptual priming test and the perceptual priming test. LPC effects were evident as the ERP difference between (1) high-meaning-old and new in the perceptual priming test, (2) low-meaning-old and new in the perceptual priming test, and (3) high-meaning-old and new in the conceptual priming test. The topographies of the old/new difference waves from 500 to 700 ms corresponding to each of these three contrasts were thus compared. All possible pairwise comparisons were made, and topographies did not differ reliably [all pairwise $F(58,1392)$ values < 1.2].

Discussion

Memory for squiggles, as assessed in tests of perceptual priming and conceptual priming, varied systematically with whether stimuli

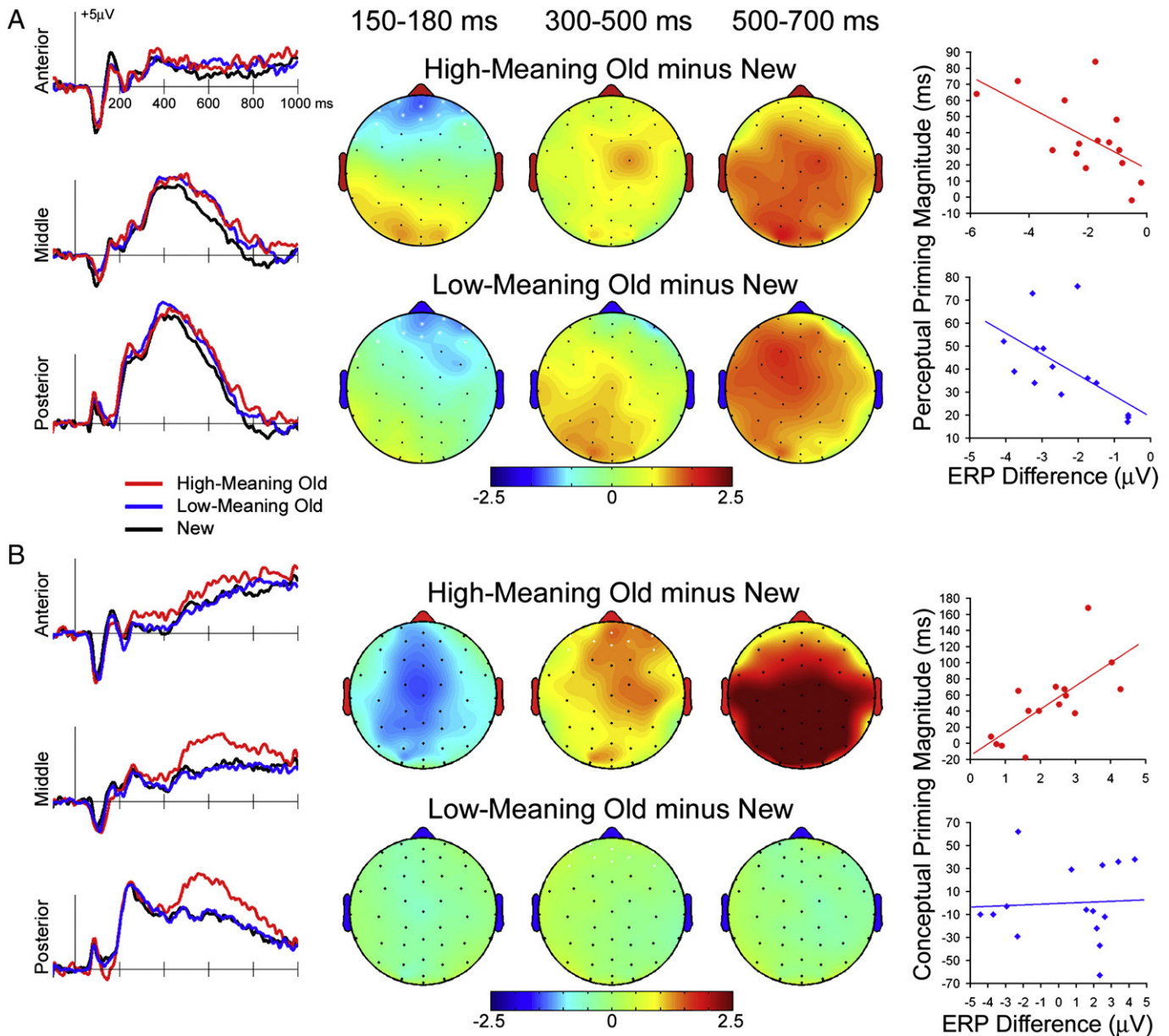


Fig. 5. Distinguishing ERP correlates of perceptual priming and conceptual priming. Panel A summarizes results from the perceptual priming test and panel B from the conceptual priming test. The left column shows ERP waveforms averaged over the anterior, middle, and posterior regions used in statistical analyses. The middle column shows old/new ERP differences plotted topographically for the high-meaning and low-meaning categories, averaged over the 150–180, 300–500, and 500–700 ms intervals. The right column shows correlations between ERP amplitudes and memory with separate scatterplots for the high-meaning category (upper plots; red) and the low-meaning category (lower plots; blue). Electrode locations in the middle column are shown as white dots for the region and latency interval that was used for the corresponding scatterplot in the right column; all other electrode locations are shown as black dots.

were meaningful. Ratings of meaningfulness given to each squiggle diverged across individuals based on the idiosyncratic extent to which conceptual knowledge in long-term memory was activated. Accessing such conceptual knowledge involves deciding that the stimulus is known based on pre-experimental experiences, akin to when an object's category is determined via semantic retrieval. Perceptual priming was indicated by faster loop-discrimination responses for old compared to new squiggles. Conceptual priming was indicated by faster meaningfulness responses only for high-meaning-old compared to new squiggles. The two types of priming also differed in associated ERP repetition effects, P170 effects for perceptual priming and FN400 effects for conceptual priming.

Frontopolar P170 potentials were reduced for old compared to new squiggles in the perceptual priming test, and P170 amplitudes correlated with priming magnitude, regardless of meaningfulness.

