

Interactive report

# Neural correlates of memory retrieval and evaluation<sup>1</sup>

Charan Ranganath<sup>2</sup>, Ken A. Paller<sup>\*</sup>

*Department of Psychology, Northwestern University, 2029 Sheridan Road, Evanston, IL 60208-2710, USA*

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## Abstract

Results from recent neuroimaging studies have led to a controversy as to whether right or left prefrontal regions are relatively more important for episodic retrieval. To address this issue, we recorded event-related brain potentials during two recognition tests with identical stimuli but differing retrieval demands. In both tests, participants viewed a sequence of object drawings, half of which were identical to ones viewed earlier except for a change in size and half of which were new. Instructions were to discriminate between old and new objects (general test) or to additionally decide whether old objects were larger or smaller at study (specific test). Frontal brain potentials that were more positive during the specific than during the general test for both old and new objects were interpreted as neural correlates of the process by which specific attributes of test cues are compared with information retrieved from memory. Another ERP difference between the specific and general tests, which was observed for old objects only, had a left posterior scalp topography and was interpreted to reflect the reactivation of memories for studied objects. Frontal and posterior potentials thus reflected two memory processes important for accurate episodic retrieval. Furthermore, our findings suggest that both left and right prefrontal regions were engaged when demands to retrieve and evaluate perceptual information increased. © 2000 Elsevier Science B.V. All rights reserved.

*Keywords:* Human memory; Event-related potentials; ERPs; Prefrontal cortex; Episodic memory; Source monitoring; Recollection

## 1. Introduction

A great deal of neuropsychological evidence has implicated prefrontal cortex in operations engaged during the formation and retrieval of memories for events [29,52,57]. Although patients with prefrontal lesions are not amnesic, they show distinctive episodic memory impairments; they are mildly impaired on tests of item recognition and cued recall [14,56,58,59,63], they are disproportionately impaired at free recall [9,12,13,16,55], and they are significantly impaired on tests of memory for context information [6,15,24,26,28]. In addition, patients with prefrontal damage may exhibit memory distortions such as false recognition [7,40,45,46,50,59], and in the extreme, confabulation [1,21,22,30,54].

Interest in the role of prefrontal cortex in episodic memory has intensified due to results from recent neuroimaging studies showing robust activation of multiple

prefrontal regions [2,5,32,33,61,62]. Findings from these studies suggest not only that prefrontal cortex is important for memory processing but also that left and right prefrontal regions make distinct contributions [32,33,61]. These laterality patterns were noted in the Hemispheric Encoding Retrieval Asymmetry (HERA) model proposed by Tulving and colleagues [61]. According to this model, left prefrontal cortex is more involved in episodic memory encoding and in semantic memory retrieval, whereas right prefrontal cortex is more involved in episodic retrieval. This view was supported by a meta-analysis conducted by Nyberg and colleagues [33] showing that of 16 positron emission tomography (PET) studies involving encoding tasks, 13 reported significant prefrontal activations, all in the left hemisphere. And of 31 PET studies of episodic retrieval, 29 reported significant prefrontal activation and 26 of these reported larger prefrontal blood flow increases in the right hemisphere. Subsequent studies using functional magnetic resonance imaging (fMRI) have also reported right prefrontal activation during episodic retrieval [3,4,38,49].

Findings of hemispheric asymmetry during episodic retrieval were interpreted differently by Nolde, Johnson, and Raye [32]. These researchers noted that findings of

<sup>\*</sup> Corresponding author. Tel.: +1-847-467-3370; Fax: +1-847-491-7859; E-mail: kap@nwu.edu; URL: <http://www.nwu.edu/people/kap>

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<sup>2</sup> Present address: Department of Neurology, University of Pennsylvania, 3 West Gates, 3400 Spruce St., Philadelphia, PA 19104-4283, USA.

right prefrontal activation were based on comparisons between episodic retrieval tasks and non-memory baseline tasks. On the other hand, comparisons in some experiments were made between difficult and relatively less difficult episodic memory tests. In these contrasts, prefrontal activations were more often left-lateralized or bilateral. For example, Nolde, Johnson, and D'Esposito [31] conducted an event-related fMRI study in which participants were scanned during recognition testing with studied words, words corresponding to studied pictures, and unstudied words. In the old/new condition, participants attempted to discriminate between words that were or were not studied (either as a picture or as a word). In the source condition, participants were asked to specify whether each word was studied as a picture, studied as a word, or previously unstudied. Thus, the source condition placed greater demands on retrieval and evaluation of specific perceptual attributes of memories than did the old/new condition. Results showed that left prefrontal regions were more active during the source condition than during the old/new condition, whereas right prefrontal regions were activated equally during the two test conditions.

To explain these results, Nolde and colleagues [32] suggested that right prefrontal regions implement 'heuristic processing' or evaluation of memories based on a single dimension, such as familiarity. In contrast, they argued that left prefrontal regions implement 'systematic processing' or evaluation of multiple memory characteristics in order to make a memory judgment. Thus, in contrast with the HERA model, these investigators proposed that left prefrontal regions play an important role in episodic retrieval.

Whereas the neuroimaging studies reviewed above used methods that rely on hemodynamic correlates of neural activity, other studies have examined patterns of frontal activity by recording event-related brain potentials (ERPs) during tests of episodic retrieval [8,19,43,44,51,60,64–68]. ERPs are scalp-recorded measures of electroencephalographic activity synchronized to an external event. ERPs thus allow direct measurement of brain activity with temporal resolution on the order of milliseconds. Although present methods do not allow for precise localization of intracranial sources of scalp-recorded ERPs, their high temporal resolution can provide a useful complement to neuroimaging methods [10,23,34,48].

In a previous experiment, we found that ERPs implicated prefrontal regions in episodic memory retrieval [44]. Participants studied pictures of objects and were tested with three types of stimuli: studied objects, studied objects with altered aspect ratios, and previously unstudied objects. Results from two memory tests were compared. In the general test, participants were instructed to disregard alterations in making old/new judgments, whereas in the specific test they were instructed to judge an object 'old' only if it was identical to a studied object and to judge all other objects 'new.' Thus, the specific test placed greater demands on the retrieval and evaluation of specific percep-

tual information than did the general test. We reasoned that frontal ERP differences between the specific and general tests could provide insights into the role of prefrontal cortex in retrieval as follows. If prefrontal regions are selectively engaged following successful retrieval of specific event information, then frontal ERP differences would be prominent only for old pictures. But if prefrontal regions implement strategic processing during retrieval attempts, then frontal ERP differences would be observed for both old and new pictures.

The central electrophysiological finding was that ERPs were enhanced during the specific test relative to the general test. These effects were maximal over left frontal scalp regions. The finding that these ERP differences were similar for old and new pictures suggested that they did not reflect successful recall of specific perceptual details of studied pictures. We concluded instead that we had recorded a neural correlate of a process wherein specific perceptual attributes of recognition cues were compared with the contents of memory. The left frontal scalp topography of this effect and the neuroimaging findings reviewed above support the hypothesis that this evaluative process is implemented by left prefrontal cortex.

