Research Article

EXPERTISE TRAINING WITH NOVEL OBJECTS LEADS TO LEFT-LATERALIZED FACELIKE ELECTROPHYSIOLOGICAL RESPONSES

B. Rossion,[1,2] I. Gauthier,[3] V. Goffaux,[2] M.J. Tarr,[1] and M. Crommelinck[2]

[1]Department of Cognitive and Linguistic Sciences, Brown University; [2]Laboratoire de Neurophysiologie and Unite de Neuropsychologie Cognitive, Université Catholique de Louvain, Brussels, Belgium; and [3]Department of Psychology, Vanderbilt University

Abstract—*Scalp event-related potentials (ERPs) in humans indicate that face and object processing differ approximately 170 ms following stimulus presentation, at the point of the N170 occipitotemporal component. The N170 is delayed and enhanced to inverted faces but not to inverted objects. We tested whether this inversion effect reflects early mechanisms exclusive to faces or whether it generalizes to other stimuli as a function of visual expertise. ERPs to upright and inverted faces and novel objects (Greebles) were recorded in 10 participants before and after 2 weeks of expertise training with Greebles. The N170 component was observed for both faces and Greebles. The results are consistent with previous reports in that the N170 was delayed and enhanced for inverted faces at recording sites in both hemispheres. For Greebles, the same effect of inversion was observed only for experts, primarily in the left hemisphere. These results suggest that the mechanisms underlying the electrophysiological face-inversion effect extend to visually homogeneous nonface object categories, at least in the left hemisphere, but only when such mechanisms are recruited by expertise.*

It is often claimed that face recognition is realized by distinct processes within dedicated brain areas (e.g., Kanwisher, 2000). Countering this claim, both behavioral (Diamond & Carey, 1986; Gauthier & Tarr, 1997; Gauthier, Williams, Tarr, & Tanaka, 1998) and neuroimaging (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Gauthier, Anderson, Skudlarski, & Gore, 2000) studies, as well as a recent event-related potential (ERP) study (Tanaka & Curran, 2001), reveal that perceptual expertise with nonface objects can recruit the same cognitive mechanisms and brain areas that are implicated in face recognition (for a review, see Tarr & Gauthier, 2000). For example, within the spatial resolution of functional magnetic resonance imaging (fMRI), expertise with novel objects ("Greebles"; Gauthier et al., 1999), birds, and cars (Gauthier et al., 2000) appears to rely on the same neural substrates as face recognition. However, because of limited temporal resolution, fMRI studies cannot specify exactly when during visual processing such expertise effects occur. In the experiment we report here, we addressed one aspect of this issue by using ERPs, which reflect the direct recordings of brain activity at the surface of the scalp. Critically, ERPs have excellent temporal resolution, which allows inferences regarding time-course differences in visual processing that arise as a consequence of expertise training.

Several studies using ERPs have obtained a difference between objects and faces at approximately 170 ms in bilateral occipitotemporal regions (i.e., Bentin, Allison, Puce, Perez, & McCarthy, 1996; Bötzel, Schulze, & Stodieck, 1995; Eimer, 1998; Rossion et al., 2000). The component of interest has been described by some authors as specific to faces (Bentin et al., 1996) or larger for faces than for other familiar objects (Bötzel et al., 1995; Eimer, 1998; Rossion et al., 2000) and has been termed the N170.

Rossion et al. (2000) hypothesized that the larger-amplitude N170 for faces as compared with objects does not provide compelling evidence for early face-specific processes for three reasons: First, the N170 may be due to low-level visual differences between faces and objects (e.g., spatial frequency). Second, the N170 amplitude difference can be larger between two nonface object categories (e.g., cars and chairs) than between faces and some other object class (e.g., faces and cars; Rossion et al., 2000). Third, a robust (and sometimes larger) N170 difference between faces and objects is observed when face-specific processes are impaired either by face inversion (Rossion et al., 2000) or prosopagnosia (Rossion, Gauthier, et al., 1999).

