

Electrophysiological Correlates of Recollecting Faces of Known and Unknown Individuals

Ken A. Paller, Brian Gonsalves, Marcia Grabowecky, Vladimir S. Bozic, and Shishin Yamada

Department of Psychology, Northwestern University, Evanston, Illinois 60208-2710

Received March 23, 1999

We recorded brain potentials from healthy human subjects during a recognition test in order to monitor neural processing associated with face recollection. Subjects first attempted to memorize 40 faces; half were accompanied by a voice simulating that person speaking (e.g., “I’m Jimmy and I was a roadie for the Grateful Dead”) and half were presented in silence. In the test phase, subjects attempted to discriminate both types of old faces (i.e., “named” and “unnamed” faces) from new faces. Recognition averaged 87% correct for named faces, 74% correct for unnamed faces, and 91% correct for new faces. Potentials to old faces were more positive than those to new faces from 300 to 600 ms after face onset. For named faces, the old–new ERP difference was observed at anterior and posterior scalp locations. For unnamed faces, the old–new ERP difference was observed only at posterior scalp locations. Results from a prior experiment suggest that these effects do not reflect perceptual priming of faces. The posterior portion of the old–new ERP difference was thus interpreted as a neural correlate of retrieval of visual face information and the anterior portion as an indication of retrieval of person-specific semantic information. © 2000 Academic Press

INTRODUCTION

A face can function as an effective memory cue, provoking the retrieval of a wealth of stored information about an individual. Yet, the brain events that allow us to remember the people we know are largely unknown. Neuropsychological studies of patients with brain damage suggest that perceiving and remembering faces depend on processing in specific cortical regions. Additional information about the relevant physiological mechanisms may be revealed by measuring brain activity during normal face processing. Here we show that measures of the electrical activity of the brain can be used toward this end.

Person recognition—defined as remembering a known individual and retrieving an assemblage of person-

specific information pertaining to that individual—generally begins with the perceptual processing of a facial image. Voice information, contextual cues, expectations, inferences, and other factors often combine to allow a person to be recognized, but the facial image in isolation can be sufficient for person recognition. The number of distinct faces that an individual can accurately recognize is exceedingly large. People become experts at recognizing faces through extensive practice over years and perhaps by virtue of specially evolved brain mechanisms (Carey, 1992). Clues about the relevant neural mechanisms have been provided by behavioral studies in patients and in healthy individuals, single-unit neurophysiology in monkeys, and neuroimaging and electrophysiological studies in humans (for recent reviews, see De Renzi, 1997; Farah *et al.*, 1998; Young, 1998). Evidence from these various sources can be interpreted within the context of the theoretical framework for face recognition first put forth by Bruce and Young (1986). Separate modules were postulated for processing physical features of a face, for determining that a face is familiar, for retrieving stored information about a person, for retrieving a name associated with a face, for expression analysis, and for facial speech analysis.

Cortical processing mechanisms specialized for face recognition have been investigated with a variety of methods. In monkeys, particular neurons in temporal cortex respond selectively to faces (Desimone, 1991; Perrett *et al.*, 1992). In humans, recordings from intracranial electrodes have demonstrated face-specific responses from small regions of the left and right fusiform and inferior temporal gyri, and electrical stimulation from these same electrodes frequently disrupted naming of faces (Allison *et al.*, 1994a). Recordings from scalp electrodes have also revealed potentials thought to be relatively face-specific (Bentin *et al.*, 1996; Bötzel and Grüsser, 1989; Jeffreys, 1989; Jeffreys *et al.*, 1992). These *event-related potentials* or ERPs generally appear 150 to 200 ms after the onset of a face and have been labeled N170 potentials, denoting their negative polarity and 170-ms peak latency. N170 and

other similar potentials have been related not only to face-specific processing, but also to eye-gaze-specific processing, and they are thought to reflect cortical activity in occipitotemporal and posterior fusiform regions (Allison *et al.*, 1994b; Puce *et al.*, 1996, 1997). Functional activation of these same cortical regions has also been associated with face processing using *magnetoencephalography* or MEG (Linkenkaer-Hansen *et al.*, 1998; Sams *et al.*, 1997), *positron emission tomography* or PET (Haxby *et al.*, 1996; Sergent *et al.*, 1992), and *functional magnetic resonance imaging* or fMRI (Clark *et al.*, 1996; Haxby *et al.*, 1999; Kanwisher *et al.*, 1997; Puce *et al.*, 1995).

Although the ability to perceptually analyze faces is generally thought to be separate from the ability to remember faces (e.g., Carlesimo and Caltagirone, 1995), it is reasonable to speculate that the inferior occipitotemporal regions where face-specific responses are produced may also be critical for remembering faces. Accordingly, person recognition may depend on interactions between these cortical regions and regions that store information pertaining to person identity. In other words, the complex recollective experience that can be cued by a face may depend on a network of stored associations between a visual representation of that face and other information such as person-specific biographical details, sets of relevant episodic memories, emotional associations, and so on.

In the present experiment, we investigated scalp-recorded brain potentials that occur when subjects engage in person recognition in response to viewing facial images. Prior investigations of ERPs and memory have usually used words instead of faces (for reviews, see Johnson, 1995; Paller, 1993, in press; Rugg, 1995). A pervasive finding in this literature is that late positive ERP amplitudes tend to be greater for repeated items compared to new items, sometimes referred to as an *old–new ERP difference* or *ERP repetition effect*. Likewise, in experiments with faces, a repeat presentation of a face generally yields a different ERP response compared to the initial response to that face (Barrett *et al.*, 1988; Begleiter *et al.*, 1995; Bentin and McCarthy, 1994; Bentin and Moscovitch, 1988; Hertz *et al.*, 1994; Münte *et al.*, 1997, 1998; Potter and Parker, 1997; Schweinberger *et al.*, 1995; Smith and Halgren, 1987; Sommer *et al.*, 1997; Uhl *et al.*, 1990). For example, Münte and colleagues (1997) studied ERPs elicited by faces in implicit and explicit memory tests. In the implicit test, subjects were required to detect famous faces interspersed in a series of nonfamous faces, some of which repeated. In the explicit test, subjects were required to discriminate previously seen faces from other, new faces. In both tests, ERP differences associated with face repetition took the form of increased positivity from about 300 to 700 ms. ERP differences were generally smaller in the implicit test than in the

explicit test, with additional topographic differences in the 300 to 500 ms interval. Presumably, subjects given the implicit memory test engaged in less recollective processing in response to repeated faces than did those given the explicit memory test.

Paller and colleagues (1999) recorded ERPs to previously seen faces and new faces, and in addition, two types of previously seen faces were compared—some faces were associated with brief biographical information in a study phase and some were not. Subjects were instructed to remember the faces with biographies and to forget the others. Despite the artificial nature of these circumstances, a face associated with a biography in this manner can be thought of as corresponding to the face of a known individual. When those known faces were presented in the experiment, recollective processing of the sort typically associated with person recognition was presumably engaged. ERPs elicited by those faces included an enhanced response over posterior scalp regions and, to a lesser extent, over anterior regions.

The present study was designed to determine whether similar ERP correlates of face recollection can also be observed during a yes–no recognition test and without differential instructions to remember. The experiment was thus arranged so that a direct comparison could be made between faces associated with biographical information and faces presented under circumstances that were identical except for the absence of associated biographical information. As a shorthand, we will refer to the former category of faces as *named faces* and to the latter category of faces as *unnamed faces*. This contrast corresponds to the real-world contrast between faces of known and unknown individuals. Faces of both types can potentially provoke recollection, as someone can remember having seen a face before regardless of whether any person-specific biographical information is known. We hypothesized that ERP repetition effects would be found for named faces and, to a lesser extent, for unnamed faces, which may in both cases reflect recollective processing.