Note that in the specific test employed in our previous study [44], participants were required to judge whether or not studied pictures had been changed, but they were not required to remember anything specific about the change. Conceivably, participants were able to evaluate the extent to which studied pictures were altered without engaging in the more active process of recalling the precise way in which studied pictures were altered. Accordingly, it remains an open question whether frontal brain potentials associated with successful retrieval would be produced if participants were given the more demanding requirement of recalling perceptual detail, rather than just evaluating whether or not there was a match between the recognition cue and the contents of memory.

In the present study, we investigated whether frontal brain potentials associated with successful retrieval would be observed if participants were encouraged to recall perceptual detail. The design of the study is schematically depicted in Fig. 1. Participants studied line drawings of






Stimuli		Correct Response	
Study	Test	General Test	Specific Test
		"Old"	"Old/Larger"
		"Old"	"Old/Smaller"
		"New"	"New"

Fig. 1. Sample stimuli and responses in each test condition.

objects and were tested with size-changed versions of studied objects and new objects. In the general test, they were required to make old–new judgments, whereas in the specific test they were additionally required to indicate whether old objects were studied in a larger or smaller size. By comparing brain potentials recorded during the specific and general test conditions, we were able to investigate frontal activity and its association with strategic retrieval and with successful recall of specific perceptual information.

## 2. Methods

### 2.1. Participants

Two men and ten women from the Northwestern University community were paid for participating in the experiment. They were right-handed and ranged in age from 18 to 22 years. Data from four additional participants were discarded (two because of technical difficulties and two because of excessive eye and muscle artifacts).

### 2.2. Stimuli

Stimuli were derived from 300 pictures of objects used in previous studies of picture memory [39,53]. Each picture was manipulated to create a small version (75% scaling) and a large version (135% scaling) so that a total of 900 pictures were used. The average picture size was approximately  $40 \times 40$  mm.

### 2.3. Procedure

Each participant was fitted with an electrode cap (see below) and seated in a sound-attenuating chamber. Participants were given task instructions and also instructed to try to relax neck and facial muscles and to avoid blinking or moving while performing the experimental tasks. Stimuli were presented on a video monitor about 140 cm away. Responses were made with a joystick held in the right hand. Participants practiced mock trials of each task before beginning the experiment to assure that they fully understood the task requirements.

The experiment consisted of 20 study-test blocks. In the study phase of each block, ten pictures (half small and half large versions) were presented twice, each time in a different random order. The exposure duration for each picture during the study phase was 630 ms. A fixation cross appeared after each picture and the next trial began 2.65 s after the response. Participants were to push the joystick to the right if the highest point on the right half of the picture was higher than the highest point on the left half, and to the left if the highest point on the left half was higher or if both points were equally high. This study task was used to ensure that participants encoded each drawing in a perceptually detailed manner. After the last picture, a filler picture was shown, followed by a rectangle, and the

participant was asked if the last picture was wider than the rectangle. This question was asked to minimize recency effects. Participants were then given feedback on their performance during the study run and allowed to blink or stretch. The average delay between the last study picture and the test phase was approximately 1 min.

At the beginning of the test phase, a cue was presented indicating whether a general test or a specific test would be given. Participants were instructed that three types of pictures would be presented during the test phase: reduced-size versions of studied pictures (old/smaller), enlarged-size versions of studied pictures (old/larger), and unstudied pictures (new). In the general test, instructions were to ignore size changes and push the joystick up for old pictures and down for new pictures. In the specific test, instructions were to push the joystick to the left for old/smaller pictures, to the right for old/larger pictures, and down for new pictures. Fifteen unscaled pictures (five of each type) were shown in a random order during the test phase of each block (the old/smaller pictures had been studied in enlarged format and the old/larger in reduced format). Each picture was presented for 300 ms and then replaced by a fixation cross. The next trial began 2.65 ms after the participant's response.

The specific and general tests were given in a pseudo-random order, with the provision that there were no more than two consecutive blocks of either test type. The mapping of pictures to tests (specific vs. general) and stimulus types (old/larger vs. old/smaller vs. new) was counterbalanced across participants. Behavioral and ERP data for studied pictures were collapsed across the old/smaller and old/larger categories because no differences were expected or observed between these two types of pictures.

### 2.4. ERP recording and analysis

Electroencephalographic recordings were made using an elastic cap with 21 tin electrodes at standard scalp locations (Fpz, Fp1, Fp2, Fz, F3, F4, F7, F8, Cz, C3, C4, Pz, P3, P4, T3, T4, T5, T6, Oz, O1, O2). Scalp electrode impedances were reduced below 5 K Ohms. Electrooculographic (EOG) recordings were made using an electrode below the right eye (vertical EOG) and electrodes lateral to each eye (horizontal EOG). The band pass was .1–100 Hz. Scalp and vertical EOG electrodes were referenced to a left mastoid electrode during recording and the reference was changed to the average of the left and right mastoid recordings off-line. Trials containing artifacts due to eye movements that occurred from 100 ms pre-stimulus to 1200 ms post-stimulus were excluded prior to averaging ( $M = 11.0\%$ ,  $SE = 3.2\%$ ).

### 2.5. ERP analysis methods

Statistical analyses were restricted to artifact-free trials on which participants correctly identified an item as old or new. We characterized the primary effects by focusing on

ERPs from a selection of eight scalp locations (F7, F8, T3, T4, P3, P4, O1, O2). Topographic maps were used to display additional distributional information. The analyses most relevant to the goals of this study concerned ERP differences between the specific and general tests, referred to as ‘test effects’. In light of findings from our previous study [44], we expected ERPs recorded during the specific test to exhibit enhanced positivity relative to those recorded during the general test, and we expected this effect to be most pronounced at frontal scalp sites. Planned comparisons were thus conducted on test effects observed at frontal sites using an alpha level of .05 for each comparison. In addition, we conducted analyses on ERP test effects observed at other scalp locations, and a Bonferroni-corrected alpha level was used for these analyses (.017), based on the number of tests computed for each epoch (three). Interaction terms that were significant by these criteria were followed up with *t*-tests to determine the source of the effect. Analyses that revealed significant Test  $\times$  Hemisphere interactions were repeated after rescaling mean amplitudes by the vector-length method to avoid confounding amplitude differences with topography differences [27].

### 3. Results

#### 3.1. Behavioral results

Recognition accuracy results are shown in Fig. 2(A). An analysis of variance (ANOVA) revealed no significant differences in item recognition accuracy between old and new pictures [ $F(1,11) < 1$ ] or between test conditions [ $F(1,11) = 1.22$ ,  $p = .294$ ] and no significant Stimulus Type  $\times$  Condition interaction [ $F(1,11) < 1$ ]. The mean accuracy of judgments of size change in the specific test was 82.5% (range = 72–92; SD = 8.7).

