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Research report

Using ERPs to dissociate recollection from familiarity in picture recognition

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Abstract

Dual process theories posit that separate recollection and familiarity processes contribute to recognition memory. Previous research, testing recognition memory for words, indicates that event-related brain potentials (ERPs) can be used to dissociate recollection from familiarity. It has been hypothesized that the FN400 ERP old/new effect (300–500 ms) varies with stimulus familiarity, but the parietal ERP old/new effect (400–800 ms) varies with recollection. The results reported here are consistent with this hypothesis, extending it to the recognition of pictures when subjects had to discriminate between studied pictures, highly familiar lures (mirror-reversals of studied pictures), and new pictures. Furthermore, the parietal old/new effect showed significant recollection-related differences only for subjects with good behavioral discrimination between studied items and similar lures.

Theme: Neural basis of behaviour

Topic: Cognition: learning and memory-humans

Keywords: Event-related potential; ERP; Recognition memory; Familiarity; Recollection

1. Introduction

According to dual process theories of recognition memory, two distinct processes contribute to our ability to discriminate between studied and non-studied items: familiarity and recollection [21,24,33,38,77]. Familiarity is often thought to arise from an assessment of the global similarity between a test item and all study-list information in memory (as in the global matching models reviewed in Refs. [4,43,46]). Recollection is a process that enables the retrieval of specific information about studied items such as physical attributes or associative/contextual/source information. Face recognition provides a classic example of this distinction because we have all had the experience of knowing a face is familiar despite an inability to recollect details such as the person's name [34].

Recent evidence suggests that familiarity and recollection processes may be dissociable with the measurement of event-related brain potentials (ERPs). Starting ~300 ms after the onset of a recognition test item, ERPs are more positive when elicited by previously studied (old) than non-studied (new) stimuli (reviewed in Refs. [27,56]). These 'ERP old/new effects' co-occur with the well-known N400 and P300 ERP components [39,65]. Recent research has suggested that an earlier aspect of the ERP old/new effect (300–500 ms) may be related to familiarity whereas a later aspect (400–800 ms) may be related to recollection (reviewed in Refs. [17,36]; also see Refs. [13,19,37,60]). The 300–500-ms familiarity-related effect has been called the 'FN400 old/new effect' [6,7] because of its similarity to the N400 component related to semantic processing [30,31]. However, the FN400 old/new effect is often more frontally distributed than the centro-parietal N400 typically observed in studies of language. The 400–800-ms recollection-related ERP effect has been called the parietal old/new effect [1,59,60,73–75].

The evidence for relating the parietal old/new effect to recollection is particularly strong. First, the parietal old/

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new effect is associated with the recollection of specific information such as study modality [75,76], speaker's voice [59,73,74], and temporal source [68]. That is, the parietal old/new effect is primarily observed when such details are correctly recollected, but not when recognition occurs without such recollections. Second, the parietal old/new effect is sensitive to variables thought to affect recollection more than familiarity such as depth of processing [40,41,57,61]. Third, when subjects are asked to introspectively differentiate words specifically 'remembered' from those merely 'known' to be old, larger parietal old/new effects are associated with 'remembering' than 'knowing' [14,59,63] (but also see Ref. [65]).

More recent studies have begun to establish a correspondence between the FN400 old/new effect and familiarity. Curran's [7] participants studied lists of singular and plural words (e.g. TABLE, CUPS) and were tested with studied words (TABLE), similar lures presented in the opposite plurality to that of studied words (CUP), and new words (following Refs. [21–23]). Participants were instructed to make affirmative recognition judgments only for words tested in their original plurality and to reject any words that switched plurality or were completely new. Assuming that the familiarity of studied and similar items is comparable, yet greater than for new items [21–23], the finding that the FN400 differentiated new from studied/similar words (new>similar=studied) was consistent with the hypothesis that it reflects familiarity. The parietal old/new effect, on the other hand, differentiated between correctly recognized studied words and falsely recognized similar lures (studied>similar=new). Assuming recollection is more prevalent for the hits than false alarms [25,78], these results are consistent with the hypothesized correspondence between recollection and the parietal old/new effect.

Several studies have tested recognition memory with semantically similar lures [8,14,37] in variants of the Deese/Roediger-McDermott (DRM) false memory paradigm [10,48].[1] In these experiments, subjects study a list of words that are all semantic associates (e.g. GLASS, PANE, DOOR . . .) of a single, non-studied critical lure (WINDOW). These types of experiments are conceptually similar to Curran's [7] experiments with plurality-reversed lures; however, they have led to some discrepant results. Using the remember-know procedure (reviewed in Refs. [18,44]), Düzel et al. [14] observed a temporo-parietal positivity in the N400 range that was similar for studied and similar words and associated with 'knowing' recognition judgments. The parietal old/new effect was larger for remembering than knowing, but it did not differ between correct recognition of studied words and false recognition of lures. Curran et al. [8] failed to find any significant FN400 old/new effects, but the parietal old/new effect was greater for true than false recognition. The results of Nessler et al. [37] were most similar to those obtained by Curran [7] with plurality-reversed lures. The FN400 differentiated new from similar and studied items (new< similar=studied), whereas the parietal old/new effect was greater for correctly recognized words than falsely recognized lures (hits>false alarms to lures=correct rejections).

Both Curran et al. [8] and Nessler et al. [37] separated and compared subjects based on their recognition performance. Nessler et al. compared subjects with high versus low false recognition rates. As expected, subjects with low false recognition rates showed larger differences between true and false recognition. In a follow-up experiment, Nessler et al. showed that their group differences might have been attributable to low-recognition subjects' more careful encoding of item-specific features. Curran et al. compared subjects whose discrimination between studied items and similar lures was good versus poor. Unexpectedly, poor performers showed a larger parietal old/new effect between true and false recognition than did good subjects. This is inconsistent with both the results of Nessler et al. and the hypothesized correspondence between the parietal old/new effect and recollection. Only good performers, on the other hand, showed late (1000–1500 ms), right frontal ERP differences between new items and studied items or lures. Thus, good performers may have benefited from more efficient post-retrieval evaluation processes that are often associated with late frontal ERP effects [1,28,45,71,74,75]. Individual differences in performance may be mediated by processes underlying the parietal ERP old/new effects in some cases (e.g. Nessler et al. [37]) and by those underlying late frontal ERP old/new effects in other cases (e.g. Curran et al. [8]). This would be expected from the view that both of these ERP old/new effects are related to different aspects of recollection [1].

Another recent study found a positive relationship between the size of the parietal old/new effect and memory performance [39]. ERPs were recorded during the presentation of words in a categorization task (e.g. BABY ANIMAL: CUB?). Words were repeated with zero to 13 intervening trials. A parietal old/new effect (called the LPC repetition effect by Olichney et al. [39]) was observed for control subjects, but not in amnesic subjects (on average), when repeated and non-repeated conditions were compared. Free recall, cued-recall, and recognition tests for the categorized words were given immediately after ERP trials. The magnitude of the late positive component (LPC, 500 and 800 ms) was positively correlated with cued-recall (both amnesic and control subjects) and free recall (control subjects only). Free- and cued-recall are presumed to depend on recollection with little contribution of familiarity, so these results suggest that the parietal old/new effect increases with recollection ability (similarly to Nessler et al. [37]).

There were two primary purposes to the present experi-

[1]Two other ERP studies of recognition memory have used the DRM paradigm, but are less relevant to the present experiment because they did not differentiate between the FN400 and parietal old/new effects [15,29].

ment. First, we wanted to further test the generality of the hypothesized correspondence of FN400 old/new effect with familiarity and the parietal old/new effect with recollection by extending it to picture recognition. Second, we wanted to re-examine the relationship between the parietal old/new effect and recollection ability. The method was similar to Curran's [7] Experiment 2 except that stimuli were pictures. Subjects studied asymmetric pictures of common objects. The recognition test required the recollection of picture orientation by intermixing studied and new pictures with similar lures that were mirror reversals of studied pictures [22,23].