Rossion et al. (2000) found that the N170 is both enhanced and delayed (by about 10 ms) when faces are presented inverted in the picture plane, but that this difference is not observed for inverted presentations of other classes of objects (for which observers are not experts; e.g., houses or shoes; Rossion et al., 2000).

This latency delay for face inversion is robust and has been observed in multiple ERP studies (Bentin et al., 1996; Eimer, 1998, 2000b; Rossion, Delvenne, et al., 1999; Rossion et al., 2000; Taylor, McCarthy, Saliba, & Degiovanni, 1999). Because the latency delay for face inversion is more clearly face-specific than the larger amplitude of the N170 to faces compared with objects (Rossion et al., 2000), and because the inversion effect has already been tied to expertise in several other studies (Diamond & Carey, 1986; Gauthier et al., 1999), we tested whether an N170 delay with inversion is obtained for new exemplars of a homogeneous object class (Greebles; see Gauthier & Tarr, 1997) for which participants have become experts. An N170 delay in this case would suggest that the earliest processing difference between faces and objects as measured by ERPs can be accounted for by the acquisition of visual expertise and not by the object class per se.

MATERIALS AND METHODS

Participants

Ten volunteers from the University of Louvain community in Louvain-la-Neuve, Belgium (average age: 25 years), participated for pay after giving informed consent.

Stimuli

Four kinds of stimuli were used: upright faces, inverted faces, upright Greebles (Gauthier & Tarr, 1997), and inverted Greebles. The faces, scanned with a three-dimensional laser scanner and obtained

---

Address correspondence to Bruno Rossion, Department of Cognitive and Linguistic Sciences, Brown University, 190 Thayer St., Box 1978, Providence, RI 02912; e-mail: bruno_rossion@brown.edu.

from Troje and Bülthoff (Max Planck Institute, Tübingen, Germany), were all cropped to the same overall shape.[1] The Greebles are photorealistically rendered three-dimensional novel objects created in Alias Sketch! (Alias Research Inc., Toronto, Ontario, Canada).[2] The set of Greebles is organized orthogonally along two categorical dimensions, such that each Greeble is a member of one of two categories (all parts pointing up or down) and one of five families (defined by the shape of the central part; Gauthier & Tarr, 1997; Gauthier et al., 1998). Each Greeble is unique and has an individual name.

Forty faces (20 males, 20 females) were used in the first ERP session, and 40 new faces (20 males, 20 females) were used in the second ERP session. Eighty Greebles were used during the sessions in the same proportions as faces: 40 Greebles of each category split 20/20 for a total of 40 Greebles shown in each session. Forty Greebles were presented during the first ERP session: Participants were taught the individual names of 20 of these Greebles during training, and the remaining 20 were used as distractors. Only new Greebles were presented during the second ERP session.

General Procedure

The experiment consisted of three phases: During the first phase, pre-expertise-training ERPs were measured using faces and Greebles in the upright and inverted orientations. The second phase consisted of expertise training with upright Greebles. During the third phase, post-expertise-training ERPs were measured using new faces and new Greebles in the upright and inverted orientations.

ERP sessions (pre- and post-expertise training)

The procedure used in the two ERP sessions was identical. The two sessions were separated by 2 weeks, during which expertise training occurred. Unfamiliar faces and Greebles were presented to participants in both sessions. Thus, participants were not familiar with the specific Greebles presented in the second, post-expertise-training session. Following 20 practice trials, participants received 16 blocks of 40 trials each. The same block order was followed for all participants. During each block, participants were instructed to maintain central fixation (at a distance of 150 cm). One-minute pauses were allowed between blocks.

The beginning of each trial was signaled by a central cross for 200 ms. Next a black screen appeared for 550 ms, followed by the first (target) stimulus, either a Greeble or a face, presented for 1,000 ms, and then a perceptual mask for 250 ms. Immediately after the mask disappeared, a probe stimulus was presented for 1,000 ms. The probe and the target were always from the same class (e.g., Greeble-Greeble). The intertrial interval was 1,800 ms. Participants decided as quickly and accurately as possible whether the target and the probe were different or the same and responded by pressing a left or right mouse key, respectively, using their right hand. Each trial lasted 4,800 ms on average (Fig. 1).