METHODS

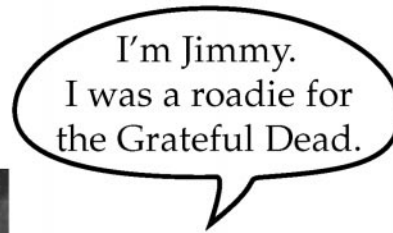
Subjects

A group of four men and eight women participated in the experiment. The mean age was 20.6 years (range 18 to 26 years). All subjects were right-handed by self-report. Subjects gave informed consent and were paid for their participation.

Stimuli

Visual stimuli included photographs of 180 faces from a 1970s high school yearbook. Each face was presented in grayscale within a rectangular area

A Study Phase



...

B Test Phase



...

FIG. 1. Schematic representation of experimental trials. (A) The study phase included faces with voices (named faces) and faces without voices (unnamed faces). (B) The test phase included faces from the study phase and new faces, with no auditory components.

measuring 12.5 by 16 cm in the center of a computer screen. Faces were viewed from a distance of 135 cm (such that the rectangular stimuli subtended 5.9 by 7.5° visual angle). A set of 40 faces was used in the study phase. These faces were shown again in the test phase along with 80 new faces. Another 60 new faces were used in a paper-and-pencil recognition test. Each set of faces included an equal number of women and men. Auditory stimuli were paired with 20 of the faces in the study phase. These stimuli were spoken by 10 women and 10 men so as to simulate the experience of meeting the people depicted. Each voice included a name and some brief biographical information (see Paller *et al.*, 1999, for additional details).

Procedure

The procedure included a study phase followed immediately by a test phase and then a paper-and-pencil

recognition test. Each subject was tested individually. To reduce artifactual contamination of EEG recordings, subjects were instructed to minimize muscle tension, eye movements, and blinks during experimental runs.

During the study phase (Fig. 1A), subjects were instructed to try to remember a series of people. They were told that 20 faces (named faces) would be presented with a spoken introduction to approximate the experience of actually meeting these people and that 20 faces (unnamed faces) would be presented in silence. Subjects were advised to try to remember all of the people for a memory test that would be given later. They were told that the test would assess their ability to recognize the faces and to recall the names and biographical information of the people who spoke. Faces were shown for 300 ms at a rate of 1 every 5 s. The onset of the voice for each named face coincided with the onset of the face presentation. The entire set of

40 faces was presented three times using different random orders. The sets of faces assigned to named and unnamed conditions were counterbalanced across subjects. In other words, each face stimulus from the set served as a named face for six subjects and as an unnamed face for the other six subjects.

During the test phase (Fig. 1B), subjects were instructed to respond after each face according to whether the face shown was old or new, pressing a button in one hand or the other (right hand for old for half of the subjects, left hand for old for the others). They were also told to use this as an opportunity to think about the biographical information that was to be remembered for the subsequent memory test. Faces were shown for 300 ms at a rate of 1 every 3 s. Faces were presented in four runs without any auditory stimuli. Named and unnamed faces were repeated across runs, whereas new faces each appeared on only one occasion. Because we wished to make comparisons with results from a prior experiment, we used stimulus sequences identical to those used previously, even though the task was changed. In the prior experiment (Paller *et al.*, 1999), target events were included by selecting 2 new faces, 2 named faces, and 2 unnamed faces in each run to be presented twice in a row. In the present experiment, subjects were told that when a face appeared twice in a row, they should respond the same way for both presentations. Responses to these immediately repeated faces were excluded from all analyses. Thus, the remaining faces in each of the four runs included a randomly ordered set of 60 faces: the 20 named faces, the 20 unnamed faces, and the 20 new faces.

For the paper-and-pencil recognition test given at the conclusion of the experiment, subjects used a set of five pages showing 20 faces per page. These 100 faces included the 40 faces from the study phase randomly mixed with 60 new faces not otherwise used in the experiment. Subjects were asked to place a letter in a corresponding box for each of the 20 named faces and each of the 20 unnamed faces and to write down the name and biographical information for each named face. Approximate wording was sufficient for recalled biographical information to be scored as correct.

Electrophysiology

Electroencephalographic recordings were made from 21 scalp electrodes embedded in an elastic cap at standard locations (Fpz, Fz, Cz, Pz, Oz, Fp1, Fp2, F3, F4, F7, F8, C3, C4, P3, P4, O1, O2, T3, T4, T5, T6). A left mastoid reference electrode was used online and the reference was changed offline to the average of left and right mastoid recordings. Two channels were used for monitoring horizontal and vertical eye movements and trials contaminated by electroocular artifacts were excluded from the analyses (7.2% on average in the test phase). Biosignals were amplified with a 0.1 to 100 Hz

band pass and sampled at a rate of 250 Hz. ERPs were computed for 1024-ms epochs beginning 100 ms prior to stimulus onset. The 300- to 600-ms interval was selected for initial analyses as this interval was used in our earlier study (Paller *et al.*, 1999). Subsequent analyses to investigate ERP time course were conducted over 100-ms latency intervals. ERP measurements were evaluated using analysis of variance (ANOVA), and critical *F* ratios were based on degrees of freedom adjusted according to the Huynh–Feldt procedure when needed to control for Type I errors in repeated-measures designs.

RESULTS

Behavioral results are summarized in Table 1. As expected, recognition was better for named faces than for unnamed faces. This difference was significant for both the test-phase recognition test [$t(11) = 3.6$, $P = 0.004$] and the subsequent paper-and-pencil recognition test [$t(11) = 2.5$, $P = 0.03$]. For named faces, successful name recall averaged 33.8% ($SE = 7.3$) and successful recall of the other biographical information averaged 60.0% ($SE = 5.6$).

Reaction time results for correct trials in the test phase (Table 1) showed that responses were equivalently fast for named faces and unnamed faces [$t(11) < 1$]. Responses to both types of old faces were faster than responses to new faces [$t(11) = 3.5$, $P = 0.01$ and $t(11) = 2.3$, $P = 0.04$, respectively].

Electrophysiological recordings during the test phase revealed systematic differences as a function of condition, as shown in Fig. 2. First, note that ERPs computed across all trials were quite similar to ERPs computed for correct trials. However, there was insufficient statistical power to analyze ERPs separately for incorrect trials. Given our concern with identifying neural correlates of accurate retrieval, ERP results for correct trials will be emphasized. Analyses of the two *study effects*—(1) ERPs to named versus new faces and (2) ERPs to unnamed versus new faces—will be described

TABLE 1

Behavioral Results from Memory Tests (*SE* Shown in Parentheses)

Measure	Condition		
	Named faces	Unnamed faces	New faces
Test-phase recognition accuracy (% correct)	87.2 (3.0)	73.9 (5.2)	90.9 (2.6)
Paper-and-pencil recognition accuracy (% correct)	73.3 (4.7)	64.2 (4.6)	89.3 (1.8)
Mean reaction time (ms)	770 (30)	784 (36)	848 (26)