Although P170 repetition effects of this specific type are novel, the present evidence for this effect and its association with RT perceptual priming is consistent with characterizations of the neurocognitive processes indexed by similar potentials. For instance, frontal-central, early positive potentials between 120 and 200 ms (known variously as vertex positive potentials [VPPs], P150 or P200) can be elicited selectively by certain categories of stimuli (e.g., faces or letterstrings relative to other objects), show similar topographic and timing characteristics, and are characteristically accompanied by a lateral occipitotemporal N170 with inverted polarity (e.g., Schendan et al., 1998; Rossion et al., 2003). The activity of neuronal populations in ventral occipitotemporal and fusiform cortex has been postulated to produce effects on both VPPs and occipitotemporal N170s with opposite polarities (Allison et al., 1999; Joyce and Rossion, 2005). Like these early potentials, in the present results, the negative-going,

frontopolar P170 repetition effects coincide with positive-going, occipitotemporal N170 repetition effects, and both potentials are reduced for old relative to new. Adaptation effects with <1-s delays show a pattern of repetition effects on the VPP/N170 similar to the repetition effects with much longer delays found here and characterized as perceptual priming (Ganis and Schendan, 2008): adaptation of meaningful objects and faces produced greater negativity on frontocentral positivity (VPP) and greater positivity on the occipitotemporal N170 (i.e., both show repetition reductions), and these repetition effects were estimated to localize to occipitotemporal cortex implicated in object and face perception. An analysis using current-source density maps for N170 effects in the present experiment also tentatively implicates occipitotemporal cortex (Supplemental Fig. 4). Repetition effects at this latency may be more common with very-short-lag repetition (e.g., Ganis and Schendan, 2008; Woollams et al., 2008). We speculate that the present design yielded 150–180 ms repetition effects, despite the long lag, due to (a) task requirements at test that focused attention on visual details, and (b) the large number of distinct, minimally-meaningful stimuli, minimizing overlapping electrophysiological signals that otherwise could have obscured such early effects (e.g., ERP correlates of object model selection, Schendan and Kutas, 2007b). Positive repetition effects at approximately the same latency have also been identified during explicit memory testing (Tsvilivis et al., 2001; Duarte et al., 2004; Friedman, 2004; Diana et al., 2005). Although their functional significance with respect to various explicit memory phenomena remains uncertain (Diana et al., 2005), some investigators have attributed these effects to priming (Friedman, 2004).