Reaction times (RTs) for correct responses are shown in Fig. 2(B). RTs were slower in the specific test than the general test [ $F(1,11) = 97.56$ ,  $p < .001$ ] and slower for old pictures than for new pictures [ $F(1,11) = 74.67$ ,  $p < .001$ ]. However, a significant Stimulus Type  $\times$  Condition interaction was also observed [ $F(1,11) = 42.91$ ,  $p < .001$ ], and *t*-tests showed that RTs were significantly slower for old than for new pictures in the specific test [ $t(11) = 7.74$ ,  $p < .001$ ] but not in the general test [ $t(11) = 1.48$ ,  $p = .167$ ].

#### 3.2. ERP results

ERPs recorded during each test condition are shown for old and new pictures in Fig. 3. Mean amplitude measurements were made over successive 200 ms intervals to calculate ERP differences between the specific and general tests (Fig. 4). Topographic maps of these ERP test effects are shown for old pictures in Fig. 5 and for new pictures in

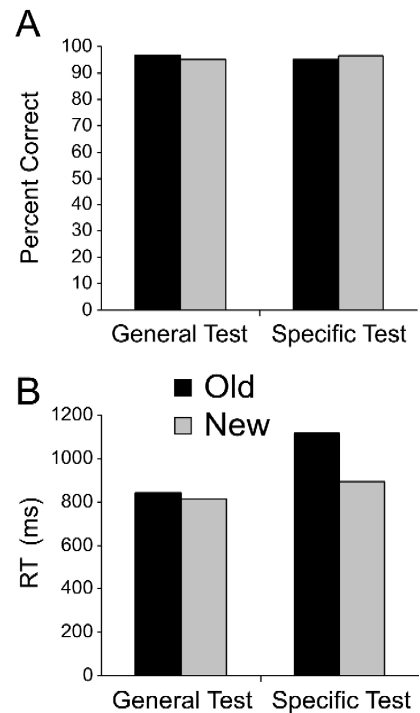


Fig. 2. Behavioral results for each condition. (A) Mean recognition accuracy. (B) Mean reaction time for correct responses.

Fig. 6. As described below in more detail, three different test effects were apparent. First, frontal potentials were more positive during the specific test than during the general test from approximately 200 to 1000 ms, and this ERP test effect was larger in magnitude for old than for new pictures. Second, a test effect maximal over left posterior scalp regions from approximately 400 to 900 ms was only seen for old pictures. Third, a test effect was observed after 900 ms at parietal and occipital scalp locations for both old and new pictures.

#### 3.3. Test effects for old pictures

Mean ERP amplitudes to old pictures recorded from pairs of left and right frontal, temporal, parietal, and occipital electrodes (as shown in the left portion of Fig. 3) were analyzed in successive 200 ms intervals from 200 to 1200 ms. Results from corresponding Test (specific vs. general)  $\times$  Hemisphere (left vs. right) ANOVAs are shown in Table 1. For the 200 to 400 ms interval, specific test ERPs were significantly more positive than general test ERPs at frontal locations with a similar trend at temporal locations. In addition, as shown in the table, a significant Test  $\times$  Hemisphere interaction was observed at occipital locations during this interval, with a similar marginal interaction at parietal sites. The interaction at occipital sites was also significant when the analysis was repeated on rescaled mean amplitudes [ $F(1,11) = 20.73$ ,  $p = .001$ ], suggesting that the interaction reflected a true topography difference between the two conditions. *T*-tests designed to

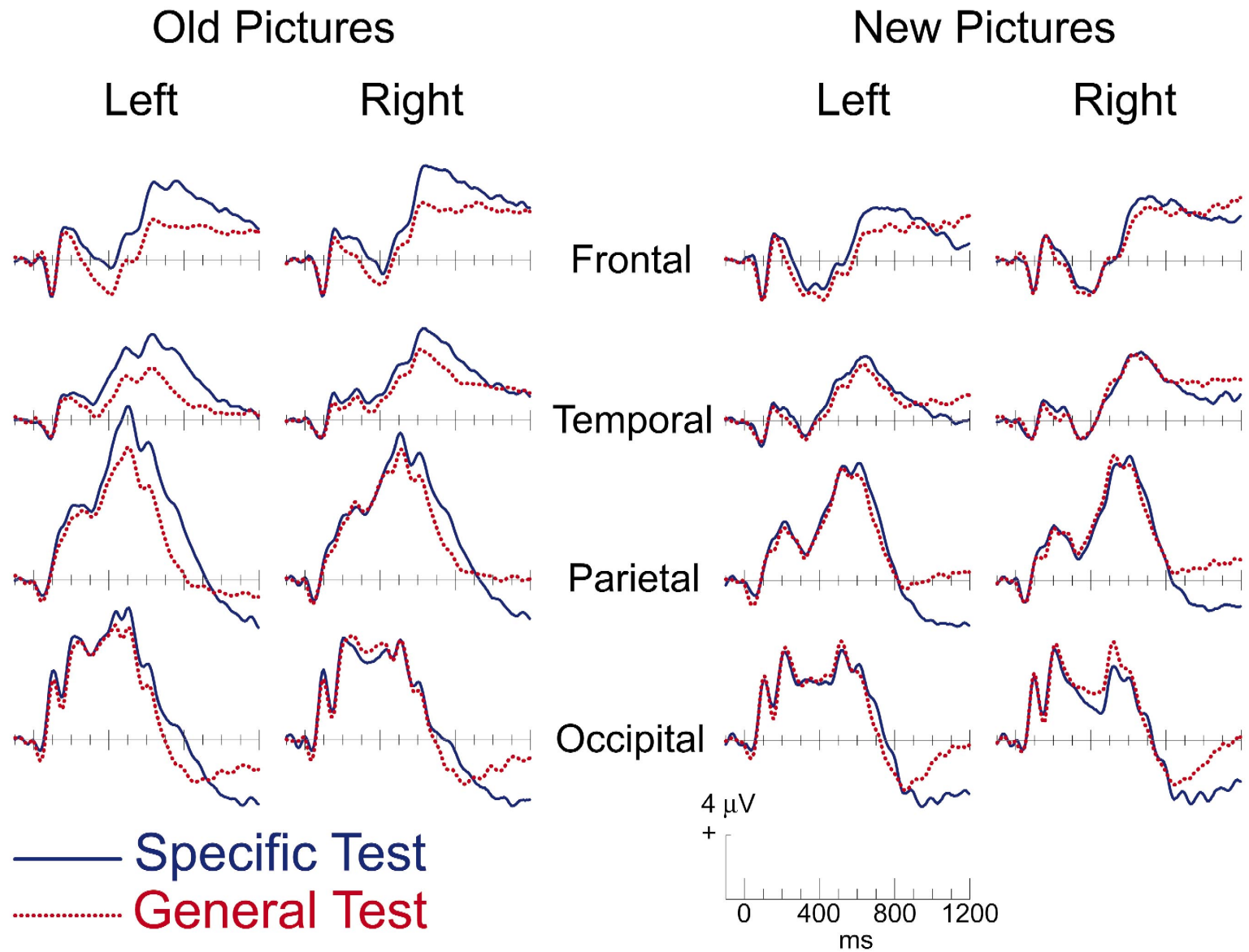


Fig. 3. ERP test effects for old and new pictures. ERPs recorded during the specific test (solid) and the general test (dotted) are shown for bilateral frontal (F7/F8), temporal (T3/T4), parietal (P3/P4), and occipital (O1/O2) sites.