2. Materials and methods

2.1. Participants

Participants were 43 right-handed students at Case Western Reserve University who participated to satisfy a research requirement in introductory psychology. After rejecting the data of participants with an insufficient number of artifact-free trials (as detailed later), 32 participants were included in the analyses.

2.2. Stimuli, design, and procedure

Each 2-h experimental session began with a practice block (eight studied and 12 tested pictures) to instruct participants and acquaint them with the procedures. Following application of the Geodesic Sensor Net, participants completed five study-test blocks. Test conditions (studied, similar, new) were manipulated within blocks. Each participant completed 100 trials per condition (20 trials per condition per block).

Stimuli were 300 asymmetric, grayscale, line drawings from a commercially available clipart database ('Art Explosion' by Nova Development, Calabasas, CA) or from Snodgrass and Vanderwart [64]. Pictures depicted a variety of objects, animals, people (e.g. football player, nurse, woman with baby carriage), and scenes. Pictures were ~3.2 cm wide×3.2 cm high and subtended a visual angle of ~3.16°. The pictures were randomly assigned to three lists that were rotated through the three test conditions for counterbalancing. Stimuli were presented on a 15″ Apple Multiscan Color Monitor.

Each study list included 40 pictures buffered by one untested picture at the beginning and the end of the list. Each study trial included a central plus sign (300-ms duration) followed by the study picture (750-ms duration). Participants were instructed to study each picture and particularly memorize its left/right orientation. A 2-min retention interval followed each study list.

Each test list contained 60 pictures: 20 studied, 20 similar, and 20 new. Similar lures were left/right mirror reversals of studied pictures (with different pictures assigned to the studied and similar test conditions). New test pictures did not appear on the study list in any form. Participants were given a self-paced rest break after every 15 trials (five trials per condition). Test order was random with the constraint that no more than three consecutive pictures came from the same condition. Participants were instructed to press a 'yes' key for studied pictures and a 'no' key for similar and new pictures. Assignment of the right index and middle fingers to the 'yes' and 'no' categories was counterbalanced across participants.

Test-trial timing was synchronized to the 15-ms screen refresh rate. Each test trial began with an open circle (3.2-cm diameter) for a variable duration (525–1005 ms). The circle was replaced by the test picture for 1995 ms, which in turn was replaced by a central question mark. The question mark remained on the screen until the participant pressed a response key. An open square (3.2-cm sides) appeared after the participant responded and remained visible throughout the 2-s interstimulus interval. EEG recording began 495 ms prior to picture onset and lasted for 2000 ms. Participants were instructed to wait until the question mark appeared before responding, to remain motionless, and to minimize eye blinks.

2.3. EEG/ERP methods

Scalp voltages were collected with a 128-channel Geodesic Sensor Net™ [69] connected to an AC-coupled, 128-channel, high input impedance amplifier (200 MΩ, Net Amps™, Electrical Geodesics, Eugene, OR). Amplified analog voltages (0.1–100-Hz bandpass, −3 dB) were digitized at 250 Hz. Individual sensors were adjusted until impedances were less than 50 kΩ.

Trials were discarded from analyses if they contained eye movements (vertical EOG channel differences greater than 70 μV) or more than five bad channels (changing more than 100 μV between samples, or reaching amplitudes over 200 μV). ERPs from individual channels that were consistently bad for a given participant were replaced using a spherical interpolation algorithm [67]. A median of 1.5 channels per participant were replaced with interpolated data (mode 0, range 0–6).

ERPs were computed within four different categories: studied[yes] (i.e. studied items given a 'yes' response), similar[yes], similar[no], and new[no]. ERPs were not computed for studied[no] responses or new[yes] categories because there were too few observations to form reliable ERPs. Data from 32 of 43 participants were retained for analysis after excluding 11 subjects who did not have at least 16 artifact-free observations within each of the four categories.[2]

[2]Participants were discarded because of excessive eye movements ($n=6$), insufficient similar[yes] trials due to high accuracy ($n=1$) or conservative response bias ($n=1$), computer malfunction ($n=1$), an improperly fitting Net ($n=1$), and a malfunctioning reference electrode ($n=1$).

ERPs were baseline-corrected with respect to a 200-ms pre-stimulus recording interval and were digitally low-pass filtered at 40 Hz. An average-reference transformation was used to minimize the effects of reference-site activity and accurately estimate the scalp topography of the measured electrical fields [2,9,11,32,42,70]. Average-reference ERPs are computed for each channel as the voltage difference between that channel and the average of all channels. Mastoid-referenced ERP plots from representative locations in the International 10–20 system [26] are presented in Appendix A to facilitate comparison with results from other laboratories.

3. Results

3.1. Behavioral results

The proportion of 'yes' responses varied across conditions: studied (mean=0.72, S.E.=0.02) > similar (mean=0.44, S.E.=0.02) > new (mean=0.13, S.E.=0.02). To investigate how ERP memory effects vary with accuracy, participants were divided according to their ability to discriminate between studied and similar pictures (following Ref. [8]). Discrimination accuracy was estimated with A′: ranging from 0 to 1 (0.5 is chance). A′ typically is used to measure discrimination between P(yes) for old items (hit rate) and new items (false alarm rate) [12]. We focused on the ability to recollect picture orientation by computing A′ between the proportions of studied[yes] and similar[yes] responses (Table 1). A median split on A′ (studied vs. similar) divided the sample into two groups: good performers and poor performers. B″D is a response bias measure ranging from −1 (extremely liberal) to 1 (extremely conservative). In addition to the expected accuracy differences, good performers were more conservative than poor performers when responding to similar and new pictures (see Table 1 for between-groups *t*-tests).

3.2. ERP results

Several assumptions guided our interpretation of the ERP results. As explained in the Introduction, we have conceptualized familiarity as a process that indexes the overall similarity between studies and tested items. Recollection, on the other hand, involves the retrieval of specific information (e.g. picture orientation) about individual items from the study list. The present approach stems from that taken in other studies which have supported the distinction between familiarity and recollection [21–23]. Following from these studies, two basic assumptions about familiarity and recollection are made. First, studied and similar pictures should be more familiar than new pictures. Given this assumption, familiarity-related ERPs should differ between studied/similar and new conditions. Second, studied and similar items should give rise to nearly similar levels of familiarity, making recollection necessary for successful discrimination between the two. Given this second assumption, recollection should be most prevalent when subjects correctly recognize studied pictures (studied[yes]) or correctly reject similar pictures (similar[no]). Presumably, subjects would not incorrectly respond 'yes' to similar items if they were able to recollect the original form of the pictures; thus, recollection is assumed to be minimal under these circumstances. The idea that recollection rarely leads to false alarms is consistent with models assuming that recollection is a high threshold process [25,78]. For the present purposes, we merely need to make the less restrictive assumption that the studied[yes] and similar[no] conditions should be associated with higher levels of recollection than the similar[yes] condition. Thus, differences between the studied[yes]/similar[no] and similar[yes] conditions were interpreted as consistent with recollection related processes.

3.2.1. FN400 results (300–500 ms)

The FN400 (300–500 ms) is typically associated with more negative amplitudes on trials with new than old items recorded over superior, frontal sites [6,7,13,17,19,36,37,60]. Most studies have referenced their recordings to the average of the two mastoid recording sites (as displayed in Figs. A1 and A2). Using the average-reference technique, we have found that the FN400 is associated with posterior, inferior (PI) differences (new>old) that have the opposite polarity to the anterior, superior

Table 1
Recognition performance

		All *S*'s	Group		*t*	S.E.	*P*
			Good	Poor			
P(yes)	Studied	0.72	0.78	0.66	3.40	0.04	<0.01
	Similar	0.44	0.38	0.50	3.88	0.03	<0.001
	New	0.13	0.10	0.16	1.61	0.04	NS
A′	Studied vs. similar	0.71	0.79	0.64	7.89	0.02	<0.001
	Similar vs. new	0.77	0.76	0.77	0.26	0.03	NS
B″D	Studied vs. similar	−0.35	−0.40	−0.29	0.89	0.11	NS
	Similar vs. new	0.76	0.85	0.67	2.05	0.09	<0.05

Two-tailed *t*-tests compared good and poor performers (df 30).