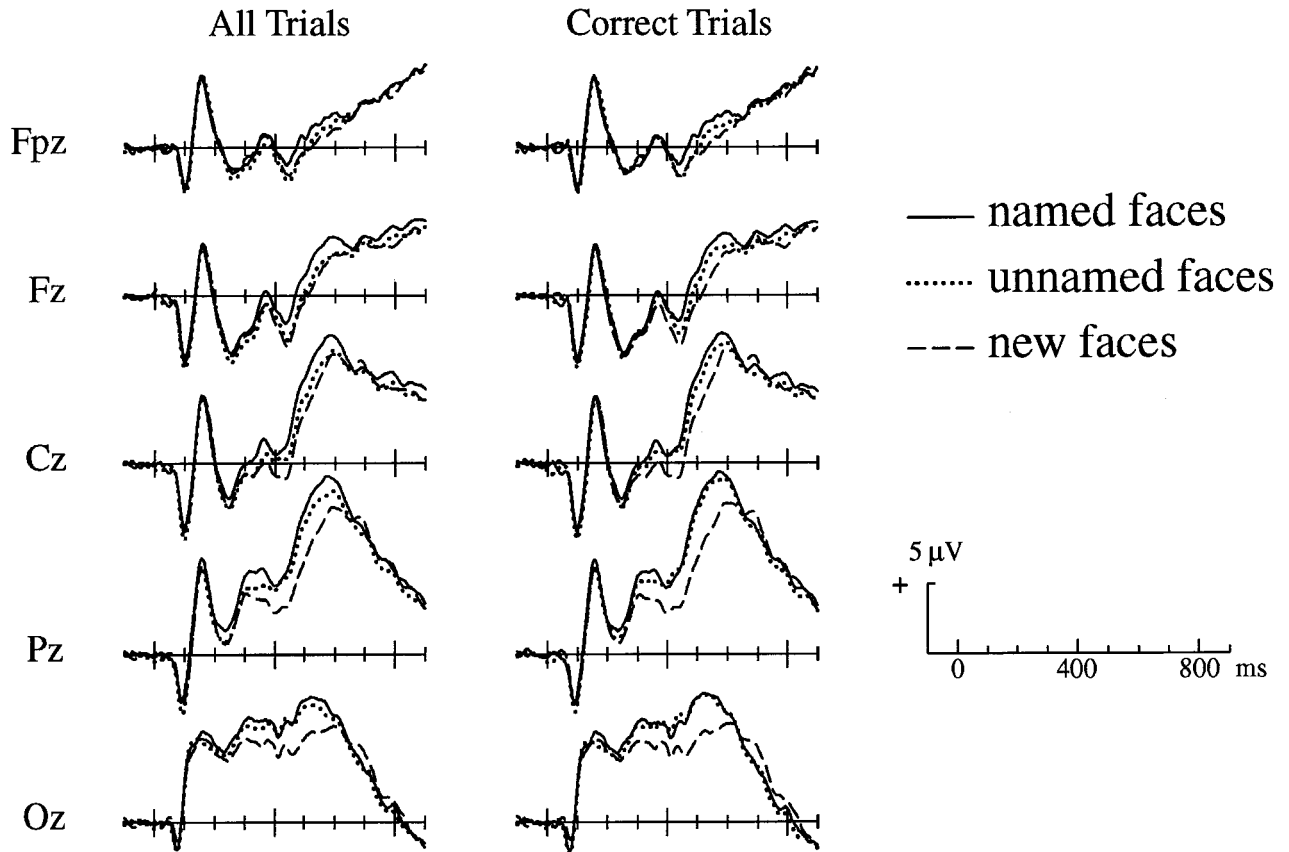


FIG. 2. ERPs recorded during the test phase for named faces, unnamed faces, and new faces. Recordings shown were from midline scalp locations arranged from anterior (top) to posterior (bottom), including all trials (left) or only correct trials (right).

in turn. Both of these study effects (or old–new ERP differences) can also be viewed as difference waves (Fig. 3).

Mean ERP amplitudes from the five midline scalp locations were initially measured over the interval from 300 to 600 ms and these measurements were submitted to ANOVAs with Condition (named vs new or unnamed vs new) and Location as factors (see Table 2). The first ANOVA showed that ERPs were significantly more positive for named than for new faces. The Condition by Location interaction reflected the finding that this study effect was significant at all midline locations except the most anterior one. ERP comparisons between unnamed and new faces revealed a similar pattern. Midline ERPs from 300 to 600 ms were also significantly more positive for unnamed than for new faces. The Condition by Location interaction reflected the finding that this study effect was significant only at the two most posterior locations. In other words, study effects at posterior locations (Pz and Oz) were reliable for named and unnamed faces, whereas study effects at anterior locations (Fz and Cz) were reliable only for named faces. The topography of the two study effects can be viewed as a series of interpolated maps

created from ERP difference measurements over consecutive 100-ms intervals (Figs. 4 and 5).

Subsequent analyses were conducted to determine the time course of the study effects by analyzing ERPs over 100-ms intervals. First, analyses focused on results from the midline parietal location, where study effect amplitudes were largest. ERPs to named faces were significantly more positive than ERPs to new faces for all three intervals from 300 to 600 ms [$F(1,11) = 8.42, 10.61, \text{ and } 11.85, P = 0.01, 0.008, \text{ and } 0.006$, respectively]. Differences were nonsignificant for all other intervals, although there was a marginal difference from 200 to 300 ms [$F(1,11) = 3.8, P = 0.08$]. ERPs to unnamed faces were also significantly more positive than ERPs to new faces for all three intervals from 300 to 600 ms [$F(1,11) = 10.84, 19.02, \text{ and } 12.17, P = 0.007, 0.001, \text{ and } 0.005$, respectively] and nonsignificant for all other intervals. Additional analyses were conducted at the midline frontal location, where only the named–new ERP difference was significant. This difference appeared to begin later than the posterior difference, as it was nonsignificant from 300 to 400 ms [$F(1,11) = 2.68, P = 0.13$], significant from 400 to 500 ms and from 500 to 600 ms [$F(1,11) = 14.00 \text{ and } 6.61, P = 0.003 \text{ and}$