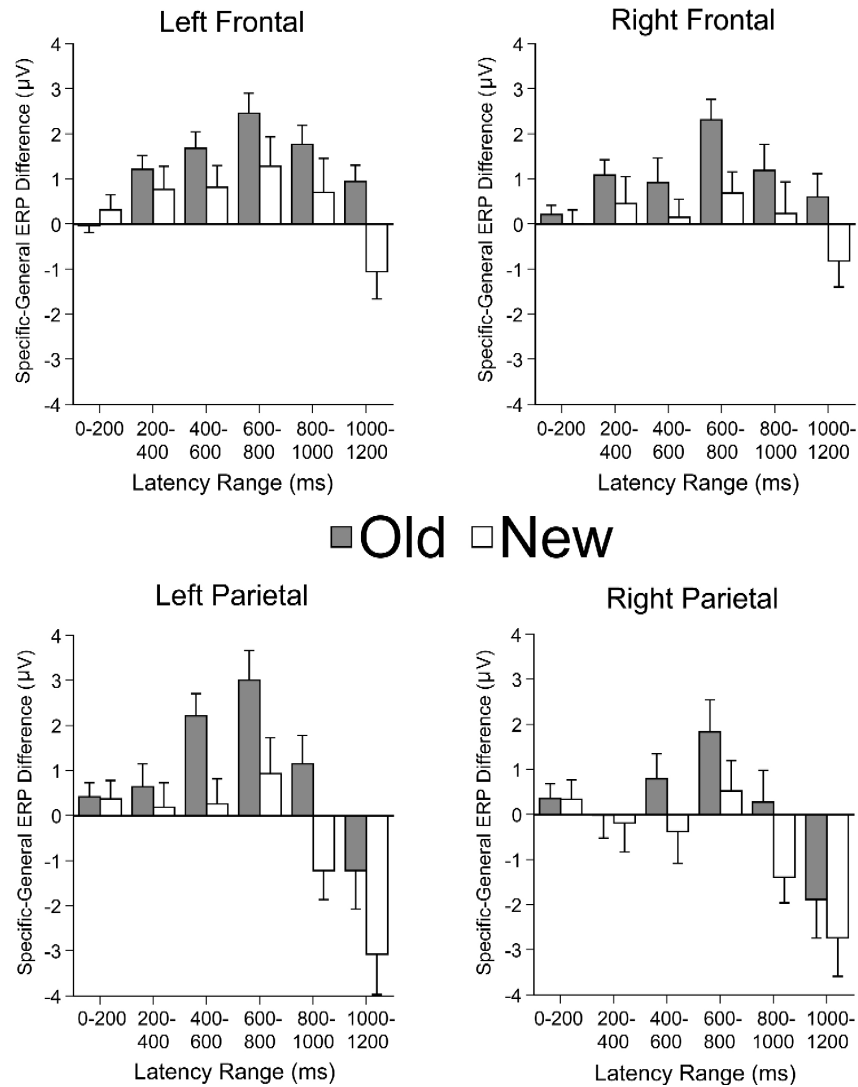


Fig. 4. Measurements of ERP test effects for frontal (F7/F8) and parietal (P3/P4) locations. Mean amplitude differences between specific test ERPs and general test ERPs are shown for consecutive 200 ms epochs from 0 to 1200 ms. Error bars show standard errors of the mean.

follow up this interaction failed to demonstrate significant test effects at either the left or the right occipital location [ $t(11)$ 's  $< 1.3$ ,  $p$ 's  $> .20$ ].

For the 400 to 600 ms interval, ERPs were reliably more positive during the specific test than during the general test at frontal, temporal, and parietal sites. In addition, significant Test  $\times$  Hemisphere interactions were observed at temporal, parietal, and occipital sites. These interactions were also significant when analyses were repeated on rescaled amplitudes [temporal:  $F(1,11) = 8.47$ ,  $p < .014$ ; parietal:  $F(1,11) = 31.68$ ,  $p < .001$ ; occipital:  $F(1,11) = 15.22$ ,  $p = .002$ ]. As shown in Figs. 3–5, these interactions reflected the tendency for test effects to be more pronounced over the left hemisphere than over the right. Follow-up  $t$ -tests confirmed that specific test ERPs were reliably more positive than general test ERPs at the

left temporal site [ $t(11) = 4.97$ ,  $p < .001$ ] and the left parietal site [ $t(11) = 4.49$ ,  $p < .001$ ] sites with a similar trend at the left occipital site [ $t(11) = 2.14$ ,  $p = .055$ ]. In contrast, differences were not statistically significant over homologous right hemisphere sites [all  $t(11)$ 's  $< 1.7$ ,  $p$ 's  $> .10$ ].

For the 600 to 800 ms interval, specific test ERPs were again more positive than general test ERPs at frontal, temporal, and parietal sites. In addition, Test  $\times$  Hemisphere interactions were observed at parietal and occipital scalp locations, with a similar trend at temporal locations. When analyses at parietal and occipital locations were repeated on rescaled data, the Test  $\times$  Hemisphere interaction was significant for parietal locations [ $F(1,11) = 11.84$ ,  $p = .006$ ] but not for occipital locations [ $F(1,11) < 1$ ]. Follow-up  $t$ -tests showed that test effects were significant