Each block of 40 trials included 10 trials for each of the four stimulus conditions (upright faces, inverted faces, upright Greebles, inverted Greebles). Each of the 40 faces and 40 Greebles appeared only once in a block, either as a target or as a probe stimulus.

Vertical and horizontal eye movements were recorded by electrooculography (EOG). The electrodes were placed on the external canthi of the eyes for horizontal movements, and in the inferior and superior areas of the ocular orbit for vertical movements. Scalp electrical activity (electroencephalogram, EEG) was recorded from 58 electrodes mounted in an electrode cap. Electrode positions included the standard 10-20 system locations and additional intermediate positions. Recordings were performed with a left-earlobe reference. The EEG was amplified by amplifiers with a gain of 30,000 through a bandpass of 0.01 to 100 Hz. Electrode impedances were kept below 5 kΩ. EEG was continuously acquired (rate = 500 Hz). After removal of EEG and EOG artifacts, epochs beginning 100 ms prior to stimulus onset and continuing for 924 ms were created and rereferenced off-line to a common average reference. Only correct trials were analyzed. Finally, the data were filtered with a low-pass filter (cutoff = 30 Hz).

Expertise training with Greebles

The overall training procedure was an adaptation of that described in Gauthier et al. (1998). Each participant underwent 14 training sessions. The first 4 sessions (approximately 1 hr each) took place on different days. Five new individual Greebles were added in each of these 4 sessions. The remaining 10 training sessions spanned 5 days (2 sessions a day). These sessions included seven tasks designed to make participants perceptual experts with Greebles (see Gauthier et al., 1998). Two tasks measured the level of expertise reached during training: naming and verification. In the naming task, a Greeble was presented and participants pressed a key corresponding to the first letter of the Greeble's name. In the verification task, a family or individual name was first presented, followed by a Greeble that remained on the screen until participants pressed a "yes" or "no" key depending on the match between the name and the picture. We used the same criterion for expertise as in Gauthier and Tarr (1997) and Gauthier et al. (1998, 1999), namely that participants were equally good at recognizing Greebles at the individual and family levels—the latter initially being much easier (Tanaka & Taylor, 1991).

Data Analyses

Grand-average ERPs were computed for all conditions, and the peak amplitudes and latencies of the N170 component at occipitotemporal sites (T5 and T6) were measured relative to a 100-ms prestimulus baseline for individual participants.

Behavioral and electrophysiological measures were analyzed using repeated measures analyses of variance (ANOVAs). For electrophysiological measures, the main analyses were run on values obtained for the second stimulus of the pair, when the participant was engaged in the active discrimination process (Rossion, Delvenne, et al., 1999).

RESULTS

Behavioral Performance

Training

The expertise criterion was reached on average after 7 to 8 training sessions. All participants underwent 14 sessions of training (about 9 hr) to ensure full expertise training with the Greebles. Although training data are not reported here, they reflected the pattern obtained in Gauthier et al. (1998).

---

[1] The faces can be viewed at the following Web site: http://faces.kyb.tuebingen.mpg.de/.

[2] The Greebles can be viewed at the following Web site: http://www.tarrlab.org/stimuli.html#gr.