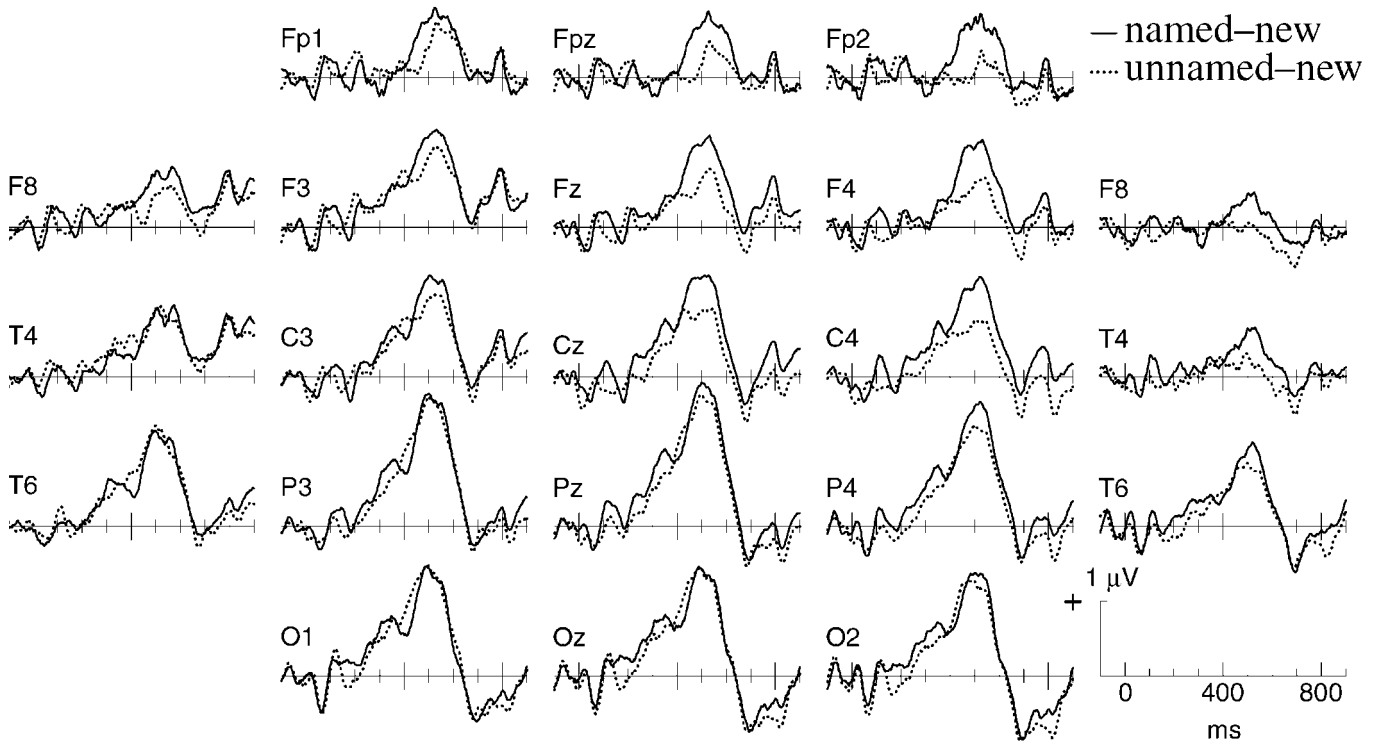


FIG. 3. ERP difference waves computed by subtracting ERPs to new faces from ERPs to old faces, including only correct trials. Recordings shown were from all scalp electrodes, arranged topographically.

TABLE 2

ERP Differences between Conditions

Comparison	μV	SE	F	P
Named–new faces				
Midline mean	1.76	0.51		
Main effect of Condition			*11.92	0.005
Condition \times Location interaction			*4.68	0.02
Midline locations				
Fpz	0.79	0.44	3.21	0.10
Fz	1.50	0.50	*9.10	0.01
Cz	1.93	0.67	*8.20	0.02
Pz	2.64	0.76	*12.06	0.005
Oz	1.95	0.48	*16.82	0.002
Unnamed–new faces				
Midline mean	1.33	0.45		
Main effect of Condition			*8.88	0.01
Condition \times Location interaction			*6.97	0.001
Midline Locations				
Fpz	0.23	0.43	0.28	0.61
Fz	0.87	0.57	2.38	0.15
Cz	1.31	0.64	4.15	0.07
Pz	2.33	0.58	*16.26	0.002
Oz	1.92	0.37	*26.38	0.0003

Note. An asterisk adjacent to the F value indicates a statistically significant effect. Degrees of freedom were 4,44 for each Condition \times Location interaction and 1,11 for all other tests.

0.03, respectively], and nonsignificant for all other intervals. In short, the posterior difference was present from 300 to 600 ms, whereas the anterior difference was present from 400 to 600 ms.

To directly assess the reliability of anterior ERP differences between named and unnamed faces, ERPs were analyzed over consecutive 100-ms intervals at midline electrodes. For the 400- to 500-ms interval, the difference was significant at Fpz [$F(1,11) = 6.49$, $P = 0.03$], marginal at Fz [$F(1,11) = 4.09$, $P = 0.07$], and nonsignificant at Cz, Pz, and Oz [$F(1,11) < 1$]. For other intervals differences were nonsignificant. In addition, ERP differences from 400 to 500 ms from all lateral locations were submitted to a Condition by Hemisphere by Location ANOVA. Although there was a tendency for ERP differences between named and unnamed faces to be larger over the right hemisphere (Fig. 3), all effects involving Hemisphere were nonsignificant.

DISCUSSION

The study-phase manipulation in the present experiment provided richer encoding for named faces than for unnamed faces. The contrast between named and unnamed faces was associated with two differences in later memory. First, named faces tended to provoke the retrieval of stored biographical information from the study phase, whereas this was not possible for un-

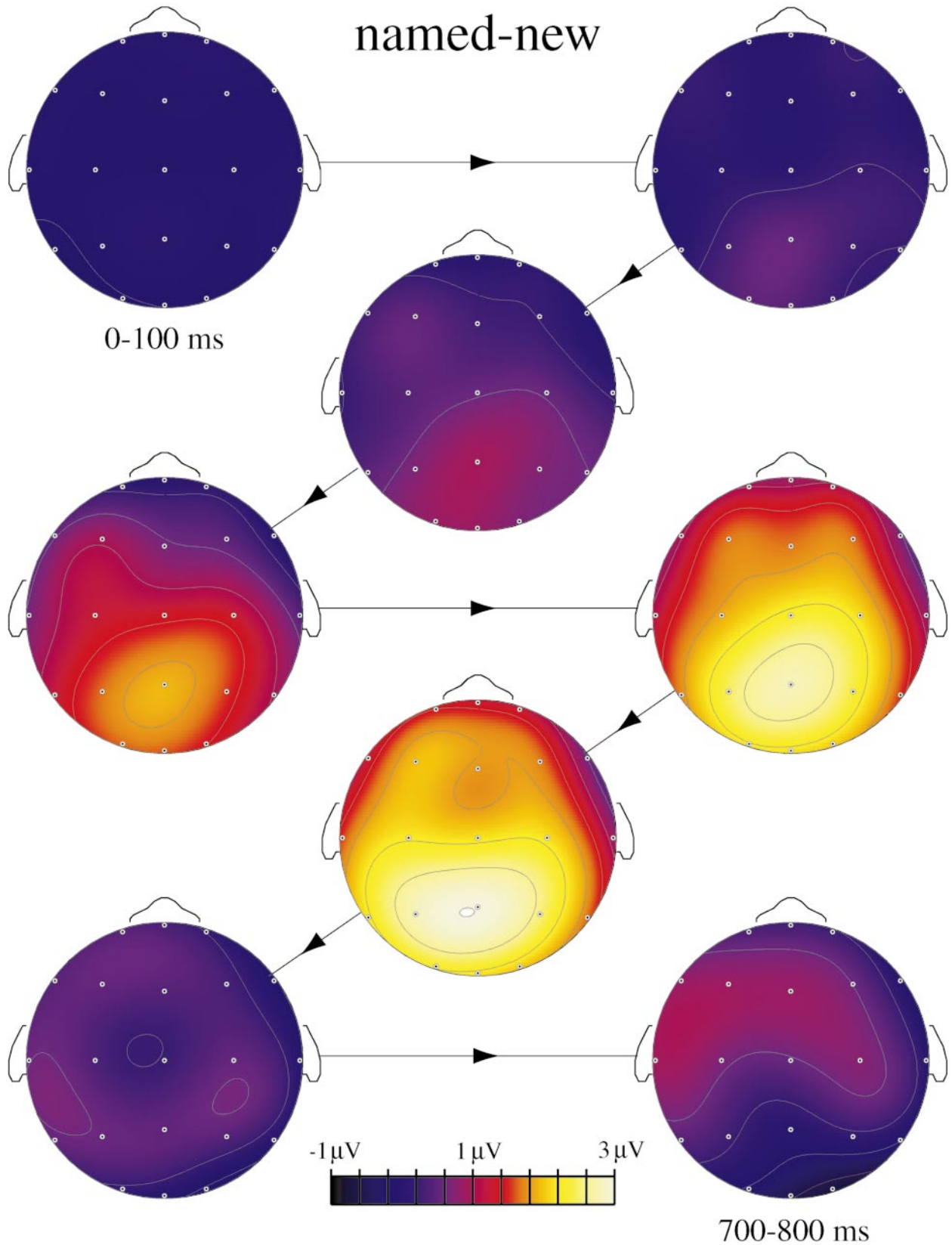


FIG. 4. Topographic maps of ERP differences across the scalp for ERPs to named faces minus ERPs to new faces. A surface spline interpolation was applied to data obtained from each electrode location (indicated by small circles on each schematic view of a head as viewed from above). Maps represent mean amplitude differences computed for consecutive 100-ms intervals starting at 0 and ending at 800 ms.