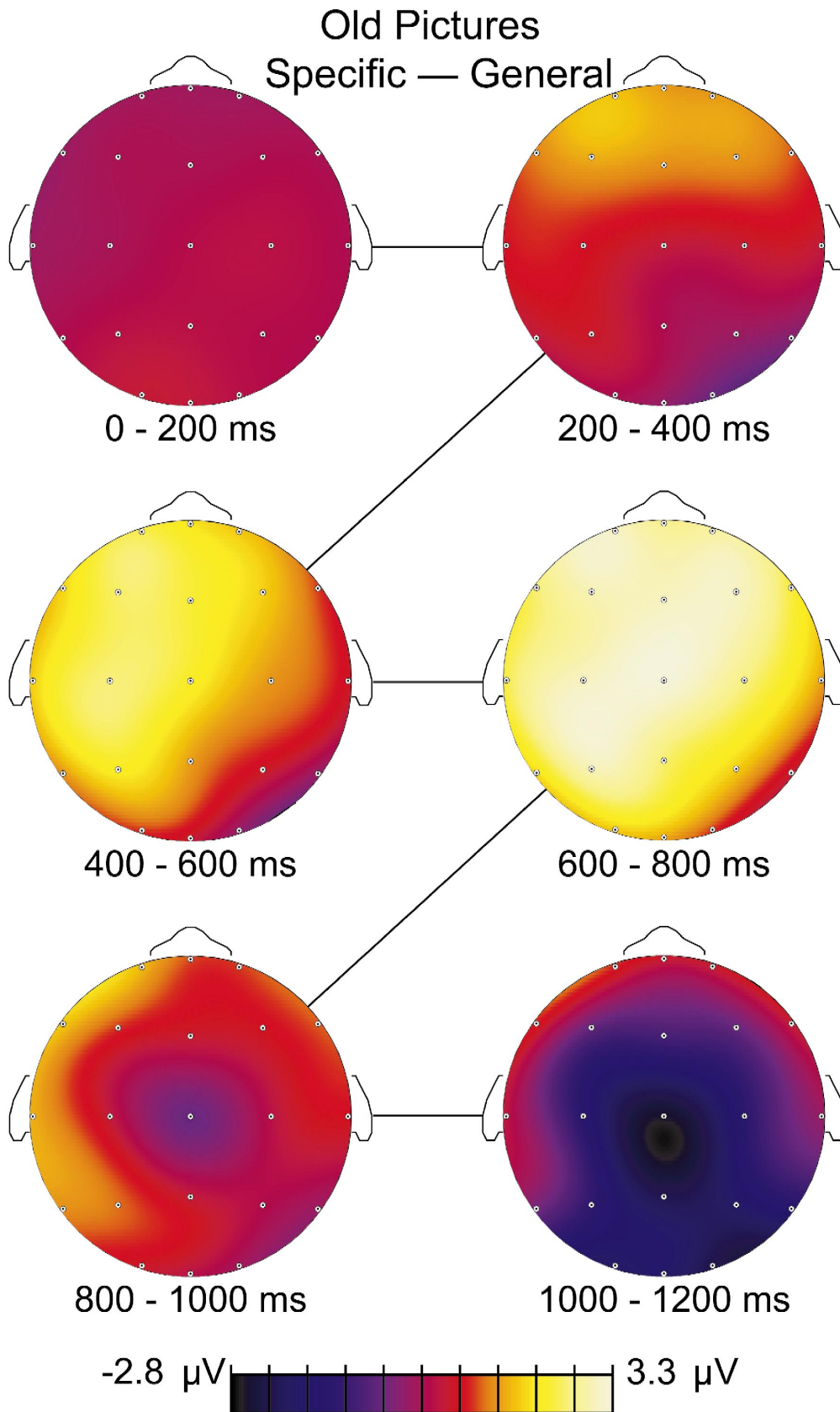


Fig. 5. Topographic maps depicting the time course of ERP test effects for old pictures. Mean amplitude differences were measured in consecutive 200 ms epochs from 0 to 1200 ms and displayed using a surface spline interpolation. Small circles represent electrode locations on a schematic head, as viewed from above.

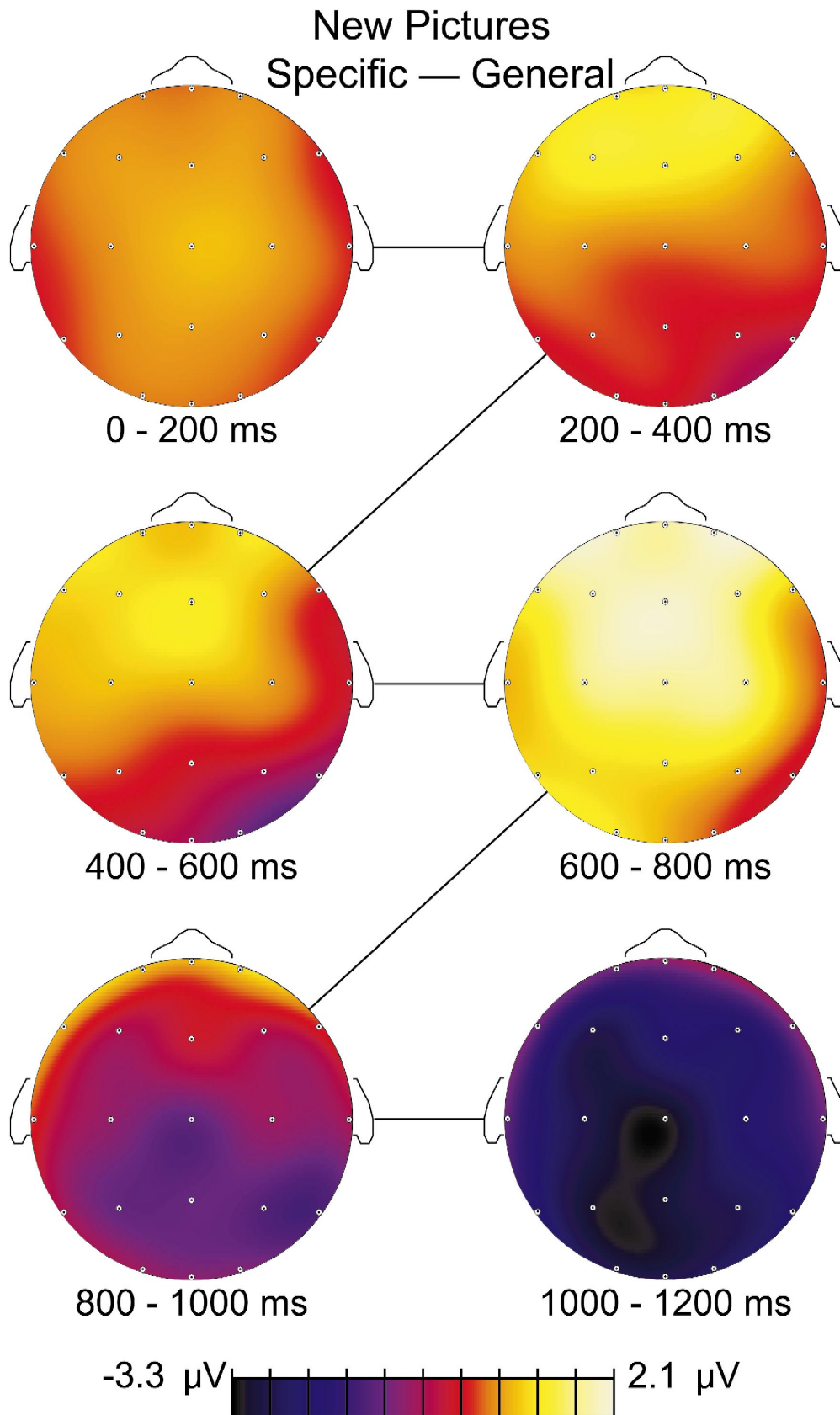


Fig. 6. Topographic maps depicting the time course of ERP test effects for new pictures. Mean amplitude differences were measured in consecutive 200 ms epochs from 0 to 1200 ms and displayed using a surface spline interpolation. Small circles represent electrode locations on a schematic head, as viewed from above.