Negative potentials at 300–500 ms were more positive for high-meaning-old squiggles compared to new squiggles in the conceptual-priming test. These potentials bear several features in common with FN400 potentials (i.e., midfrontal old/new effects) that have often been described in recognition paradigms (Friedman and Johnson, 2000; Rugg and Curran, 2007; Voss and Paller, 2008). Indeed, in a previous report (Voss and Paller, 2007), we described ERP correlates of familiarity-based recognition for the same squiggle stimuli used in the current report within a highly similar paradigm. As in the current experiment, study-phase meaningfulness ratings were used to sort squiggles into meaningfulness categories. The main difference was that subjects took recognition tests rather than priming tests. FN400 potentials were identified in conjunction with familiarity-based recognition. As in the current experiment, FN400 repetition effects were elicited by high-meaning squiggles and not by low-meaning squiggles, even though low- and high-meaning squiggles elicited similar levels of familiarity-based recognition. We thus attribute FN400 repetition effects in both studies to conceptual priming following repetition of high-meaning squiggles, regardless of test format. As discussed below, this finding is counter to the prominent supposition that FN400 repetition effects are generic markers of familiarity (Rugg and Curran, 2007). FN400 repetition effects have also been linked to conceptual priming for other stimulus categories, including faces (Voss and Paller, 2006) and words (Voss et al., *in press*). Notably, the perceptual priming ERPs in the present study also run counter to a familiarity interpretation of the FN400. Both conceptual and perceptual priming tests could incidentally activate memory underlying a nonspecific feeling of familiarity, predicting FN400-like effects in both tests. To the contrary, only the conceptual priming test showed the FN400 repetition effect.

Positive potentials after 500 ms were identified during both the perceptual and conceptual priming tests, and these potentials closely resembled repetition effects known in the literature as the late positive complex or LPC (Friedman and Johnson, 2000; Paller et al., 2007; Rugg and Curran, 2007; Voss and Paller, 2008). Substantial evidence indicates that LPC potentials signal episodic retrieval from long-term memory (Friedman and Johnson, 2000; Mecklinger, 2000; Paller et al., 2007; Rugg and Curran, 2007; Voss and Paller, 2008), and

that this retrieval is distinct from implicit memory (e.g., Paller and Kutas, 1992). Indeed, in our previous report (Voss and Paller, 2007), we found that the accuracy of familiarity-based recognition was strongly correlated with the magnitude of LPC repetition effects for both high-meaning and low-meaning squiggles. Given that incidental retrieval of encoding episodes often occurs during priming tests (Schacter, 1987; Richardson-Klavehn and Bjork, 1988; Henson, 2003), it is plausible that LPC effects during priming tests reflect incidental explicit episodic memory retrieval, which may have varied with task demands (e.g., Stenberg et al., 2006). We propose that incidental retrieval targeted primarily (a) physical features during the perceptual-priming test, leading to similar LPC effects for both meaningful conditions, and (b) conceptual features during the conceptual-priming test such that only high-meaning items evoked LPC effects. Consistent with our first proposal, LPC repetition effects during priming tests are remarkably sensitive to repetition of exact physical features (Schendan and Kutas, 2007b). Consistent with our second proposal, LPC effects are minimal when visual images evoke little or no meaningful idea about an object on an entry-level categorization task that encourages recruitment of meaningful processing (Schendan and Maher, 2009), like the meaning rating task used here to assess conceptual priming.

Collectively, our results indicate that perceptual and conceptual priming can occur for novel stimuli following only a single viewing, and that the former is indexed by earlier frontopolar P170 repetition effects, whereas the latter is indexed by later FN400 repetition effects. These findings have broad implications for the use of novel or “nonsense” stimuli when measuring memory and other cognitive processes, in that participants can readily treat these stimuli like exemplars from well-learned categories, which have been shown to produce FN400-like effects (Ganis et al., 1996; Ganis and Kutas, 2003). Furthermore, many stimuli activate conceptual representations in a highly idiosyncratic manner (Fig. 1), and this happens consistently such that meaningfulness ratings can remain stable at delays of at least one year (Voss and Paller, 2007).

The present results also yielded novel evidence on the time course of implicit memory, indicating that neural processes of perceptual priming (150–180 ms) precede those of conceptual priming (300–500 ms). The patterns of ERP effects that we identified for perceptual and conceptual priming suggest that these processes might operate differently for novel stimuli than for stimuli with which subjects have extensive perceptual and conceptual expertise. Specifically, ERPs indicated that task requirements led to the differential engagement of perceptual and conceptual priming; frontopolar P170 repetition effects attributed to perceptual priming were not identified during the conceptual priming test, and FN400 correlates of conceptual priming were not identified during the perceptual priming test. Both forms of priming are often characterized as relatively automatic and insensitive to retrieval demands for categories of well-learned stimuli (Richardson-Klavehn and Bjork, 1988). When novel geometric shapes are viewed for the first time, however, perceptual and conceptual information storage may be far less elaborate than when viewing a familiar stimulus, such that retrieval during a later priming test occurs with far less automaticity.