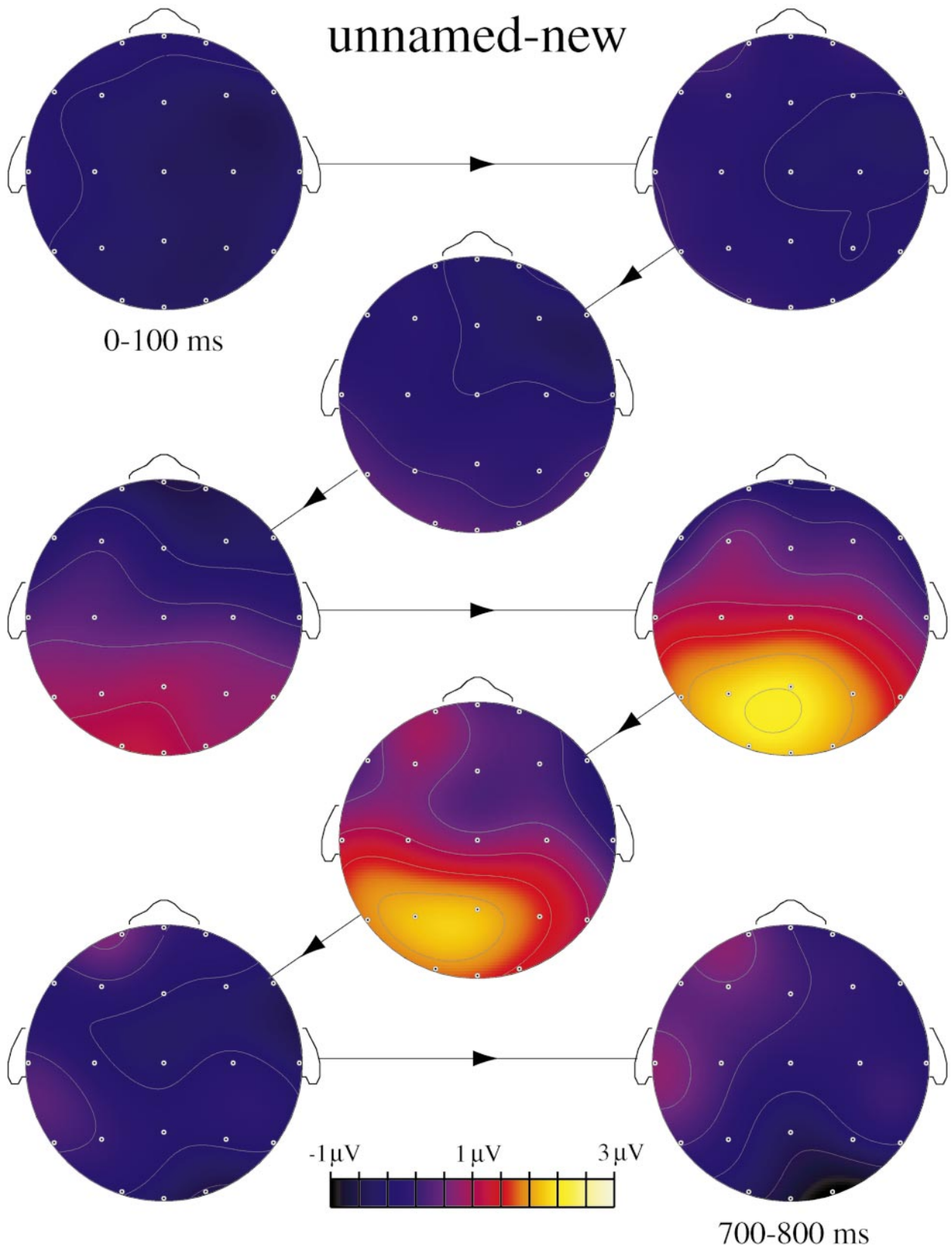


FIG. 5. Topographic maps of ERP differences between unnamed faces and new faces. Topographic maps were created as in Fig. 4.

named faces. Second, superior recognition performance was observed for named compared to unnamed faces. Subjects recognized named faces more accurately, but reaction times for correct responses did not differ between named and unnamed faces. Furthermore, reaction time distributions for named and unnamed faces appeared extremely similar. Thus, ERP comparisons for named versus unnamed faces in the test phase were not complicated by confounding differences in reaction time, nor were there any systematic physical stimulus differences (by virtue of the counterbalanced experimental design). Although significant old–new ERP differences were present for both types of old faces, for named faces these effects were found at anterior and posterior scalp locations (Fig. 4), whereas for unnamed faces these effects were restricted to posterior scalp locations (Fig. 5).

In prior experiments conducted with the same named and unnamed faces, subjects were instructed in the study phase to remember the named faces and to forget the unnamed faces (Paller *et al.*, 1999). In a test phase in which perceptually degraded faces were presented for fame decisions (i.e., “famous” vs “nonfamous”), priming was measured as a facilitation in both decision accuracy and latency (Paller *et al.*, 1999, Experiment 1). Importantly, the magnitude of priming did not differ between the two types of studied faces (referred to as *remember faces* and *forget faces*). Indeed, differential processing induced by remember versus forget instructions at study generally affects later recall and recognition but does not affect priming performance (Basden *et al.*, 1993; Golding and MacLeod, 1998; Johnson, 1994; Paller, 1990; Roediger and McDermott, 1993). The high degree of similarity between procedures used in our prior ERP experiment (Paller *et al.*, 1999, Experiment 2) and in the present experiment allows for straightforward cross-experiment comparisons. The only two ways in which the design of the present experiment differed were that (1) all faces shown in the study phase were to be remembered and (2) the task in the test phase was to make overt recognition responses. Accordingly, it is reasonable to speculate that priming would likewise be matched between named and unnamed faces in the present experiment. In contrast, recognition was superior for named compared to unnamed faces whether or not directed forgetting instructions were included.

ERPs elicited in the test phase in the prior ERP experiment (Paller *et al.*, 1999, Experiment 2) were found to differ between remember and forget faces. These effects were interpreted in light of the behavioral results that the study-phase manipulation influenced recognition but not priming. Note that no overt recognition responses were made when ERPs were recorded. Subjects were instructed to retrieve learned biographical information when shown a remember face but to make no overt response for either remember faces or

forget faces. Recollection, but not priming, thus differed between remember and forget faces. Electrophysiological correlates of priming would thus be absent in comparisons between the two types of old faces (though ERP correlates of priming have been observed with words, e.g., Paller and Gross, 1998). ERP differences between the two types of old faces (remember faces–forget faces) were thus interpreted as electrophysiological correlates of recollective processing, divorced from the influence of priming and other nonspecific factors. Figure 6 shows the spatiotemporal pattern of these effects.