(AS) differences (new<old) which are normally observed [6,7] (see Fig. 1 for specification of these regions). Thus, the FN400 can be quantified by a cross-over interaction between conditions (e.g. old, new) and regions (AS, PI). In the present experiment, the polarity reversal between the AS and PI regions was quantified by correlating subjects' mean AS and PI voltages within each condition. Each condition showed a highly significant negative correlation between AS and PI voltages (r ranged from -0.78 to -0.92, all P's<0.01, two-tailed).

Waveform plots are shown separately for good (Fig. 2) and poor (Fig. 3) performers. Part of the logic behind the experimental design rests on the assumption that studied and similar items are more familiar than new items. If the FN400 is sensitive to familiarity, FN400 old/new effects should be observed when the new condition is compared with each of the studied and similar conditions. The purest familiarity-related comparison is between the similar[yes] and new[no] conditions because recollection should be minimal in each case. These predictions were examined in a series of pairwise group (good vs. poor performers) ×condition×region (AS, PI)×hemisphere mixed-model ANOVAs with mean amplitude from 300 to 500 ms as the dependent measure. The results of these ANOVAs are summarized in Table 2. All significant effects involving either the condition or group variables are presented along with non-significant effects that are theoretically relevant. The relevant means and standard deviations within each condition/region are shown in Table 3. As shown in the first three rows of Table 2, the predicted condition by region interactions were significant when the new[no] condition was compared with each of the other conditions (studied[yes], similar[yes], similar[no]). In each case, anterior, superior (AS) amplitude was more negative for new items than for the other conditions, whereas posterior, inferior (PI) voltages were more positive for new items. Given the nature of this cross-over interaction, the magnitude of the FN400 effects is well summarized in terms of the PI–AS differences that are shown in Fig. 4.

The FN400 is hypothesized to be unrelated to recollection. Recollection should primarily influence performance when subjects correctly respond 'yes' to studied pictures or when subjects correctly reject similar lures. Recollection should be less prevalent when subjects incorrectly respond 'yes' to similar pictures because they have not correctly remembered the original orientation of the picture. Therefore, comparison among these conditions (which are assumed to have similar levels of familiarity) should be indicative of recollection-related processing. As predicted, when the similar[yes] condition (recollection absent) was

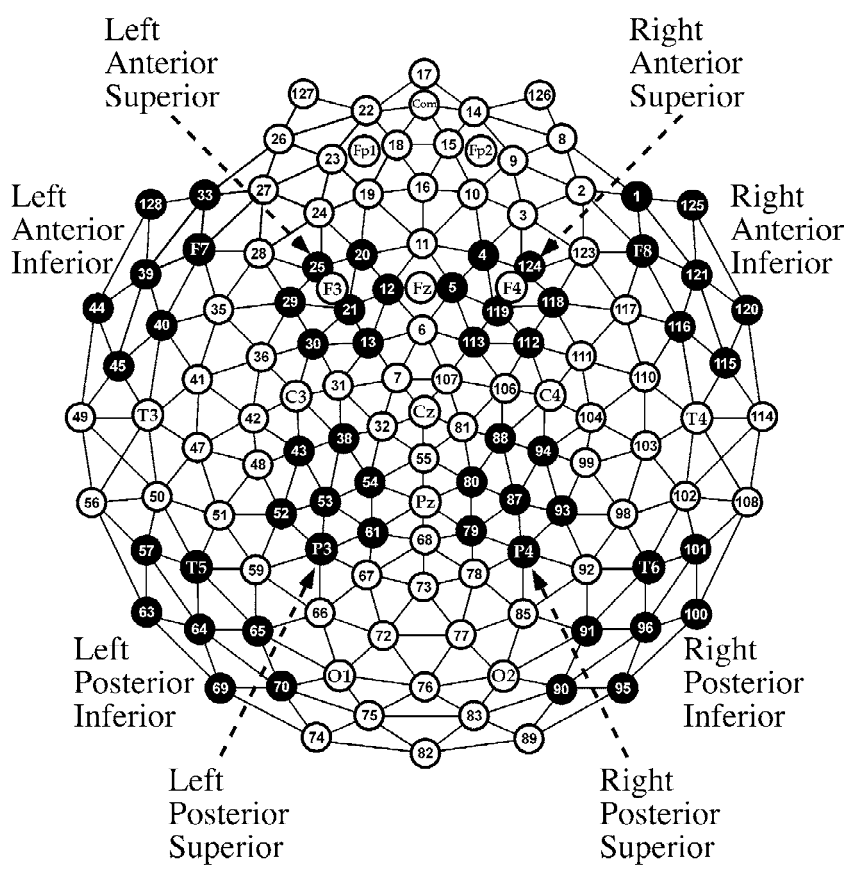

Fig. 1. Approximate channel locations on the Geodesic Sensor Net. Locations from the International 10–20 system are shown for reference. The eight clusters of black channels depict the locations used for analyses (right/left×anterior/posterior×inferior/superior).