The current findings are also relevant to the debate over whether familiarity and recollection derive from one or two memory-retrieval processes, a debate in which ERP evidence has played a pivotal role. Some investigators take the position that familiarity and recollection are relatively less-successful versus more-successful outcomes of the same retrieval processes (e.g., Squire et al., 2007; Shrager et al., 2008). Others argue that familiarity and recollection result from the operation of dual retrieval processes (Yonelinas, 2002; Eichenbaum et al., 2007).

Crucial evidence cited as support for this *dual-process account* includes dissociations between electrophysiological markers of each memory type. Recollection has been strongly associated with LPC

potentials (Friedman and Johnson, 2000; Voss and Paller, 2008), whereas familiarity has been associated with FN400 potentials (reviewed in Rugg and Curran, 2007). On the other hand, we have pointed out a number of ways in which the evidence taken to support a link between FN400 and familiarity is weak, and that much of the same evidence could instead support a link between FN400 and conceptual priming (Paller et al., 2007). This casts doubt on the use of putative associations between FN400 potentials and familiarity as support for dual-process models (Yonelinas, 2002; Curran et al., 2006; Eichenbaum et al., 2007; Rugg and Curran, 2007). With squiggles, we showed that FN400 old/new effects during recognition testing were only present for meaningful stimuli, and this inferred meaning was essential for conceptual priming (Voss and Paller, 2007). Furthermore, in the current experiment, FN400 amplitudes correlated with conceptual priming magnitude. We demonstrated a similar direct relationship between FN400 magnitude and conceptual-priming magnitude using famous faces (Voss and Paller, 2006). We thus attribute FN400 potentials to differential conceptual fluency.

In contrast, LPC potentials were associated with familiarity for squiggles (Voss and Paller, 2007). This finding is in accord with findings from other studies of ERP correlates of familiarity as distinct from those of conceptual priming (Yovel and Paller, 2004; MacKenzie and Donaldson, 2007; Voss and Paller, 2006, 2007, 2009). We thus conclude that electrophysiological evidence overall is consistent with the interpretation that familiarity and recollection are supported by a set of explicit episodic retrieval processes that are indexed by LPC potentials, and that FN400 potentials are often observed during recognition tests not in conjunction with familiarity-based recognition, but as a result of concurrent conceptual priming. Overall, the present electrophysiological findings clearly dissociate neural processes underlying perceptual and conceptual priming, thereby providing evidence that early perceptual priming indexed by P170 potentials is distinct from later conceptual priming indexed by FN400 potentials, both of which are distinct from explicit episodic memory processes that also vary with perceptual and conceptual task demands indexed by LPC potentials.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2009.09.012.

References

- Allison, T., Puce, A., Spencer, D.D., McCarthy, G., 1999. Electrophysiological studies of human face perception: I. Potentials generated in occipitotemporal cortex by face and non-face stimuli. *Cereb. Cortex* 9, 415–430.
- Barsalou, L.W., 2008. Grounded cognition. *Annu. Rev. Psychol.* 59, 617–645.
- Biederman, I., 1987. Recognition-by-components: a theory of human image understanding. *Psychol. Rev.* 94, 115–147.
- Crites Jr., S.L., Delgado, P., Devine, J.V., Lozano, D.I., 2000. Immediate and delayed stimulus repetitions evoke different ERPs in a serial-probe recognition task. *Psychophysiology* 37, 850–858.
- Curran, T., Tepe, K.L., Piatt, C., 2006. ERP explorations of dual processes in recognition memory. In: Zimmer, H.D., Mecklinger, A., Lindenberger, U. (Eds.), *Handbook of Binding and Memory: Perspectives from Cognitive Neuroscience*. Oxford University Press, Oxford, pp. 467–492.
- Danker, J.F., Hwang, G.M., Gauthier, L., Geller, A., Kahana, M.J., Sekuler, R., 2008. Characterizing the ERP Old-New effect in a short-term memory task. *Psychophysiology* 45, 784–793.
- Delorme, A., Makeig, S., 2004. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J. Neurosci. Meth.* 134, 9–21.
- Diana, R.A., Vilberg, K.L., Reder, L.M., 2005. Identifying the ERP correlate of a recognition memory search attempt. *Brain Res. Cogn. Brain Res.* 24, 674–684.
- Duarte, A., Ranganath, C., Winward, L., Hayward, D., Knight, R.T., 2004. Dissociable