Table 1  
ANOVA results for ERPs to old pictures for main effect of test and test by hemisphere interaction

Location	Effect	Epoch (ms)									
		200 to 400		400 to 600		600 to 800		800 to 1000		1000 to 1200	
		<i>F</i> (1,11)	<i>p</i>	<i>F</i> (1,11)	<i>p</i>	<i>F</i> (1,11)	<i>p</i>	<i>F</i> (1,11)	<i>p</i>	<i>F</i> (1,11)	<i>p</i>
Frontal (F7/F8)	Test effect	<b>20.55</b>	<b>.001</b>	<b>9.59</b>	<b>.01</b>	<b>38.20</b>	<b>&lt; .001</b>	<b>13.19</b>	<b>.004</b>	4.39	.06
	Interaction	–	–	3.73	.080	–	–	–	–	–	–
Temporal (T3/T4)	Test effect	6.73	.025	<b>12.73</b>	<b>.004</b>	<b>36.08</b>	<b>&lt; .001</b>	<b>15.99</b>	<b>.008</b>	–	–
	Interaction	–	–	<b>8.08</b>	<b>.016</b>	6.02	.032	2.06	–	–	–
Parietal (P3/P4)	Test effect	–	–	<b>8.52</b>	<b>.014</b>	<b>12.85</b>	<b>.004</b>	1.21	–	3.30	.097
	Interaction	<b>7.83</b>	<b>.017</b>	<b>38.73</b>	<b>&lt; .001</b>	<b>12.66</b>	<b>.004</b>	6.68	.025	4.36	.061
Occipital (O1/O2)	Test effect	–	–	1.04	–	3.23	–	–	–	<b>11.62</b>	<b>.006</b>
	Interaction	<b>20.12</b>	<b>.001</b>	<b>30.73</b>	<b>&lt; .001</b>	<b>10.15</b>	<b>.009</b>	3.21	–	1.63	–

Note: Only *F*-values > 1 and *p*-values < .1 are shown. Significant effects are shown in bold (using alpha = .05 for frontal locations and alpha = .017 for other locations, as described in Section 2.5).

at parietal sites on both sides and at the left occipital site [ $t(11)$ 's > 2.30,  $p$ 's < .05], but not at the right occipital site [ $t(11) = 1.25$ ,  $p = .237$ ].

For the 800 to 1000 ms interval, main effects for test were only seen at frontal and temporal scalp locations. Finally, during the 1000 to 1200 ms interval, ERPs were significantly more negative during the specific test than during the general test at occipital sites. This effect was maximal at the central midline site.

Overall, analyses on ERPs to old pictures confirmed three results. First, ERPs recorded at bilateral frontal and temporal scalp locations were more positive during the specific test than during the general test from 200 to 1000 ms. Second, ERPs recorded at parietal scalp locations were also more positive during the specific test from 400 to 800 ms, and this test effect was left-lateralized. Third, at 1000 ms ERPs became more negative during the specific test than during the general test at posterior scalp locations.

### 3.4. Test effects for new pictures

Results from ANOVAs on ERPs to new pictures measured over successive 200 ms intervals from 200 to 1200

ms are shown in Table 2. For the 200 to 400 ms interval, no significant differences between specific and general test ERPs were found. Analyses for the 400 to 600 ms interval showed significant Test  $\times$  Hemisphere interactions at frontal and temporal locations with a similar trend at occipital locations. The Test  $\times$  Hemisphere interactions at frontal and temporal locations were also significant when analyses were repeated on rescaled mean amplitudes [ $F(1,11)$ 's > 5.10,  $p$ 's < .05]. Follow-up *t*-tests failed to demonstrate significant test effects on either left [ $t(11)$ 's < 2,  $p$ 's > .08] or right [ $t(11)$ 's < 1.55,  $p$ 's > .15] sides during this interval.

For the 600 to 800 ms interval, ERPs were significantly more positive during the specific test than during the general test at frontal sites. In addition, a marginal Test  $\times$  Hemisphere interaction was observed at occipital sites. For the 800 to 1000 ms interval, ERPs were marginally more negative during the specific test than during the general test at parietal scalp locations. This negative test effect was significant during the 1000 to 1200 ms interval at parietal and occipital scalp locations, with a similar trend at temporal locations.

Table 2  
ANOVA results for ERPs to new pictures for main effect of test and test by hemisphere interaction

Location	Effect	Epoch (ms)									
		200 to 400		400 to 600		600 to 800		800 to 1000		1000 to 1200	
		<i>F</i> (1,11)	<i>p</i>	<i>F</i> (1,11)	<i>p</i>	<i>F</i> (1,11)	<i>p</i>	<i>F</i> (1,11)	<i>p</i>	<i>F</i> (1,11)	<i>p</i>
Frontal (F7/F8)	Test effect	1.49	–	1.33	–	<b>6.19</b>	<b>.03</b>	–	–	3.01	–
	Interaction	–	–	<b>5.30</b>	<b>.042</b>	–	–	–	–	–	–
Temporal (T3/T4)	Test effect	–	–	–	–	–	–	–	–	7.62	.019
	Interaction	–	–	<b>9.52</b>	<b>.01</b>	1.46	–	3.02	–	–	–
Parietal (P3/P4)	Test effect	2.50	–	–	–	1.09	–	5.11	.045	<b>11.41</b>	<b>.006</b>
	Interaction	–	–	2.27	–	–	–	–	–	–	–
Occipital (O1/O2)	Test effect	–	–	1.06	–	–	–	3.21	–	<b>12.61</b>	<b>.005</b>
	Interaction	3.32	.095	7.63	.018	7.73	.018	–	–	–	–

Note: Only *F*-values > 1 and *p*-values < .1 are shown. Significant effects are shown in bold (using alpha = .05 for frontal locations and alpha = .017 for other locations, as described in Section 2.5).

In sum, test effects for new pictures were apparent at frontal locations from 600 to 800 ms. As shown in Figs. 3–6, this frontal ERP difference was smaller in magnitude but topographically similar to the frontal test effect for old pictures. In addition, ERPs were more negative during the specific test than during the general test at parietal and occipital locations from 1000 to 1200 ms. This effect was similar to the late negative test effect for old pictures. The left posterior test effect observed for old pictures from 400 to 800 ms was not observed for new pictures.

### 3.5. Comparison of test effects for old and new pictures

Further analyses were conducted to directly compare the scalp topographies of test effects between old and new pictures. In these analyses, specific-general ERP differences for each epoch were normalized by the vector-length method [27]. Measures from all 21 electrode locations

were submitted to a Location  $\times$  Stimulus Type ANOVA for each 200 ms epoch from 200 to 1200 ms, corresponding to the maps shown in Figs. 5 and 6. No reliable topographic differences were revealed by these comparisons [ $F(20,220)$ 's  $< 1$ ].