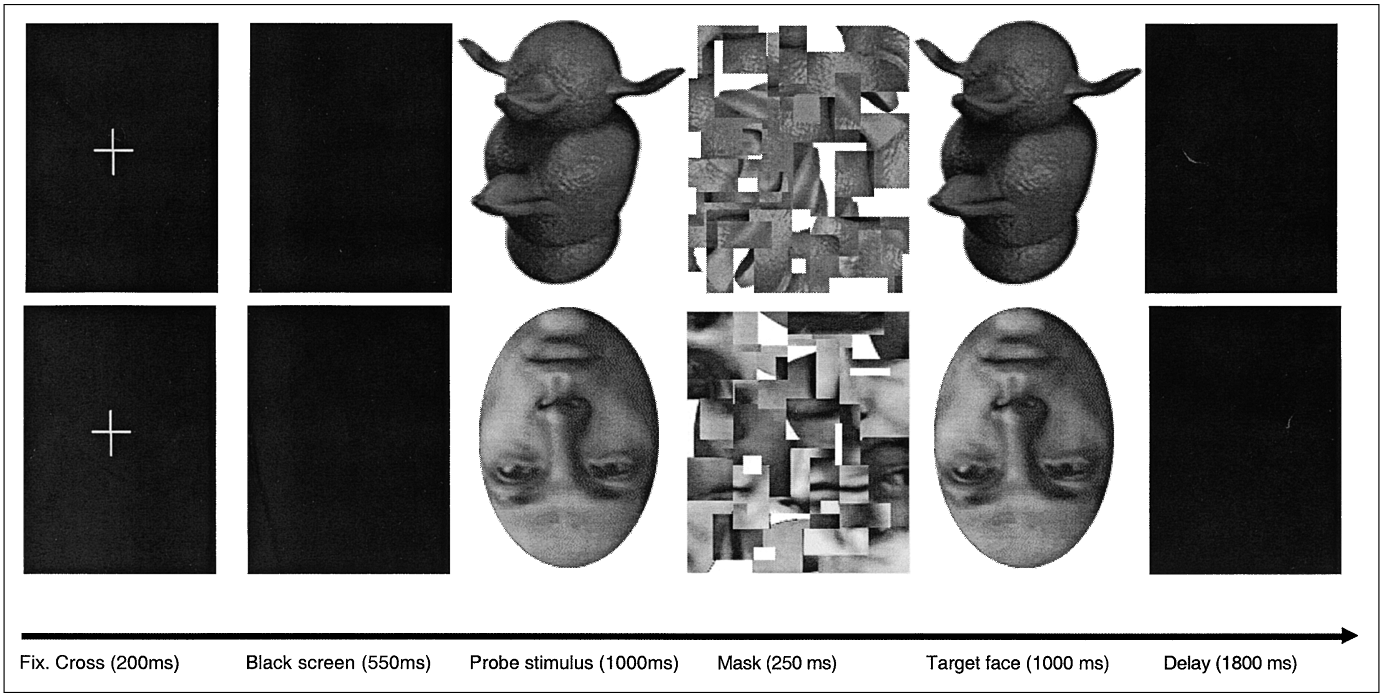

Fig. 1. Time course of one trial with upright Greebles and one trial with inverted faces.

ERP sessions

Mean percentages of correct responses and mean response times (RTs) for correct responses during the two ERP sessions are shown in Table 1. Accuracy varied between 88% and 97%, indicating that the participants performed the task quite accurately.

Same/different judgments were faster during the second than the first ERP session, $F(1, 12) = 10.5$, $p < .01$, and were faster for upright than inverted stimuli, $F(1, 12) = 39.2$, $p < .001$. There was also a significant interaction between category (face vs. Greeble) and orientation, $F(1, 12) = 31.9$, $p < .001$, the inversion effect being larger for faces than for Greebles across the two sessions (Table 1). A separate 2 $\times$ 2 ANOVA for faces showed main effects of session, $F(1, 12) = 11.5$, $p < .005$, and orientation, $F(1, 12) = 28.8$, $p < .001$. A separate 2 X 2 ANOVA for Greebles also showed main effects of session, $F(1, 12) = 13.1$, $p < .005$, and orientation, $F(1, 12) = 27.2$, $p < .001$, plus a Session X Orientation interaction, $F(1, 12) = 10.8$, $p < .01$. This interaction was due to the inversion effect (mean RT difference between upright and inverted) being larger following expertise training with the Greebles than before the training (see Table 1).