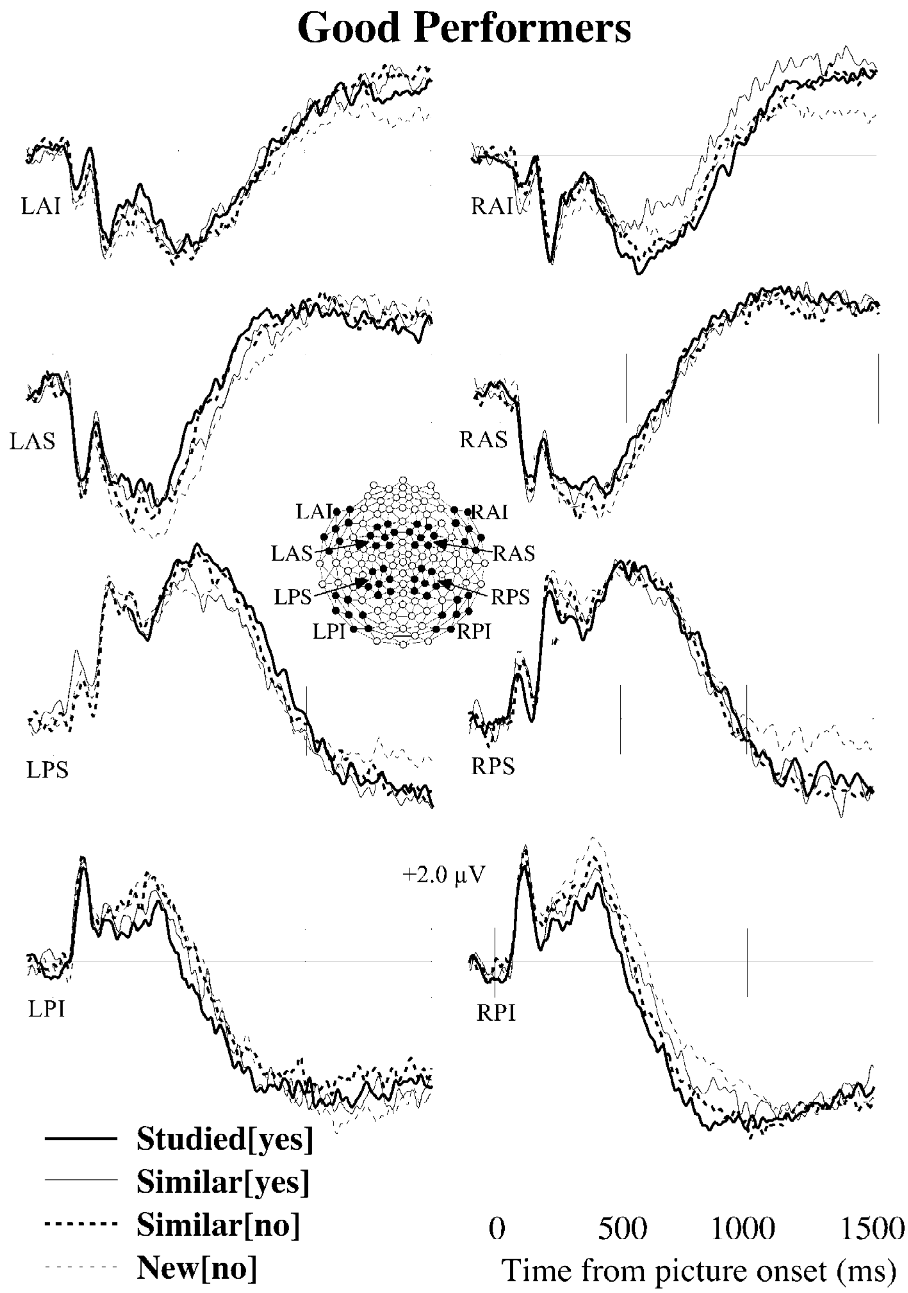

Fig. 2. Mean average-referenced ERPs for good performers who were above the median in discriminating studied from similar pictures. Region abbreviations: A, anterior; I, inferior; L, left; P, posterior; R, right; S, superior.

compared to the conditions with recollection present (studied[yes] and similar[no]), no significant FN400 effects were observed (last two rows of Table 2). In addition, the ANOVAs summarized in Table 2 showed no statistically reliable group differences.

3.2.2. Parietal effects (400–800 ms)

As mentioned with regard to the FN400, the spatial distribution of the parietal old/new effect is somewhat more complicated with average-referenced ERPs than typically observed with mastoid-referenced ERPs. Relative to a mastoid reference, parietal (posterior, superior) scalp regions are more positive for old than new conditions between about 400 and 800 ms (reviewed in Refs [17,36,56]). The average-reference captures these posterior, superior differences (old>new) as well as opposite polarity differences (old<new) over anterior, inferior regions [6–8]. Thus, condition (e.g. old, new)×region (PS, AI) interactions are indicative of the parietal old/new effect. The polarity reversal between the PS and AI regions was quantified by correlating subjects' mean PS and AI voltages within each of the present conditions. Each

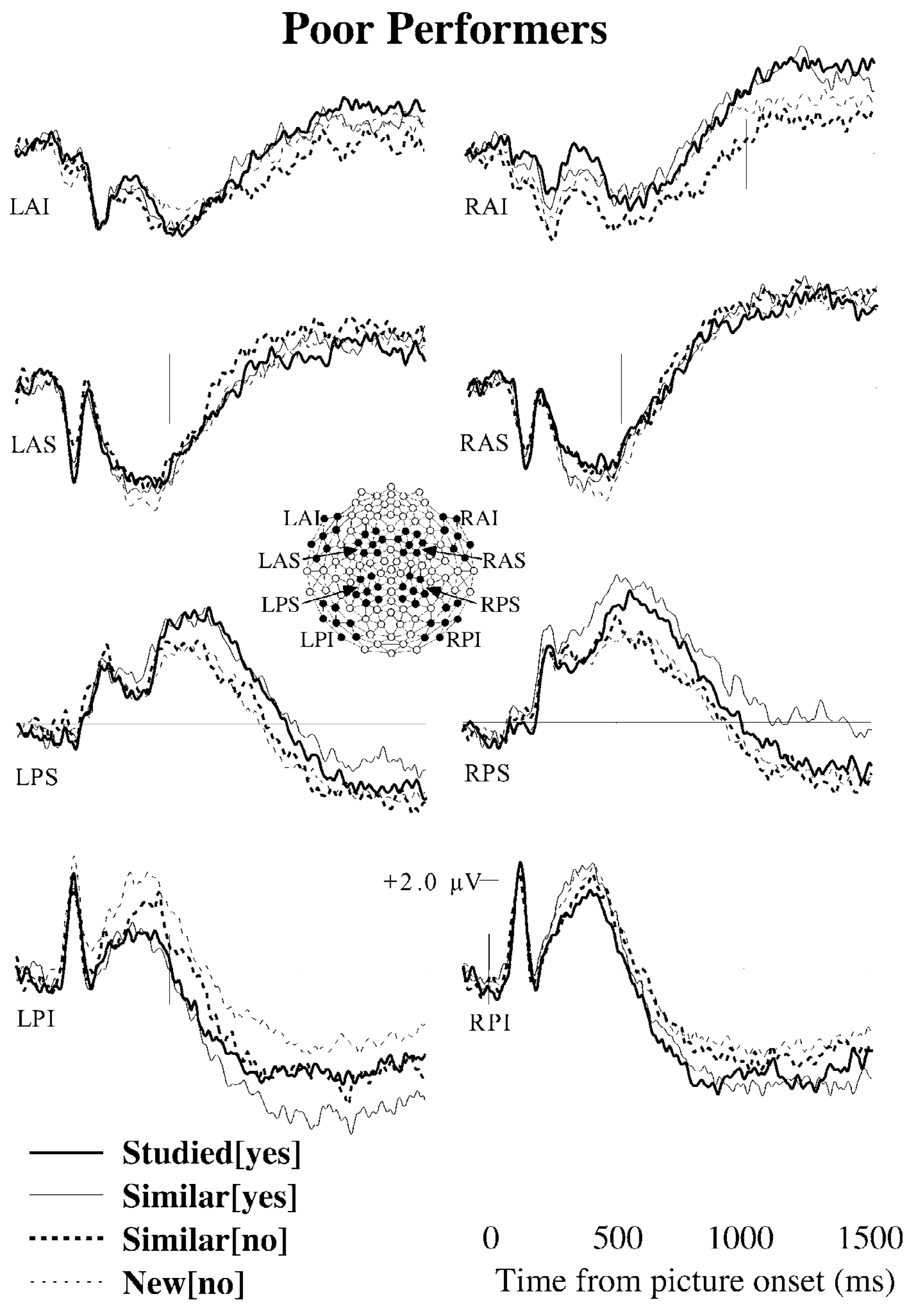

Fig. 3. Mean average-referenced ERPs for poor performers who were below the median in discriminating studied from similar pictures. Region abbreviations: A, anterior; I, inferior; L, left; P, posterior; R, right; S, superior.

Table 2
FN400 ANOVAs (300–500 ms)

	Conditions compared	Effect	df	F	MSE	P
1	Studied[yes]/new[no]	Cond×region	1, 30	18.36	1.94	<0.001
2	Similar[yes]/new[no]	Cond×region	1, 30	4.95	3.04	<0.05
3	Similar[no]/new[no]	Cond×region	1, 30	6.03	1.52	<0.05
4	Studied[yes]/similar[yes]	Cond×region	1, 30	1.52	2.88	>0.10
5	Similar[no]/similar[yes]	Cond×region	1, 30	0.21	3.4	>0.10

Cond, Condition; df, degrees of freedom. Region refers to the anterior, superior (AS) and posterior, inferior (PI) regions included in the ANOVAs.