### 3.6. Effects of reference electrode

To confirm that the topographies of the ERP test effects we observed were not corrupted by differential electro-physiological activity at one of the mastoid electrodes, left- and right- mastoid referenced ERPs were also calculated using re-referencing, and the topographies of ERP test effects using these different referencing methods were compared. As shown in Fig. 7, although the magnitude of ERP test effects varied slightly according to which referencing method was used, the topography of ERP test effects remained stable. These findings suggest that the

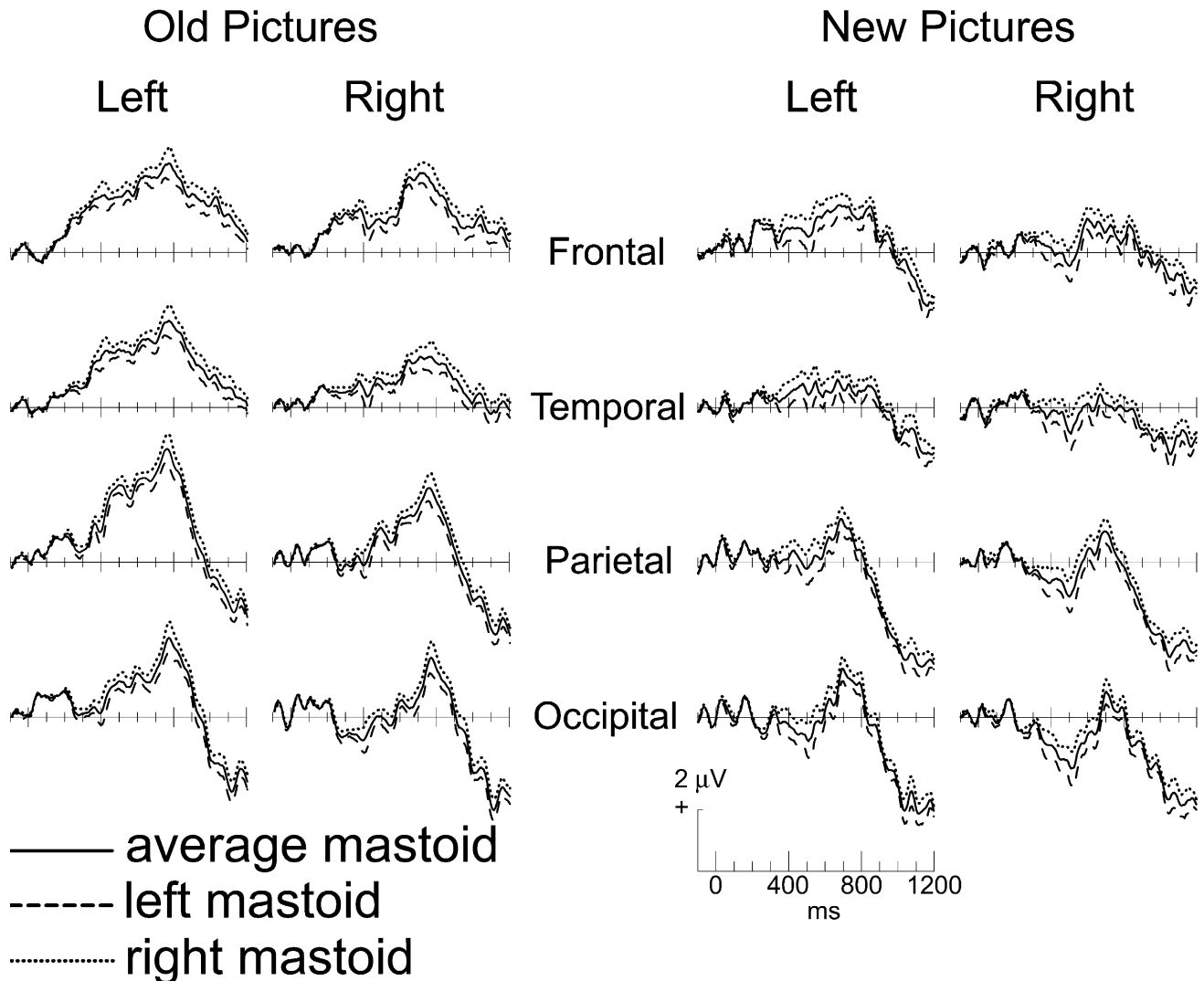


Fig. 7. ERP difference waves (specific test–general test) calculated with three different reference methods: averaged-mastoid (solid), left-mastoid (dashed), and right-mastoid (dotted).

pattern of results was not corrupted by using average mastoid referenced ERPs for our statistical analyses.

#### 4. Discussion

The purpose of this experiment was to monitor left and right frontal brain potentials during retrieval and evaluation of learned information. Brain potentials were compared between a general test that required memory for the gist of studied pictures and a specific test that additionally required recall of the relative size of studied pictures. Comparisons revealed multiple ERP differences between the specific and general test conditions.

First, ERPs were more positive during the specific test than during the general test at frontal scalp sites. This test effect was statistically reliable for old pictures from 200 to 1000 ms, and largest from 600 to 800 ms. For new pictures, a frontal test effect was observed from 600 to 800 ms with smaller differences visible earlier. Whereas these frontal test effects were produced for both old and new pictures, another distinctive test effect was elicited only by old pictures. This effect had a left posterior scalp topography and was significant from 400 to 800 ms. Finally, in the latter part of the epoch, ERPs to old and new pictures were more negative during the specific test than during the general test. We will discuss the frontal test effects first and then turn to the two additional test effects.

In general, frontal test effects can be attributed to either (1) strategic processing engaged more in the specific test than in the general test, (2) greater reactivation of size or other information from the study phase, or (3) both. However, the assumption that new pictures did not evoke successful retrieval makes it possible to narrow down the alternatives. Specifically, frontal test effects that were similar for old and new pictures, as in the 600 to 800 ms interval, can be firmly attributed to strategic processing. Larger frontal test effects for old than for new pictures can be explained by assuming that strategic processing was enhanced for old pictures. Another plausible alternative is that frontal test effects reflected a combination of strategic processing plus, for old pictures only, activity related to successful retrieval. Moreover, if some frontal activity was associated with successful retrieval, it may have been related to the left posterior test effect discussed below.

In our previous experiment [44], left frontal ERPs to old and new pictures were more positive during the specific test than the general test and there were minimal differences between results for old and new pictures. In the present experiment, a topographically similar, but less strongly lateralized test effect was evident for old and new pictures. In both experiments, participants were prompted to evaluate the correspondence between recognition cues and information retrieved from memory. The comparison of specific perceptual attributes of recognition cues with retrieved information was more likely to be engaged in the

specific test than in the general test. Frontal test effects in both experiments can thus be taken as neural correlates of the more extensive evaluation of specific perceptual attributes in the specific test.

Findings from a series of behavioral studies suggest that this memory monitoring process may be crucial for accurate episodic memory. For example, several studies have demonstrated that specific perceptual attributes of memories are critical for specifying the context of an event, termed ‘source memory’ [17]. Prior behavioral evidence suggests that the availability of detailed perceptual information at retrieval supports the phenomenological experience of conscious recollection [25,42]. Specific perceptual information is also a major cue in differentiating memories of thoughts, mental images, or imagined events from memories of experienced events [18,20].