Table 1. *Accuracy rates and mean response times (RTs) before and after training*

	Before training (novices)		After training (experts)	
Measure	Faces	Greebles	Faces	Greebles
	Upright stimuli			
Accuracy (%)	97	91	96	93
RT (ms)	703	733	622	631
	Inverted stimuli			
Accuracy(%)	90	88	89	95
RT (ms)	772	758	697	677

ERPs

Figure 2 presents grand-average ERPs elicited by upright (gray line) and inverted (black line) face (top panel) and Greeble (bottom panel) probe stimuli at selected occipitotemporal electrodes (T5 and T6) during the first ERP session. N170 potentials were observed in all conditions in all participants, at the right and left occipitotemporal electrodes.[3]

During the first ERP session, on average, the N170 peaked at 175 ms (T5) and 173 ms (T6) for upright faces (mean latency extracted manually on each participant, see Table 2). It was delayed and larger for inverted faces compared with normal faces (Fig. 2, Table 2). The N170 latency for upright Greebles was later than the peak evoked by upright faces and was substantially smaller in amplitude (Table 2). There were no reliable differences between normal and inverted Greebles in the amplitude or latency of the N170 component prior to expertise training (Fig. 2, Table 2). These findings largely replicate previous observations: Faces evoke large occipitotemporal activities around 170 ms following stimulus onset. These potentials are also evoked by nonface stimuli, including Greebles (Rossion et al., 2000).

---

[3] For 3 participants, the peak measurements in all conditions were made at electrodes CB1 and CB2, slightly posterior to T5 and T6, because the shape of the N170 allowed a better peak measurement at the former electrodes.