Table 3
FN400 means and standard errors (300–500 ms)

		Good				Poor			
		LAS	LPI	RAS	RPI	LAS	LPI	RAS	RPI
New[no]	Mean	−3.07	1.60	−2.56	2.26	−2.37	1.90	−2.14	1.91
	(S.E.)	(0.54)	(0.56)	(0.56)	(0.54)	(0.42)	(0.61)	(0.39)	(0.64)
Similar[no]	Mean	−2.58	1.56	−2.35	1.78	−1.93	1.23	−1.68	1.67
	(S.E.)	(0.60)	(0.62)	(0.59)	(0.58)	(0.48)	(0.82)	(0.48)	(0.60)
Similar[yes]	Mean	−2.73	1.08	−1.99	1.99	−2.30	1.50	−2.07	1.65
	(S.E.)	(0.55)	(0.55)	(0.48)	(0.88)	(0.49)	(0.55)	(0.47)	(0.67)
Studied[yes]	Mean	−2.16	0.87	−2.01	1.19	−1.95	0.71	−1.57	1.38
	(S.E.)	(0.53)	(0.49)	(0.57)	(0.55)	(0.56)	(0.59)	(0.48)	(0.74)

A, anterior; I, inferior; L, left; P, posterior; R, right; S, superior; S.E., standard error.

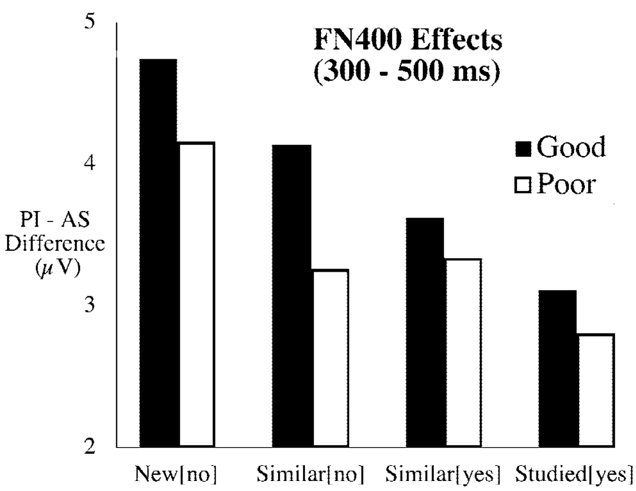

Fig. 4. Mean voltage difference between the posterior, inferior (PI) and anterior, superior (AS) regions between 300 and 500 ms within each condition.

condition showed a highly significant negative correlation between PS and AI (r ranged from −0.45 to −0.69, all P's<0.01, two-tailed).

A series of pairwise group (good vs. poor performers) ×condition×region (PS, AS)×hemisphere ANOVAs was conducted with mean amplitude from 400 to 800 ms as the dependent measure (Tables 4 and 5). The studied[yes]/new[no]×region interaction (Table 4, #1; PS: old>new; AI: old<new) replicates previous results [6–8]. Consistent with the hypothesized correspondence between the parietal effect and recollection, the studied[yes]/similar[yes] by region interaction was larger for good than poor performers (significant group × condition × regions interaction; Table 4, #2). Separate ANOVAs on each group showed a significant condition×region interaction for good subjects, but not for poor subjects.

The similar[yes] and new[no] conditions should primarily differ according to familiarity, so we did not expect parietal effects. However, the group×similar[yes]/new-[no]×region interaction was significant (Table 4, #3). Separate ANOVAs on each group showed a significant condition×region interaction for poor subjects, but not for good subjects. The magnitude of the parietal effect can be summarized with the PS–AS differences plotted in Fig. 5. The good performers statistically replicated the pattern of recollection-related parietal effects (studied[yes]> similar[yes]=new[no]) observed using words with plurality-reversed lures [7], but the poor subjects showed more of a familiarity-sensitive pattern (studied[yes]= similar[yes]>new[no]).

Recollection can contribute to the similar[no] condition if subjects recollect the orientation of the originally studied pictures and use that as the basis for correctly rejecting similar lures (a 'recall-to-reject' strategy [4,21,51–53,77]; also see Discussion). Corresponding parietal differences would be expected from the similar[no]/new[no] and

Table 4
Parietal ANOVAs (400–800 ms)

	Conditions compared	Groups	Effects	df	F	MSE	P
1	Studied[yes]/new[no]	Both	Cond×Reg	1, 30	7.36	0.84	<0.05
2	Studied[yes]/similar[yes]	Both	Grp×Cond×Reg	1, 30	4.46	0.77	<0.05
		Good	Cond×Reg	1, 15	7.26	0.7	<0.05
		Poor	Cond×Reg	1, 15	0.16	0.84	>0.10
3	Similar[yes]/new[no]	Both	Grp×Cond×Reg	1, 30	5.45	1.2	<0.05
		Good	Cond×Reg	1, 15	0.88	1.32	>0.10
		Poor	Cond×Reg	1, 15	5.4	1.27	<0.05
4	Similar[no]/new[no]	Both	Cond×Reg	1, 30	1.97	1.6	>0.10
5	Similar[no]/similar[yes]	Both	Cond×Reg	1, 30	0.14	2.88	>0.10

Cond, condition; df, degrees of freedom; Grp, group. Reg refers to the posterior, superior (PS) and anterior, inferior (AI) regions included in the ANOVAs.

Table 5
Parietal means and standard errors (400–800 ms)

		Good				Poor			
		LAI	LPS	RAI	RPS	LAI	LPS	RAI	RPS
New[no]	Mean	−1.70	2.65	−1.43	2.98	−1.03	1.31	−0.60	1.65
	(S.E.)	(0.47)	(0.63)	(0.45)	(0.63)	(0.39)	(0.43)	(0.45)	(0.42)
Similar[no]	Mean	−1.78	3.13	−1.67	2.93	−1.36	1.42	−1.20	1.64
	(S.E.)	(0.42)	(0.54)	(0.38)	(0.66)	(0.40)	(0.70)	(0.47)	(0.54)
Similar[yes]	Mean	−1.47	2.45	−0.82	2.77	−0.85	1.28	−0.29	1.71
	(S.E.)	(0.85)	(0.78)	(0.54)	(0.60)	(0.41)	(0.59)	(0.36)	(0.43)
Studied[yes]	Mean	−1.54	3.29	−1.91	2.91	−1.25	2.03	−0.61	2.30
	(S.E.)	(0.49)	(0.64)	(0.53)	(0.57)	(0.44)	(0.40)	(0.32)	(0.33)

A, anterior; I, inferior, L, left; P, posterior; R, right; S, superior; S.E., standard error.

similar[no]/similar[yes] comparisons, but neither was significant (Table 4, #4 and #5). Despite the absence of group×condition×region interactions, the PS–AI differences plotted in Fig. 5 suggest relevant differences between the similar[no] and similar[yes] conditions for good performers. An ANOVA on the good performers showed a marginally significant similar[no]/similar[yes]×region interaction, $F(1, 15)=3.58$, MSE$=1.17$, $P=0.08$. Thus, evidence that the parietal old/new effect is related to recall-to-reject processing was weak.

The weakness of parietal differences between similar[no]/similar[yes] conditions could be attributable to these conditions differing in familiarity more so than recollection. Although FN400 differences between these conditions were not significant, a trend toward familiarity differences is apparent in Fig. 4. It is possible that neither FN400 nor parietal differences between these conditions were significant because the comparison confounds familiarity and recollection in a manner that dilutes possible effects on either component.

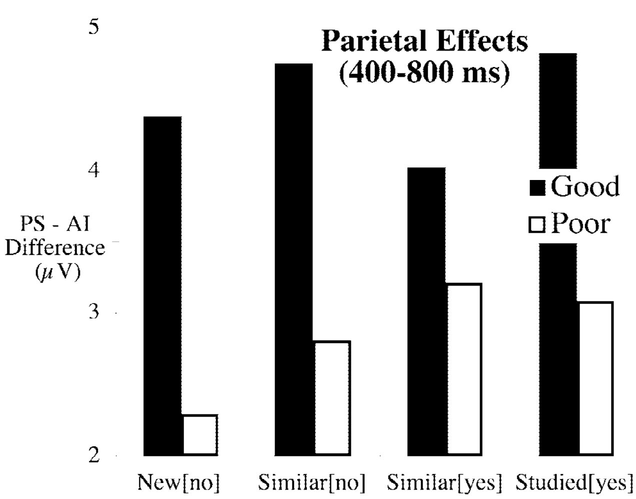

Fig. 5. Mean voltage difference between the posterior, superior (PS) and anterior, inferior (AI) regions between 400 and 800 ms within each condition.