Inspection of Figs. 4, 5, and 6 suggests that similar neurophysiological phenomena were recorded across experiments, although there were differences in the latency of the observed response. Apparently, these electrophysiological manifestations of face recollection were evident whether or not subjects made overt recognition responses and whether or not faces were associated with biographical information. Interestingly, the latency of old–new effects was shorter in the present experiment than in the prior experiment. A reasonable explanation for this difference is that retrieval processing occurred more quickly following face presentations in the present experiment due to the recognition task requirement, which demanded a quick manual response to each face. The comparison across experiments is also relevant for several other reasons. Old–new ERP effects in the present experiment could have been influenced by response-related processing, given that reaction times differed between old and new faces. However, the old–new ERP differences cannot be explained by a relative increase in temporal variability of processing elicited by new face presentations, because reaction time variability was less for new faces compared to old faces, as shown in Table 1.

The contrast between named–new and unnamed–new ERP differences in the present experiment makes it possible to ask whether a portion of the effect is specifically related to retrieval of biographical information. Again, note that this named/unnamed contrast is free from any physical stimulus effects (due to counterbalancing) and from response factors (given the absence of corresponding reaction time differences). If one were to assume that nearly all of the old–new ERP effect reflected biographical retrieval, then the effect would be expected to be much larger for named faces than for unnamed faces. On the contrary, if one were to assume that nearly all of the old–new ERP effect reflected face retrieval, then the effect would be expected to be the same for named and unnamed faces.

Indeed, at posterior locations the old–new ERP effect was highly similar for named and unnamed faces. This posterior portion of the effect can thus be taken as an index of face recollection associated with visual processing of the facial image just presented and of retrieved

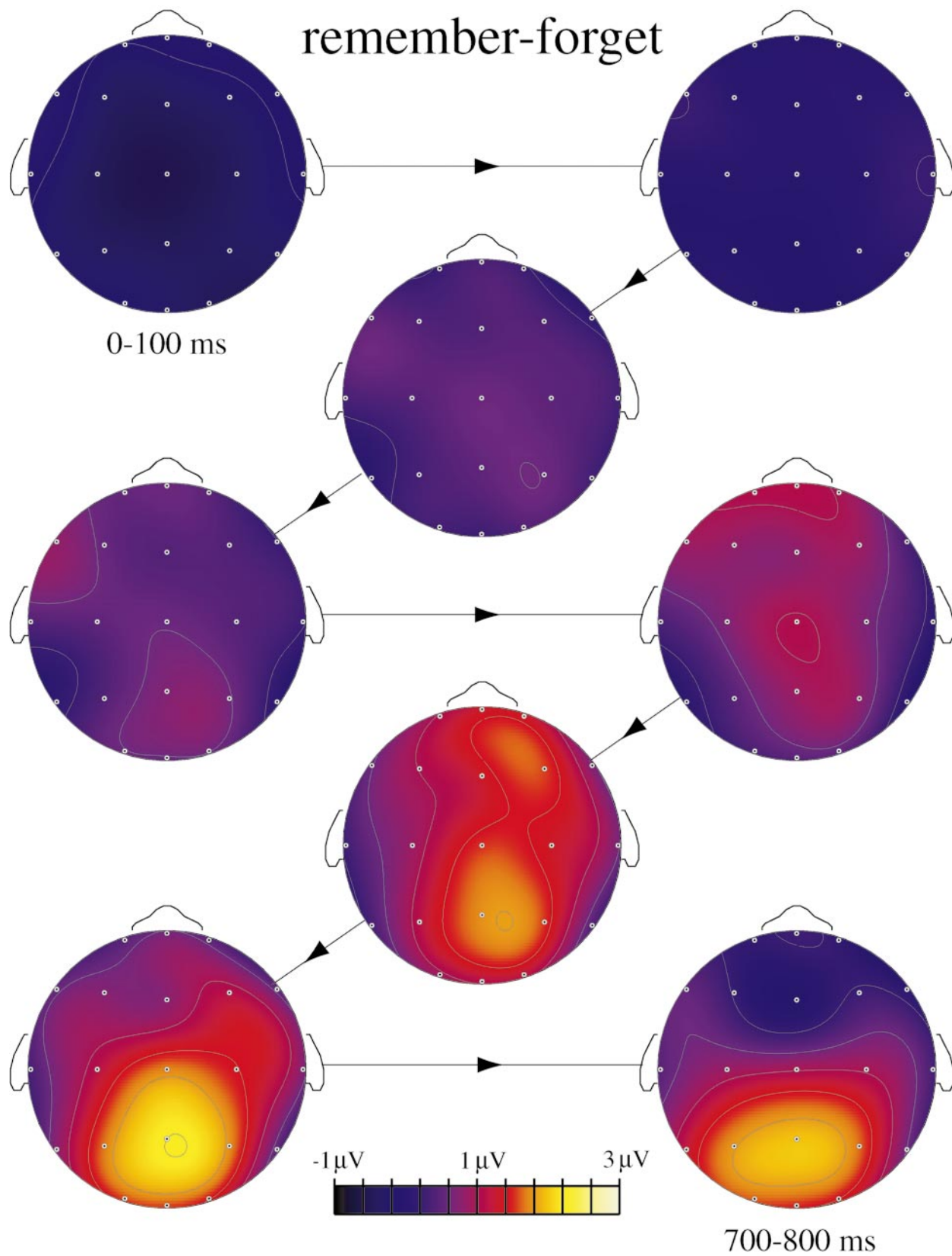


FIG. 6. Results from Paller *et al.* (1999) for the ERP difference between remember faces and forget faces. Topographic maps were created as in Figs. 4 and 5.

representations of the face viewed at study. At anterior locations, the old–new ERP effect was observed for named faces but was smaller and unreliable for unnamed faces. This anterior portion of the effect can thus be taken as an index of person recollection connected to the biographical information heard at study.

In addition, part of the anterior portion of the old–new ERP effect for named faces may reflect frontal activity engaged in the service of strategic retrieval operations. Prior neuroimaging and ERP results suggest that both left and right frontal regions tend to be activated during retrieval, although left frontal regions appear to be particularly relevant for evaluation processes critical for accurate retrieval (e.g., Buckner, 1996; Fletcher *et al.*, 1997; Nolde *et al.*, 1998; Nyberg *et al.*, 1996; Ranganath and Paller, 1999; Tulving *et al.*, 1994; Wilding, 1999; Wilding and Rugg, 1996). Similarly, the problem of retrieving the appropriate name and biographical information for each named face may call on prefrontal processing for accurate retrieval to take place. Prefrontal regions could also contribute to processing of contextual information that occurs after initial face retrieval; however, the early timing of the anterior portion of the old–new ERP effect suggests that it does not reflect postretrieval processing.

An alternative explanation for the ERP differences for named versus unnamed faces is that they reflect differential recognition accuracy for the two types of studied faces. This alternative could apply even for analyses restricted to correct trials, because recognition could have been stronger for named than for unnamed faces (e.g., fewer lucky guesses). Nonetheless, topographically specific differences for named versus unnamed faces, as observed here, would not be predicted based on differences in recognition strength alone. The fact that ERPs at posterior scalp locations were so remarkably similar for named and unnamed faces suggests that this portion of the old–new ERP effect reflected memory-related processing that supported accurate recognition judgments in both conditions.