The importance of retrieval and evaluation of specific perceptual information during episodic recollection was emphasized in the source monitoring framework proposed by Johnson and her colleagues [17,21]. According to this view:

... on average, memories from a specific external source (television) will have different qualities (sound, motion, and many visual details) than the memories from another source (the newspaper). Memory monitoring processes capitalize on such differences by evaluating memories (or mental experiences in general) for the expected characteristics of a given source (Ref. [21], p.138).

We postulate that our frontal ERP test effects represent neural correlates of these memory-monitoring processes. The bilateral topography of ERP test effects in this study and the strongly left-lateralized topography of frontal test effects in our previous study [44] are inconsistent with the view that right-prefrontal regions are more involved than homologous left prefrontal regions in episodic retrieval [33,61]. Of course, ERP asymmetries observed in scalp recordings do not imply that frontal neural activity is equivalently asymmetric, given that activity in one hemisphere can generate scalp potentials over the contralateral hemisphere. Nonetheless, findings from neuroimaging [11,31,32,44] converge on the view that left and right prefrontal regions are important in implementing these memory monitoring processes.

Furthermore, our findings converge with neuropsychological results suggesting that these monitoring processes break down in patients with prefrontal lesions. For example, the breakdown of monitoring processes to evaluate specific perceptual attributes of memories may explain the disproportionate impairment of source memory [6,15,24,26,28] and the incidence of memory distortions [7,21,22,30,40,45,46,50,54,59] in patients with prefrontal lesions. These patients may have access to specific perceptual attributes of memories but fail to attend to this infor-

mation when attempting to recall the source of a memory [7].

In addition to the frontal test effects described above, a left parietal test effect was apparent for old but not for new pictures (Figs. 3–6). This ERP test effect was topographically similar to ERP modulations reported in previous studies of source memory conducted by Wilding and colleagues [64–68]. In these studies, participants studied words spoken in a male or female voice. Next, they were given a recognition test with visual words and were asked to specify the gender of the speaker for words judged old. Across these studies, ERPs to old items were more positive-going than those to new items, with these differences largest over left posterior and right frontal scalp regions. Furthermore, these ‘old–new effects’ were larger in magnitude when the speaker’s voice was correctly recalled, suggesting that they were associated with recollection of the voice information associated with studied words. We have also linked posterior ERPs to recollective processing in prior studies that made use of memory dissociations between implicit and explicit memory tests [35–37].

Although our primary intentions in the present experiment were to focus on differences in brain potentials between the two test conditions, it should be noted that the left posterior test effect can also be conceptualized as a type of old–new effect. ERPs to old and new pictures in each condition at the left parietal scalp site are shown in Fig. 8. An old–new effect was observed in both test conditions from 200 to 500 ms, but old–new differences continued from 500 to 1200 ms during the specific test. In light of various findings associating similar ERP effects with recollection (see Ref. [47] for review), we propose that the left posterior test effect seen in this study reflects the recollection of additional details of studied pictures in the specific test. Our ERP results thus demonstrated a dissociation between posterior activity reflecting the reactivation of stored information and anterior activity reflecting the monitoring and evaluation of retrieved information. These findings parallel recent neuroimaging results associating posterior cortical activity with reactivation of stored information and prefrontal activity with the monitoring and manipulation of that information [41].

The finding that ERPs after about 900 ms were more negative during the specific test than during the general test was unexpected, given that no such effect was apparent in our previous study [44]. The posterior distribution of this effect may have been exaggerated due to overlap with anterior test effects of the opposite polarity from 200 to 1000 ms. The finding that the late test effect appeared to begin earlier and to have a broader topography for new than for old pictures may have actually been related to the fact that the overlapping frontal test effect was smaller for new pictures, rather than to differences in the late effect per se. In light of the late onset of the negative test effect relative to reaction times, however, it is unlikely that it reflects processes that were critical for making memory

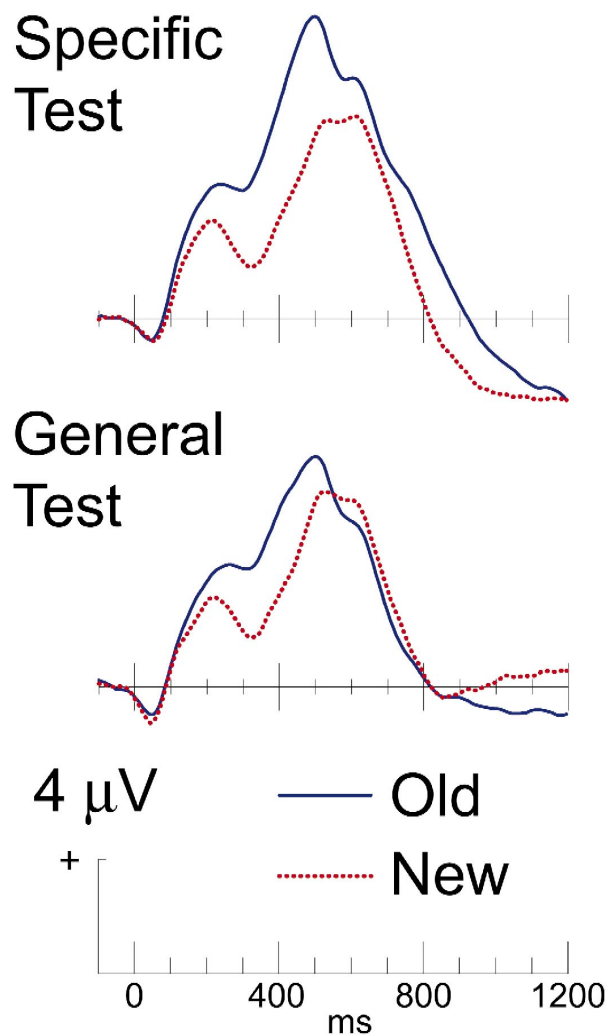


Fig. 8. Old–new ERP effects during each test condition for the left parietal scalp location.

judgments in either test condition. Instead, the effect may reflect a divergence in cognitive activities between the two test conditions that occurred after participants made recognition decisions. For example, it is possible that participants were more confident in recognition responses made during the general test than in responses made during the specific test. It is also possible that continued processing and evaluation of relative size information continued in the specific test but not in the general test, and that this post-decision processing was associated with widespread negative potentials.

In summary, results from the present study have revealed several insights into the role of prefrontal cortex in episodic memory retrieval. First, in contrast to the HERA model, our results support the view that left and right prefrontal regions both make important contributions to episodic retrieval. Second, our results demonstrate that frontal activity can be associated both with the reactivation of stored information (for old pictures) and with evaluative processing (for old and new pictures). We also observed

left posterior activity related to the reactivation of stored information. Although it remains unclear exactly how left and right prefrontal regions differ in their functions during episodic retrieval, our results indicate that these asymmetries are more complex than suggested by models such as HERA.

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