3.2.3. Topographic comparison of FN400 and parietal effects

If the FN400 familiarity effect and the parietal recollection effect were associated with qualitatively different scalp topographies, the view that these effects arise from separate brain mechanisms would be supported. Curran [6,7] has found evidence for such qualitative differences in three of four experiments. Hypotheses relating the FN400 old/new effect to familiarity and the parietal old/new effect to recollection primarily were supported by the results from good performers, so only these subjects were included in the topographic analyses. ERP differences between similar[yes] and new[no] categories were used to estimate familiarity effects. ERP differences between studied[yes] and similar[yes] categories were used to estimate recollection effects. To minimize temporal overlap between these effects which would obscure topographic differences, analyses focused on 40-ms windows that centered around the peak amplitude of the similar[yes]/new[no] and studied[yes]/similar[yes] differences (following Ref. [7]). To adjust for inter-subject variability in the peak latencies of these differences, peak latencies were determined for each subject separately and the mean amplitude differences were taken within each individual subject's 40-ms peak window.[3] The peak of the FN400 familiarity differences (similar[yes]−new[no]) averaged between 397 and 437 ms. The peak of the parietal recollection differences (studied[yes]−similar[yes]) averaged between 642 and 682 ms. The complete topographies of these differences are displayed with spherical spline interpolations in Fig. 6. To assess qualitative differences, unbiased by the relative magnitude of the recollection and familiarity differences, the ERP differences were normalized across the eight regions of interest (left/right×anterior/posterior×inferior/superior) according to the vector length method [35]. The normalized differences were compared in a 2 difference (familiarity: similar[yes]−new[no], recollection: studied[yes]−

[3]We thank the reviewer who suggested determining the latencies of the peak differences for each subject separately.

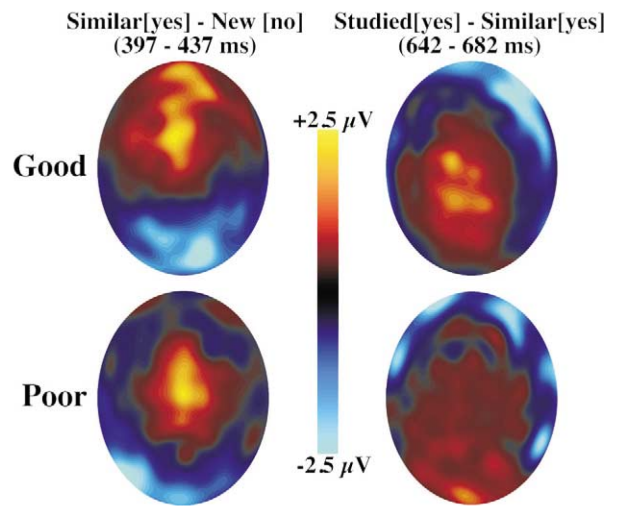

Fig. 6. Topographic distribution of ERP differences associated with the FN400 familiarity effect (left: similar[yes]−new[no]) and parietal recollection effect (right: studied[yes]−similar[yes]). Topographies are plotted separately for good (top) and poor (bottom) performers. The figure was constructed by finding the 40-ms window in which these differences peaked for each subject, computing each subject's mean difference within this window for each electrode, averaging the mean differences across subjects, and interpolating the mean differences with a spherical spline algorithm. The mean FN400 window was 397–437 ms. The mean parietal window was 642–682 ms. Each oval depicts the head from above (front of head on top of oval, left on left, etc.).

similar[yes])×2 hemisphere×2 anterior/posterior×2 inferior/superior repeated measures ANOVA. The difference×anterior/posterior interaction was highly significant, $F(1, 15)=17.33$, $MSE=0.24$, $P<0.001$. The FN400 familiarity effect was associated with positive-going differences over anterior regions and negative-going differences over posterior regions whereas the parietal recollection differences showed the opposite pattern.

3.2.4. Late frontal effects (1000–1500 ms)

In general, late frontal voltages were more positive for studied and similar than new conditions (most prominently over the right hemisphere; Figs. 2 and 3). This pattern is broadly consistent with late frontal ERP old/new effects that are often observed (reviewed in Refs. [1,17,36]). When the late frontal effects were analyzed within the anterior/superior and anterior/inferior regions, significant differences were observed between ERPs to new items and each of the other three conditions (studied[yes], similar[yes], similar[no]). These differences were observed for both good and poor performers, with the exception of poor subjects not showing significant late frontal differences between the similar[no] and new[no] conditions. However, the poor subjects did show significant similar[no]/new[no] differences at other right frontal locations that did not happen to correspond to the anterior/superior and anterior/inferior regions. Because we had no a priori basis for predicting or understanding the subtle topographic differences among the late frontal effects shown by good and poor performers, these results are not addressed further and the statistical tests are omitted.

4. Discussion

4.1. Overview

Previous research comparing memory for studied items and similar lures has dissociated recollection from familiarity on the basis of their ERP correlates. The present study extended this method of dissociation to picture recognition. At test, participants were asked to discriminate between studied pictures and their mirror-reversed images (similar lures). The results are consistent with the claim that the FN400 ERP old/new effect is related to familiarity and the parietal old/new effect is related to recollection (the 'ERP familiarity/recollection hypothesis'). FN400 differences were observed between ERPs elicited by new items and the other higher-familiarity conditions (studied and similar). FN400 differences were not observed when conditions most likely associated with recollection (studied[yes], similar[no]) were contrasted with the similar[yes] condition, which is more likely to be associated with familiarity than with recollection. The present study also supports the notion that there is a correspondence between behavioral performance and the parietal recollection effect. Recollection-related differences were observed with respect to the parietal old/new effect (studied[yes]>similar[yes]), but only for subjects with good behavioral discrimination between studied items and similar lures.

4.2. FN400 old/new effects

The present results converge with other recent experiments in showing that the FN400 reflects the activity of a process that differentiates old (studied) from new items, but treats similar lures the same as actually studied items. In this regard, the FN400 appears to be related to familiarity processes. This pattern has been observed when similar lures are plurality-reversed words [7], semantically similar words [37] (but see Ref. [8]), and mirror-reversed pictures (the present experiment). The convergence of these results suggests that the FN400 is not merely sensitive to idiosyncratic aspects of the similarity manipulations used in any single experiment. Lures are semantically similar to studied items in each of these experiments, so semantics may be one dimension of similarity that drives the FN400 response. If the FN400 is related to the N400 which is often observed in ERP studies of language comprehension [30,31], such semantic sensitivity would be expected [39]. However, another recent experiment has shown that the FN400 is sensitive to physical similarity when memory for novel visual shapes is tested [5], so the FN400 also may be sensitive to perceptual similarity.

4.3. Parietal old/new effects

4.3.1. Relationship to recollection

The present results also compliment other studies showing a relationship between recollection and the parietal old/new effect. Several approaches have been used to investigate this problem. One approach has been to manipulate variables thought to differentially affect recollection and familiarity. This approach can be problematic without a compelling theoretical consensus for how the chosen variables affect recollection and familiarity. Examples of such theoretically ambiguous variables include word versus pseudowords [6], word frequency [54,55,58], and level of processing [40,41,57,61]. A second approach has emphasized the fact that the parietal old/new effect is larger when subjects judge that recognition is based upon 'remembering' than 'knowing' [14,59,63]. However, Spencer et al. [65] have recently shown that differences between remembering and knowing may be an artifact of greater trial-to-trial latency variability for 'know' trials. The third approach, as adopted here, has been to show that the parietal old/new effect is associated with the ability to recollect specific attributes for studied items. Any single experiment adopting this approach is subject to the criticism that only a limited dimension of recollection is being addressed, but this criticism is undermined by generalization to a variety of different attributes including study modality [75,76], speaker's voice [59,73,74], temporal source [68], word plurality [7], and picture orientation (the present experiments). Each of these approaches has its limitations, but together they converge on the view that the parietal old/new effect is related to the recollection of specific information.