These results provide a foothold for further research aimed at establishing the nature of neural processing responsible for person recognition. Prosopagnosic impairments in which patients fail to recollect familiar faces generally result from damage to inferior temporal regions, although the precise anatomical details of this association are controversial and perhaps quite variable across patients (e.g., Damasio *et al.*, 1982; De Renzi, 1997; Ettlín *et al.*, 1992). Prior neuroimaging results with PET and fMRI have associated various brain regions with memory for known and unknown faces (Andreasen *et al.*, 1996; Dubois *et al.*, 1999; Gorno Tempini *et al.*, 1998; Haxby *et al.*, 1996; Kapur *et al.*, 1995; Sergent *et al.*, 1992). For example, right prefrontal, bilateral parietal, and ventral occipital regions

were implicated by Haxby and colleagues (1996). More limited regions of activation in the fusiform gyrus, left lingual gyrus, and right parietal cortex were found by Andreasen and colleagues (1996). Additional studies are needed to delineate the various cortical networks required for person recognition and link them to specific memory functions. Old–new ERP effects appeared to reflect multiple aspects of memory for faces. These included (a) processing of visual information corresponding to the match between a recognition probe and stored representations of facial images viewed at study—which was associated with posterior ERP differences beginning at approximately 300 ms—and (b) strategic processing critical for retrieving person-specific biographical information heard at study—which was associated with anterior ERP differences beginning at approximately 400 ms.

ACKNOWLEDGMENTS

This research was supported by Grant NS34639 from the National Institute of Neurological Diseases and Stroke. We thank Ted Whalen for technical support.

REFERENCES

- Allison, T., Ginter, H., McCarthy, G., Nobre, A. C., Puce, A., Luby, M., and Spencer, D. D. 1994a. Face recognition in human extrastriate cortex. *J. Neurophysiol.* **71**: 821–825.
- Allison, T., McCarthy, G., Nobre, A., Puce, A., and Belger, A. 1994b. Human extrastriate visual cortex and the perception of faces, words, numbers, and colors. *Cereb. Cortex* **4**: 544–554.
- Andreasen, N. C., O'Leary, D. S., Arndt, S., Cizadlo, T., Hurtig, R., Rezaei, K., Watkins, G. L., Ponto, L. B., and Hichwa, R. D. 1996. Neural substrates of facial recognition. *J. Neuropsychiatry Clin. Neurosci.* **8**: 139–146.
- Barrett, S. E., Rugg, M. D., and Perrett, D. I. 1988. Event-related potentials and the matching of familiar and unfamiliar faces. *Neuropsychologia* **26**: 105–117.
- Basden, B. H., Basden, D. R., and Gargano, G. J. 1993. Directed forgetting in implicit and explicit memory tests: A comparison of methods. *J. Exp. Psychol. Learn. Memory Cognit.* **19**: 603–616.
- Begleiter, H., Porjesz, B., and Wang, W. 1995. Event-related brain potentials differentiate priming and recognition to familiar and unfamiliar faces. *Electroencephalogr. Clin. Neurophysiol.* **94**: 41–49.
- Bentin, S., Allison, T., Puce, A., Perez, E., and McCarthy, G. 1996. Electrophysiological studies of face perception in humans. *J. Cognit. Neurosci.* **8**: 551–565.
- Bentin, S., and McCarthy, G. 1994. The effects of immediate stimulus repetition on reaction time and event-related potentials in tasks of different complexity. *J. Exp. Psychol. Learn. Memory Cognit.* **20**: 130–149.
- Bentin, S., and Moscovitch, M. 1988. The time course of repetition effects for words and unfamiliar faces. *J. Exp. Psychol. Gen.* **117**: 148–160.
- Bötzel, K., and Grüsser, O. J. 1989. Electric brain potentials evoked by pictures of faces and non-faces: A search for “face-specific” EEG-potentials. *Exp. Brain Res.* **77**: 349–360.
- Bruce, V., and Young, A. 1986. Understanding face recognition. *Br. J. Psychol.* **77**: 305–327.