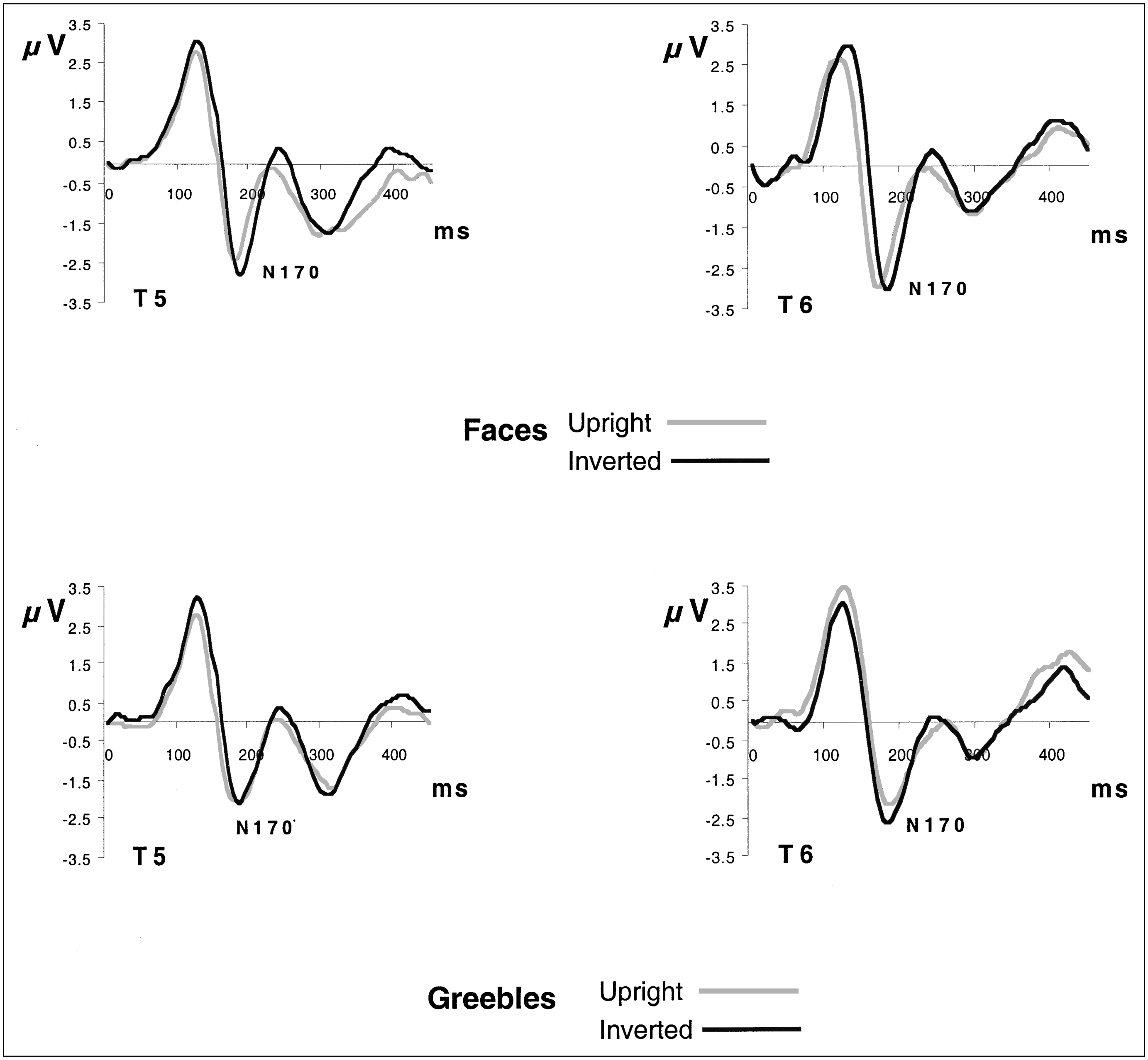

Fig. 2. Waveforms obtained at electrode sites T5 and T6 before expertise training. The graphs at the top show results for faces; those at the bottom show results for Greebles.

Following expertise training with Greebles, the N170 latencies for the two categories of stimuli were similar (Fig. 3, Table 2). There was also a general increase of N170 voltage amplitude, regardless of condition[4] (Table 2). The latency delay for inverted faces was similar before and after expertise training with Greebles (Figs. 2 and 3, Table 2), but ERPs to Greebles showed training effects: After training, there was a substantial delay and increase of amplitude for inverted Greebles as compared with upright Greebles at electrode T5 (Fig. 3, Table 2). These training effects were also observed for the target item (the first stimulus of the pair in the matching task). However, they were not observed in the grand-averaged data for the right hemisphere (electrode T6; see Fig. 3), although there was a slight latency difference between normal and inverted Greebles in the individual measurements (Table 2).

---

[4] Overall, the signal-to-noise ratio was better during the second ERP session, probably a general effect of practice with the EEG procedure. Amplitudes of other components (P1 at OZ, P2 at CZ) were also higher for all conditions during the second session than during the first session.

Table 2. *Amplitude and latency values of the N170 following the probe stimulus presentation before and after expertise training*

Measure and electrode	Before training				After training			
	Faces		Greebles		Faces		Greebles	
	Upright	Inverted	Upright	Inverted	Upright	Inverted	Upright	Inverted
Latency (ms)								
T5 (left)	174.8 ± 10.5	186.2 ± 10.1	182.6 ± 12.8	183.8 ± 9.7	177.6 ± 14.9	187.6 ± 10.2	179.8 ± 14.3	185 ± 11.1
T6 (right)	173.4 ± 14.1	184 ± 12.4	184.8 ± 14.1	180.6 ± 9.4	173.4 ± 16.3	183.4 ± 12.1	180.6 ± 11.9	182.2 ± 10.5
Amplitude (μV)								
T5 (left)	−2.52 ± 1.9	−2.94 ± 2.2	−2.14 ± 1.6	−2.18 ± 1.8	−3.21 ± 2.3	−4.07 ± 2.3	−2.64 ± 1.8	−3.13 ± 2
T6 (right)	−3.26 ± 2.4	−3.57 ± 2.6	−2.65 ± 1.9	−2.90 ± 1.9	−3.94 ± 2.3	−5.20 ± 3.3	−4.41 ± 2.4	−3.91 ± 2.4

Statistical analyses for N170 peak latency values

An ANOVA with session, category, orientation, and lateralization as factors was conducted on the N170 latency. This analysis revealed the expected inversion effect for faces, larger than that for Greebles. A main effect of orientation was found, $F(1, 9) = 23.4$, $p < .001$, as was a significant interaction between category and orientation, $F(1, 9) = 22.0$, $p < .001$. The interaction among session, category, and orientation, which reflected the delay of the N170 to inverted Greebles following expertise training, was only marginally significant, $F(1, 9) = 3.79$, $p = .08$.