An alternative possibility is that parietal differences between studied and similar pictures may be related to perceptual priming rather than recollection. In general, changes in the physical format of stimuli influence perceptual priming (or 'implicit memory') more so than explicit memory (reviewed by Ref. [50]), so parietal differences between studied and similar items could merely reflect that activity of priming-related processes responding more weakly when pictures are presented in mirror-reversed orientation. This alternative explanation is undermined by several considerations. First, although physical changes often do reduce priming, several studies have shown that priming is invariant when pictorial stimuli are mirror reversed as they were in the present experiment [3,16,62,66]. Second, changing the visual/auditory modality of words between study and test lists does not reduce the size of the parietal old/new effects (Curran, unpublished), so unlike many perceptual priming effects, the parietal old/new effect is not sensitive to physical stimulus changes. Third, when the present results were re-averaged without regard to accuracy, the studied/similar×PS/AI interaction did not approach significance ($F<1$). Thus, the parietal studied/similar differences reported here are dependent upon accuracy differences between the studied[yes] and similar[yes] conditions rather than reflecting the effects of orientation changes per se. Fourth, we found that the magnitude of the parietal studied[yes]/similar[yes] difference was larger for subjects with good than poor recollection ability. Thus, the magnitude of the parietal recollection effect is related to a behavioral manifestation of recollection.

4.3.2. Parietal versus late frontal old/new effects

The finding that the parietal ERP recollection effect (studied[yes]>similar[yes], 400–800 ms) is greater for subjects with good than poor discrimination between studied items and similar lures supports a correspondence with recollection. This result is consistent with others showing a relationship between the parietal old/new effect and low false recognition of semantically similar lures [37] and high recall ability [39]. However, not all studies have shown this relationship. Although Curran et al. [8] used a DRM paradigm similar to that of Nessler et al. [37], Curran et al. did not find greater parietal old/new effects for good compared to poor discrimination subjects. Instead, late frontal old/new effects were greater for good than poor performers. Given the view that the parietal and late frontal old/new effects reflect the activity of dissociable processes related to different forms of recollection [1], it makes sense that recollection ability would vary with the parietal old/new effect under some conditions but vary with the late frontal old/new effect in other conditions. Whereas the parietal old/new effect may be sensitive to the quality or quantity of retrieved information [1,58,72,73], the late frontal old/new effect may be related to post-retrieval evaluation processes [1,28,45,71,74,75]. Thus, good recollection could be the product of effective retrieval (indexed by the parietal old/new effect, as in the present experiment and that of Nessler et al. [37]) or effective evaluation processes (indexed by the late frontal old/new effect; Curran et al. [8]). The conclusion of Nessler et al. [37] that low false alarm rates were attributable to careful encoding of item-specific features is consistent with this view in that retrieval processes underlying the parietal old/new effect should be more effective following thorough encoding of details.

4.3.3. Theoretical accounts

Roediger and colleagues have developed an activation/monitoring framework to account for false memory effects in the DRM paradigm [49], which may also account for the differences that are found regarding parietal and late frontal old/new effects. According to the activation/monitoring account, studied items activate related lures during the study episode, and false recognition results from a failure to correctly monitor the source of this activation [49]. From this perspective, it seems reasonable to assume that the quantity/quality of information retrieved in response to lures will increase with the amount of study-time

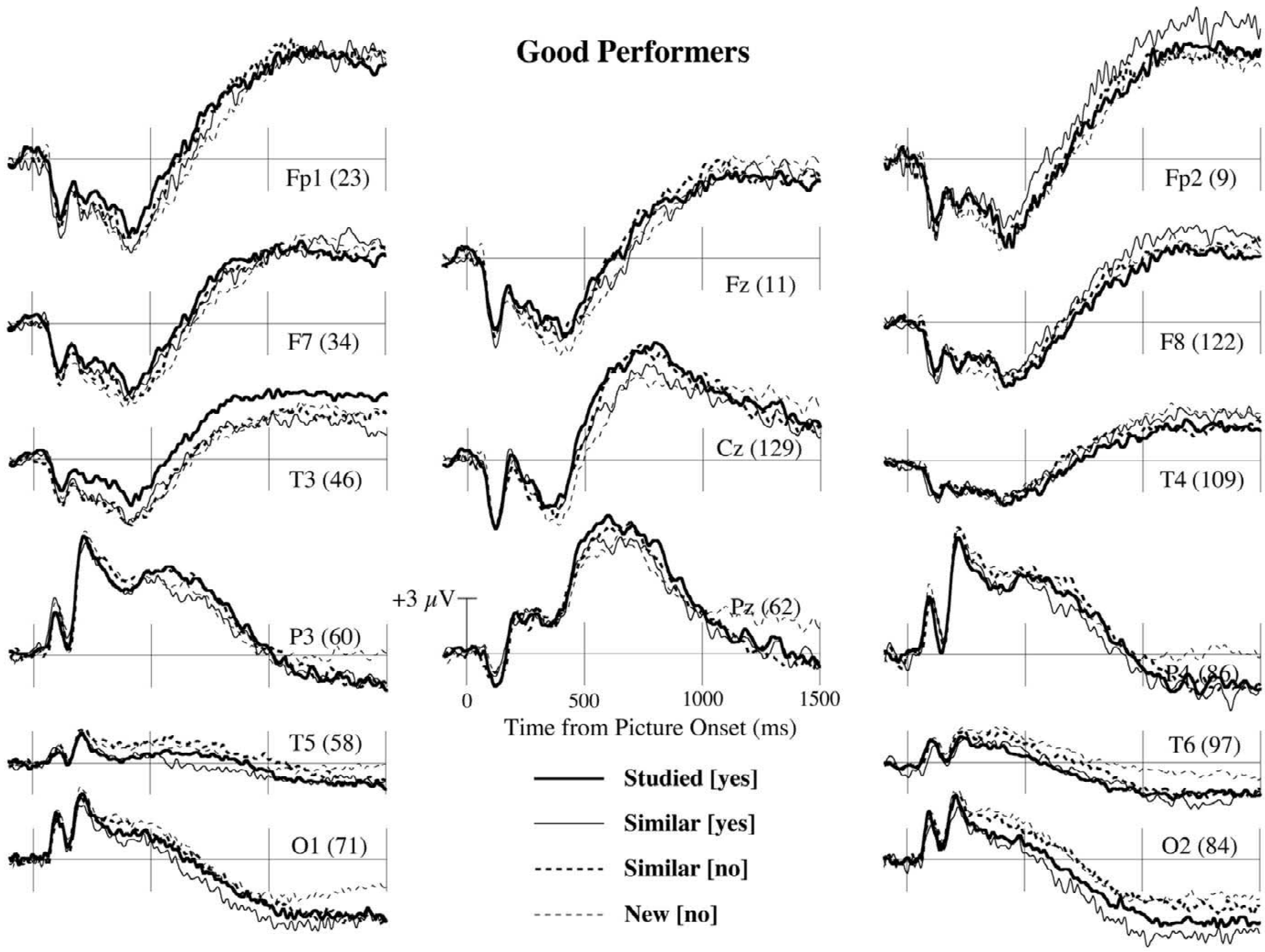

Fig. A.1. Mean mastoid-referenced ERPs for good performers from channels nearest to several locations of the International 10–20 system.

activation. The subjects of Nessler et al. [37] studied sets of five categorically related words (in addition to a category label that was provided) and were tested on five related lures from each category. The subjects of Curran et al. [8] studied sets of 12 semantic associates and were tested on four related lures from each set. Given that the false recognition levels increase with the number of studied associates [20,47], overall activation was probably higher in the experiment of Curran et al. This assumption is supported by the higher critical false alarm rates shown by the subjects of Curran et al. (53%) compared to those of Nessler et al. (26%). The lower level of lure activation may have enabled the subjects of Nessler et al. to differentiate true and false memories based on the quality/quantity of information (indexed by the parietal old/new effect). The higher level of lure activation may have required the subjects of Curran et al. to rely on post-retrieval monitoring processes (indexed by the late frontal old/new effect).