- Buckner, R. L. 1996. Beyond HERA: Contributions of specific prefrontal brain areas to long-term memory retrieval. *Psychonomic Bull. Rev.* **3**: 149–158.
- Carey, S. 1992. Becoming a face expert. *Philos. Trans. R. Soc. London Ser. B Biol. Sci.* **335**: 95–102. [Discussion pp. 102–103]
- Carlesimo, G. A., and Caltagirone, C. 1995. Components in the visual processing of known and unknown faces. *J. Clin. Exp. Neuropsychol.* **17**: 691–705.
- Clark, V. P., Keil, K., Maisog, J. M., Courtney, S., Ungerleider, L. G., and Haxby, J. V. 1996. Functional magnetic resonance imaging of human visual cortex during face matching: A comparison with positron emission tomography. *NeuroImage* **4**: 1–15.
- Damasio, A. R., Damasio, H., and Van Hoesen, G. W. 1982. Prosopagnosia: Anatomic basis and behavioral mechanisms. *Neurology* **32**: 331–341.
- De Renzi, E. 1997. Prosopagnosia. In *Behavioral Neurology and Neuropsychology* (T. E. Feinberg, and M. J. Farah, Eds.), pp. 245–255. McGraw–Hill, New York.
- Desimone, R. 1991. Face-selective cells in the temporal cortex of monkeys. *J. Cognit. Neurosci.* **3**: 1–8.
- Dubois, S., Rossion, B., Schiltz, C., Bodart, J. M., Michel, C., Bruyer, R., and Crommelinck, M. 1999. Effect of familiarity on the processing of human faces. *NeuroImage* **9**: 278–289.
- Ettlin, T. M., Beckson, M., Benson, D. F., Langfitt, J. T., Amos, E. C., and Pineda, G. S. 1992. Prosopagnosia: A bihemispheric disorder. *Cortex* **28**: 129–134.
- Farah, M. J., Wilson, K. D., Drain, M., and Tanaka, J. N. 1998. What is “special” about face perception? *Psychol. Rev.* **105**: 482–498.
- Fletcher, P. C., Frith, C. D., and Rugg, M. D. 1997. The functional neuroanatomy of episodic memory. *Trends Neurosci.* **20**: 213–218.
- Golding, J. M., and MacLeod, C. M. 1998. *Intentional Forgetting: Interdisciplinary Approaches*. Erlbaum, Mahwah, NJ.
- Gorno Tempini, M. L., Price, C. J., Josephs, O., Vandenberghe, R., Cappa, S. F., Kapur, N., and Frackowiak, R. S. 1998. The neural systems sustaining face and proper-name processing. *Brain* **121**: 2103–2118. [Published erratum appears in *Brain* **121**: 2402]
- Haxby, J. V., Ungerleider, L. G., Clark, V. P., Schouten, J. L., Hoffman, E. A., and Martin, A. 1999. The effect of face inversion on activity in human neural systems for face and object perception. *Neuron* **22**: 189–199.
- Haxby, J. V., Ungerleider, L. G., Horwitz, B., Maisog, J. M., Rapoport, S. I., and Grady, C. L. 1996. Face encoding and recognition in the human brain. *Proc. Natl. Acad. Sci. USA* **93**: 922–927.
- Hertz, S., Porjesz, B., Begleiter, H., and Chorlian, D. 1994. Event-related potentials to faces: The effects of priming and recognition. *Electroencephalogr. Clin. Neurophysiol.* **92**: 342–351.
- Jeffreys, D. A. 1989. A face-responsive potential recorded from the human scalp. *Exp. Brain Res.* **78**: 193–202.
- Jeffreys, D. A., Tukmachi, E. S., and Rockley, G. 1992. Evoked potential evidence for human brain mechanisms that respond to single, fixated faces. *Exp. Brain Res.* **91**: 351–362.
- Johnson, H. M. 1994. Processes of successful intentional forgetting. *Psychol. Bull.* **116**: 274–292.
- Johnson, R., Jr. 1995. Event-related potential insights into the neurobiology of memory systems. In *Handbook of Neuropsychology* (F. Boller, and J. Grafman, Eds.), Vol. 10, pp. 135–163. Elsevier, Amsterdam.
- Kanwisher, N., McDermott, J., and Chun, M. M. 1997. The fusiform face area: A module in human extrastriate cortex specialized for face perception. *J. Neurosci.* **17**: 4302–4311.
- Kapur, N., Friston, K. J., Young, A., Frith, C. D., and Frackowiak, R. S. 1995. Activation of human hippocampal formation during memory for faces: A PET study. *Cortex* **31**: 99–108.
- Linkenkaer-Hansen, K., Palva, J. M., Sams, M., Hietanen, J. K., Aronen, H. J., and Ilmoniemi, R. J. 1998. Face-selective processing in human extrastriate cortex around 120 ms after stimulus onset revealed by magneto- and electroencephalography. *Neurosci. Lett.* **253**: 147–150.
- Müntz, T. F., Brack, M., Grootheer, O., Wieringa, B. M., Matzke, M., and Johannes, S. 1997. Event-related brain potentials to unfamiliar faces in explicit and implicit memory tasks. *Neurosci. Res.* **28**: 223–233.
- Müntz, T. F., Brack, M., Grootheer, O., Wieringa, B. M., Matzke, M., and Johannes, S. 1998. Brain potentials reveal the timing of face identity and expression judgments. *Neurosci. Res.* **30**: 25–34.
- Nolde, S. F., Johnson, M. K., and Raye, C. L. 1998. The role of prefrontal cortex during tests of episodic memory. *Trends Cognit. Sci.* **2**: 399–406.
- Nyberg, L., Cabeza, R., and Tulving, E. 1996. PET studies of encoding and retrieval: The HERA model. *Psychonomic Bull. Rev.* **3**: 135–148.
- Paller, K. A. 1990. Recall and stem-completion priming have different electrophysiological correlates and are modified differentially by directed forgetting. *J. Exp. Psychol. Learn. Memory Cognit.* **16**: 1021–1032.
- Paller, K. A. 1993. Elektrophysiologische Studien zum Menschlichen Gedächtnis [Electrophysiological studies of human memory]. *Z. Elektroenzephalogr. Elektromyogr. Gebiete* **24**: 24–33.
- Paller, K. A. Neurocognitive foundations of human memory. In *The Psychology of Learning and Motivation* (D. L. Medin, Ed.), Vol. 40. Academic Press, San Diego, in press.
- Paller, K. A., Bozic, V. S., Ranganath, C., Grabowecy, M., and Yamada, S. 1999. Brain waves following remembered faces index conscious recollection. *Cognit. Brain Res.* **7**: 519–531.
- Paller, K. A., and Gross, M. 1998. Brain potentials associated with perceptual priming versus explicit remembering during the repetition of visual word-form. *Neuropsychologia* **36**: 559–571.
- Perrett, D. I., Hietanen, J. K., Oram, M. W., and Benson, P. J. 1992. Organization and functions of cells responsive to faces in the temporal cortex. In *Processing the Facial Image* (V. Bruce, A. Cowey, A. W. Ellis, and D. I. Perrett, Eds.), pp. 23–30. Clarendon/Oxford Univ. Press, Oxford.
- Potter, D. D., and Parker, D. M. 1997. Dissociation of event-related potential repetition effects in judgments of face identity and expression. *J. Psychophysiol.* **11**: 287–303.
- Puce, A., Allison, T., Asgari, M., Gore, J. C., and McCarthy, G. 1996. Differential sensitivity of human visual cortex to faces, letter-strings, and textures: A functional magnetic resonance imaging study. *J. Neurosci.* **16**: 5205–5215.
- Puce, A., Allison, T., Gore, J. C., and McCarthy, G. 1995. Face-sensitive regions in human extrastriate cortex studied by functional MRI. *J. Neurophysiol.* **74**: 1192–1199.
- Puce, A., Allison, T., Spencer, S. S., Spencer, D. D., and McCarthy, G. 1997. A comparison of cortical activation evoked by faces measured by intracranial field potentials and functional MRI: Two case studies. *Hum. Brain Mapp.* **5**: 298–305.
- Ranganath, C., and Paller, K. A. 1999. Frontal brain potentials during recognition are modulated by requirements to retrieve perceptual detail. *Neuron* **22**: 605–613.
- Roediger, H. L., III, and McDermott, K. B. 1993. Implicit memory in normal human subjects. In *Handbook of Neuropsychology* (F. Boller, and J. Grafman, Eds.), Vol. 8, pp. 63–131. Elsevier, Amsterdam.
- Rugg, M. D. 1995. Event-related potential studies of human memory. In *The Cognitive Neurosciences* (M. S. Gazzaniga, Ed.), pp. 789–801. MIT Press, Cambridge, MA.
- Sams, M., Hietanen, J. K., Hari, R., Ilmoniemi, R. J., and Lounas-

- ma, O. V. 1997. Face-specific responses from the human inferior occipito-temporal cortex. *Neuroscience* **77**: 49–55.
- Schweinberger, S. R., Pfitze, E.-M., and Sommer, W. 1995. Repetition priming and associative priming of face recognition: Evidence from event-related potentials. *J. Exp. Psychol. Learn. Memory Cognit.* **21**: 722–736.
- Sergent, J., Ohta, S., and MacDonald, B. 1992. Functional neuroanatomy of face and object processing. A positron emission tomography study. *Brain* **115**: 15–36.
- Smith, M. E., and Halgren, E. 1987. Event-related potentials elicited by familiar and unfamiliar faces. *Electroencephalogr. Clin. Neurophysiol. Suppl.* **40**: 422–426.
- Sommer, W., Komoss, E., and Schweinberger, S. R. 1997. Differential localization of brain systems subserving memory for names and faces in normal subjects with event-related potentials. *Electroencephalogr. Clin. Neurophysiol.* **102**: 192–199.
- Tulving, E., Kapur, S., Craik, F. I., Moscovitch, M., and Houle, S. 1994. Hemispheric encoding/retrieval asymmetry in episodic memory: Positron emission tomography findings. *Proc. Natl. Acad. Sci. USA* **91**: 2016–2020.
- Uhl, F., Lang, W., Spieth, F., and Deecke, L. 1990. Negative cortical potentials when classifying familiar and unfamiliar faces. *Cortex* **26**: 157–161.
- Wilding, E. L. 1999. Separating retrieval strategies from retrieval success: An event-related potential study of source memory. *Neuropsychologia* **37**: 441–454.
- Wilding, E. L., and Rugg, M. D. 1996. An event-related potential study of recognition memory with and without retrieval of source. *Brain* **119**: 889–905. [Published erratum appears in *Brain* **119**: 1416]
- Young, A. W. 1998. *Face and Mind*. Oxford Univ. Press, Oxford.