- neural correlates for familiarity and recollection during the encoding and retrieval of pictures. *Brain Res. Cogn. Brain Res.* 18, 255–272.
- Eichenbaum, H., Yonelinas, A.P., Ranganath, C., 2007. The medial temporal lobe and recognition memory. *Annu. Rev. Neurosci.* 30, 123–152.
- Friedman, D., 2004. ERP studies of recognition memory: differential effects of familiarity, recollection, and episodic priming. *Cogn. Sciences* 1, 81–121.
- Friedman, D., Johnson Jr, R., 2000. Event-related potential (ERP) studies of memory encoding and retrieval: a selective review. *Microsc. Res. Tech.* 51, 6–28.
- Ganis, G., Kutas, M., 2003. An electrophysiological study of scene effects on object identification. *Brain Res. Cogn. Brain Res.* 16, 123–144.
- Ganis, G., Schendan, H.E., 2008. Visual mental imagery and perception produce opposite adaptation effects on early brain potentials. *Neuroimage* 42, 1714–1727.
- Ganis, G., Kutas, M., Sereno, M.I., 1996. The search for common sense: an electrophysiological investigation of the semantic analysis of words and pictures in sentences. *J. Cogn. Neurosci.* 8, 89–106.
- Groh-Bordin, C., Zimmer, H.D., Ecker, U.K., 2006. Has the butcher on the bus dyed his hair? When color changes modulate ERP correlates of familiarity and recollection. *Neuroimage* 32, 1879–1890.
- Henson, R.N., 2003. Neuroimaging studies of priming. *Prog. Neurobiol.* 70, 53–81.
- Horner, A.J., Henson, R.N., 2008. Priming, response learning and repetition suppression. *Neuropsychologia* 46, 1979–1991.
- Joyce, C., Rossion, B., 2005. The face-sensitive N170 and VPP components manifest the same brain processes: the effect of reference electrode site. *Clin. Neurophysiol.* 116, 2613–2631.
- MacKenzie, G., Donaldson, D.J., 2007. Dissociating recollection from familiarity: electrophysiological evidence that familiarity for faces is associated with a posterior old/new effect. *Neuroimage* 36, 454–463.
- McCarthy, G., Wood, C.C., 1985. Scalp distributions of event-related potentials: an ambiguity associated with analysis of variance models. *EEG Clin. Neurophysiol.* 62, 203–208.
- Mecklinger, A., 2000. Interfacing mind and brain: a neurocognitive model of recognition memory. *Psychophysiology* 37, 565–582.
- Paller, K.A., Kutas, M., 1992. Brain potentials during memory retrieval provide neurophysiological support for the distinction between conscious recollection and priming. *J. Cogn. Neurosci.* 4, 375–391.
- Paller, K.A., Voss, J.L., Boehm, S.G., 2007. Validating neural correlates of familiarity. *Trends Cogn. Sci.* 11, 243–250.
- Peterson, M.A., Enns, J.T., 2005. The edge complex: implicit memory for figure assignment in shape perception. *Percept. Psychophys.* 67, 727–740.
- Richardson-Klavehn, A., Bjork, R.A., 1988. Measures of memory. *Annu. Rev. Psychol.* 39, 475–543.
- Roediger III, H.L., 1990. Implicit memory. Retention without remembering. *Am. Psychol.* 45, 1043–1056.
- Rossion, B., Joyce, C.A., Cottrell, G.W., Tarr, M.J., 2003. Early lateralization and orientation tuning for face, word, and object processing in the visual cortex. *Neuroimage* 20, 1609–1624.
- Rugg, M.D., Curran, T., 2007. Event-related potentials and recognition memory. *Trends Cogn. Sci.* 11, 251–257.
- Rugg, M.D., Doyle, M.C., 1994. Event-related potentials and stimulus repetition in direct and indirect tests of memory. In: Heinze, H.J., Munte, T., Mangun, G.R. (Eds.), *Cognitive Electrophysiology*. Birkhauser, Boston, pp. 124–148.
- Schacter, D.L., 1987. Implicit memory: history and current status. *J. Exp. Psychol. Learn Mem. Cogn.* 13, 501–518.
- Schacter, D.L., Dobbins, I.G., Schnyer, D.M., 2004. Specificity of priming: a cognitive neuroscience perspective. *Nat. Rev. Neurosci.* 5, 853–862.
- Schacter, D.L., Wig, G.S., Stevens, W.D., 2007. Reductions in cortical activity during priming. *Curr. Opin. Neurobiol.* 17, 171–176.
- Schendan, H.E., Kutas, M., 2002. Neurophysiological evidence for two processing times for visual object identification. *Neuropsychologia* 40, 931–945.
- Schendan, H.E., Kutas, M., 2003. Time course of processes and representations supporting visual object identification and memory. *J. Cogn. Neurosci.* 15, 111–135.
- Schendan, H.E., Kutas, M., 2007a. Neurophysiological evidence for transfer appropriate processing of memory: processing versus feature similarity. *Psychon. Bull. Rev.* 14, 612–619.
- Schendan, H.E., Kutas, M., 2007b. Neurophysiological evidence for the time course of activation of global shape, part, and local contour representations during visual object categorization and memory. *J. Cogn. Neurosci.* 19, 734–749.
- Schendan, H.E., Maher, S.M., 2009. Object knowledge during entry-level categorization is activated and modified by implicit memory after 200 ms. *Neuroimage* 44, 1423–1438.
- Schendan, H.E., Ganis, G., Kutas, M., 1998. Neurophysiological evidence for visual perceptual categorization of words and faces within 150 ms. *Psychophysiology* 35, 240–251.
- Shrager, Y., Kirwan, C.B., Squire, L.R., 2008. Activity in both hippocampus and perirhinal cortex predicts the memory strength of subsequently remembered information. *Neuron* 59, 547–553.
- Squire, L.R., Zola-Morgan, S., 1991. The medial temporal lobe memory system. *Science* 253, 1380–1386.
- Squire, L.R., Zola-Morgan, S., Clark, R.E., 2007. Recognition memory and the medial temporal lobe: a new perspective. *Nat. Rev. Neurosci.* 8, 872–883.
- Stenberg, G., Johansson, M., Rosen, I., 2006. Conceptual and perceptual memory: retrieval orientations reflected in event-related potentials. *Acta Psychol.* 122, 174–205.
- Tsvilivis, D., Otten, L.J., Rugg, M.D., 2001. Context effects on the neural correlates of recognition memory: an electrophysiological study. *Neuron* 31, 497–505.
- Tulving, E., 1972. Episodic and semantic memory. In: Tulving, E., Donaldson, W. (Eds.), *Organization of Memory*. Academic Press, New York, pp. 381–403.