Although the parietal ERP old/new effect appears to be related to quantity/quality of recollected information, more specific theoretical formulations are lacking. Some theorists have drawn a distinction between two different respects in which recollection could aid recognition memory performance. First, a 'recall-to-accept' process/strategy could facilitate correct responses to studied items through the recollection of details about the target item. Second, a 'recall-to-reject' process/strategy could counteract a tendency to false alarm to similar items by recollecting attributes of the actually studied item [4,21,51–53,77]. In the present experiment, for example, a 'recall-to-reject' process might lead a person to reject a picture of a dog facing rightward by recollecting the same dog facing leftward on the study list. Such a process is less likely to influence performance when semantically similar lures are used because recollecting 'dream' does not necessarily mean that 'sleep' was not studied. Several lines of evidence have supported the existence of recall-to-reject processing [4,21,51–53,77], but it has been argued that it is more likely to occur in associative- than item-recognition tasks [51].

Parietal ERP differences between studied[yes] and similar[yes] conditions are clearly consistent with a recall-to-accept process [7] (also the present experiment). Curran

[7] sought evidence for recall-to-reject processing by comparing the similar[no] and studied[no] conditions, and found corresponding parietal ERP differences in only one of two experiments. In the present experiment, recall-to-reject processing was evaluated by comparing the similar[no] and similar[yes] conditions. This analysis revealed marginally significant parietal ERP differences for good, but not for poor, performers. Overall, the evidence for a relationship between the parietal ERP old/new effect and recall-to-reject processing is suggestive but weak. Future research will be needed to determine the reasons why the parietal ERP old/new effect seems more associated with recall-to-accept than recall-to-reject processing. Such research would lead to a better specification of the recollection processes underlying the parietal old/new effect.

Acknowledgements

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Appendix A

Figs. A1 and A2 show mastoid-referenced ERPs (average of left and right mastoids, channels 57 and 101) from representative locations in the International 10–20 system [26]. For good performers (Fig. A1), FN400 effects are best seen at Fz (300–500 ms) and parietal effects are best seen at P3 (400–800 ms). For poor performers (Fig. A2), the FN400 effect is best seen at Cz. One discrepancy between the average-referenced and mastoid-referenced ERP can be seen with respect to the parietal old/new

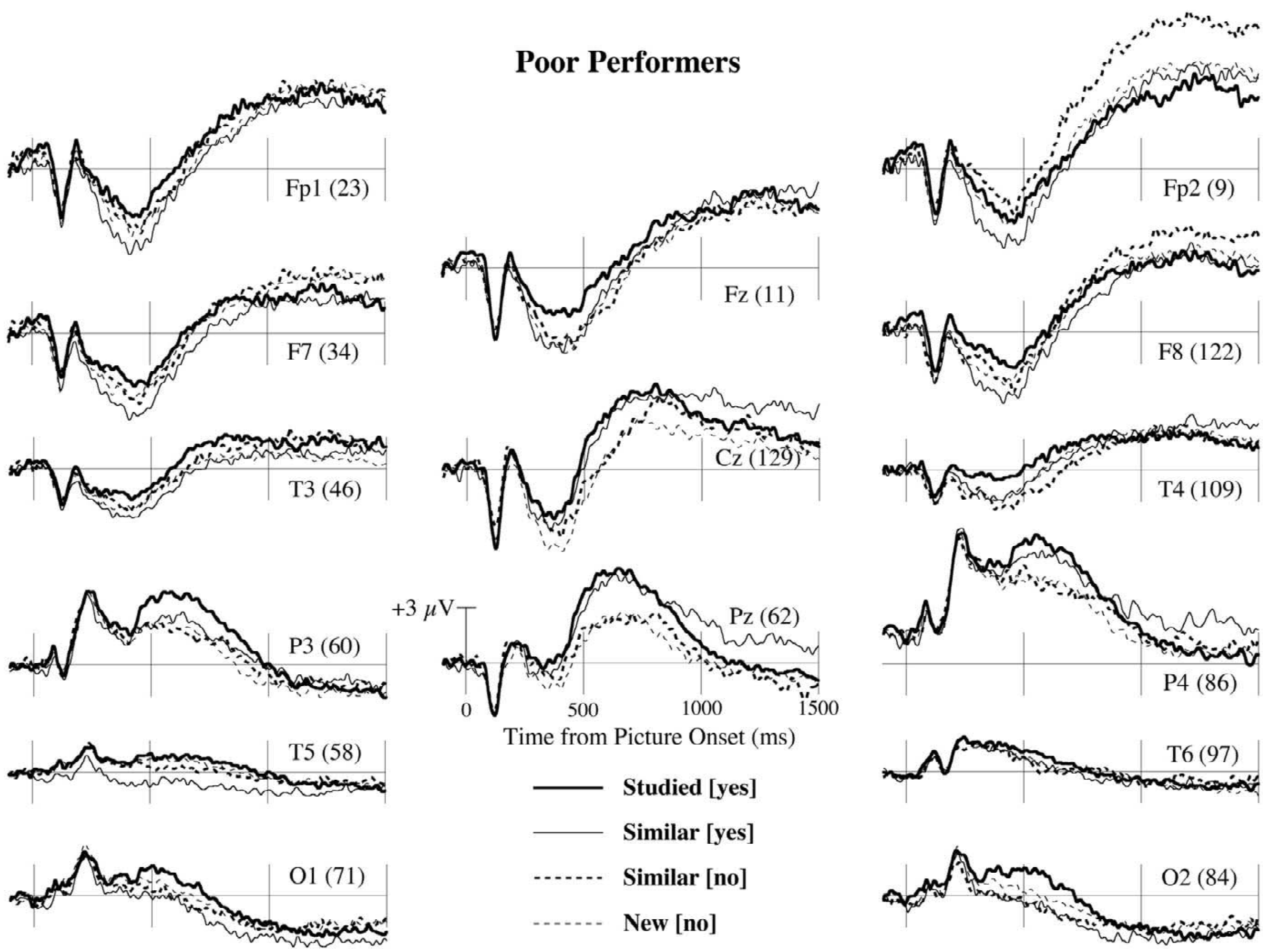

Fig. A.2. Mean mastoid-referenced ERPs for poor performers from channels nearest to several locations of the International 10–20 system.

effect. Average-referenced ERPs indicated no parietal difference between studied[yes] and similar[yes] conditions, but such a difference is apparent in the mastoid-referenced ERPs at channel P3 (Fig. A2). Fig. 6 (lower, right) shows an opposite polarity (similar[yes]> studied[yes]) near the right mastoid (with respect to the average reference). Keeping in mind that electrical fields originating near the mastoids will appear as opposite polarity fields at distant channels in mastoid-referenced ERPs, the greater positivity for studied[yes] than similar[yes] conditions in the mastoid-referenced data at P3 can be attributed to the opposite-polarity difference near the right mastoid. In fact, the right mastoid difference is primarily attributable to a single subject who had the lowest number of acceptable trials in studied[yes] and similar[yes] conditions (studied[yes]=24 trials, similar[yes]= 20 trials).

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