- Tulving, E., Schacter, D.L., 1990. Priming and human memory systems. *Science* 247, 301–306.
- Urbach, T.P., Kutas, M., 2002. The intractability of scaling scalp distributions to infer neuroelectric sources. *Psychophysiology* 39, 791–808.
- Voss, J.L., Paller, K.A., 2006. Fluent conceptual processing and explicit memory for faces are electrophysiologically distinct. *J. Neurosci.* 26, 926–933.
- Voss, J.L., Paller, K.A., 2007. Neural correlates of conceptual implicit memory and their contamination of putative neural correlates of explicit memory. *Learn. Mem.* 14, 259–267.
- Voss, J.L., Paller, K.A., 2008. Neural substrates of remembering: electroencephalographic studies. In: Byrne, JH (Ed.), *Learning and Memory: A Comprehensive Reference*. Elsevier, Oxford, pp. 79–97.
- Voss, J.L., Paller, K.A., 2009. Remembering and knowing: electrophysiological distinctions at encoding but not retrieval. *Neuroimage* 46, 280–289.
- Voss, J.L., Lucas, H., Paller, K.A., in press. Conceptual priming and familiarity: two different expressions of memory during recognition testing with distinct neurophysiological correlates. *J. Cogn. Neurosci.* doi:10.1162/jocn.2009.21341.
- Woollams, A.M., Taylor, J.R., Karayanidis, F., Henson, R.N., 2008. Event-related potentials associated with masked priming of test cues reveal multiple potential contributions to recognition memory. *J. Cogn. Neurosci.* 20, 1114–1129.
- Yonelinas, A.P., 2002. The nature of recollection and familiarity: a review of 30 years of research. *J. Mem. Lang.* 46, 441–517.
- Yovel, G., Paller, K.A., 2004. The neural basis of the butcher-on-the-bus phenomenon: when a face seems familiar but is not remembered. *Neuroimage* 21, 789–800.