Although the inversion effect was large for faces in both sessions, the same effect for Greebles increased with expertise. Because the interaction between category and orientation was significant, separate three-way ANOVAs for faces and Greebles were conducted. For faces, there was only a significant effect of orientation, $F(1, 9) = 30.0$, $p < .001$, reflecting the delay observed at each session and both electrode sites for inverted stimuli (Figs. 2 and 3, Table 2). For Greebles, the only significant effect was an interaction between session and orientation, $F(1, 9) = 5.86$, $p < .05$. The latency difference between normal and inverted Greebles increased following training (Fig. 3, Table 2). This effect was mainly observed at T5, and there was a marginally significant interaction between lateralization and orientation, $F(1, 9) = 5.03$, $p < 05$. For Greebles, the ANOVA was further divided across the two sessions (with orientation and lateralization as factors). There was no significant effect prior to expertise training, but there was a significant orientation effect for Greebles following expertise training, $F(1, 9) = 10.2$, $p < .01$. The effect of orientation was also significant at T5 ($p < .05$) and marginally significant at T6 ($p = .07$).

Statistical analyses for N170 peak amplitude values

The N170 peak amplitude revealed effects similar to those for latency, with a significant expertise effect in the orientation effect for Greebles at the left electrode. We conducted an ANOVA on the N170 peak amplitude values, with session, category, orientation, and lateralization as factors. There was a main effect of orientation, $F(1, 9) = 10.6$, $p < .01$, reflecting the larger activity for inverted than for upright stimuli, and the effect of session was marginally significant, $F(1, 9) = 3.41$, $p = .10$, reflecting a general increase of amplitude. A significant interaction between category and orientation was found, $F(1, 9) = 6.71$, $p < .05$, with the amplitude difference between normal and inverted stimuli larger for faces than for Greebles.

Separate three-way ANOVAs were conducted for Greebles and faces. For faces only, there was a significant effect of orientation, $F(1, 9) = 9.77$, $p < .01$. For Greebles, there was a main effect of lateralization, $F(1, 9) = 5.17$, $p < .05$, and the interaction among orientation, session, and lateralization was also significant, $F(1, 9) = 6.29$, $p < .05$. This interaction reflects the amplitude difference between normal and inverted Greebles at the left hemisphere only following expertise training (Figs. 2 and 3, Table 2).

DISCUSSION

This study replicates previous observations of a larger N170 for faces than for Greebles and an electrophysiological inversion effect (delay and increase) on this component for faces. We extend those results by demonstrating an electrophysiological inversion effect for a visually homogeneous nonface stimulus class—Greebles—following expertise training. It should be noted that in a previous study with Greeble novices (Rossion et al., 2000), we did not observe such an effect with these or other nonface objects (chairs, houses, cars, shoes). This result supports our hypothesis that the electrophysiological ERP inversion effect obtained in the present study is mediated by expertise rather than the category of faces per se. However, it is important to note that this expertise effect was larger on the left than the right side—although the interaction of lateralization, orientation, and session was significant for peak amplitudes only, and not for peak latencies. In contrast, most expertise effects assessed using fMRI are either bilateral (Gauthier et al., 1999) or found only on the right (Gauthier et al., 2000).

Similar differences between measures of brain activity were found by Liu, Higuchi, Marantz, and Kanwisher (2000) in a recent magnetoencephalography (MEG) study that obtained larger M170 responses in the left hemisphere to faces whereas the very same stimuli elicited greater right-hemisphere activation in fMRI in the "fusiform face area" (FFA). Such discrepancies are not surprising given that ERP and fMRI record different kinds of signals (electrical and metabolic) at different time scales. Moreover, the results Liu et al. (2000) obtained suggest that it is unlikely that the N170 component reflects only the activity of the FFA. Given current evidence, it appears that the same Greeble expert would show an expertise effect for Greebles that is stronger in the right hemisphere in fMRI (Gauthier et al., 1999, 2000) and stronger in the left hemisphere in ERPs, perhaps reflecting somewhat independent effects of expertise. Collecting fMRI and ERP data within the same participants may help resolve questions regarding the

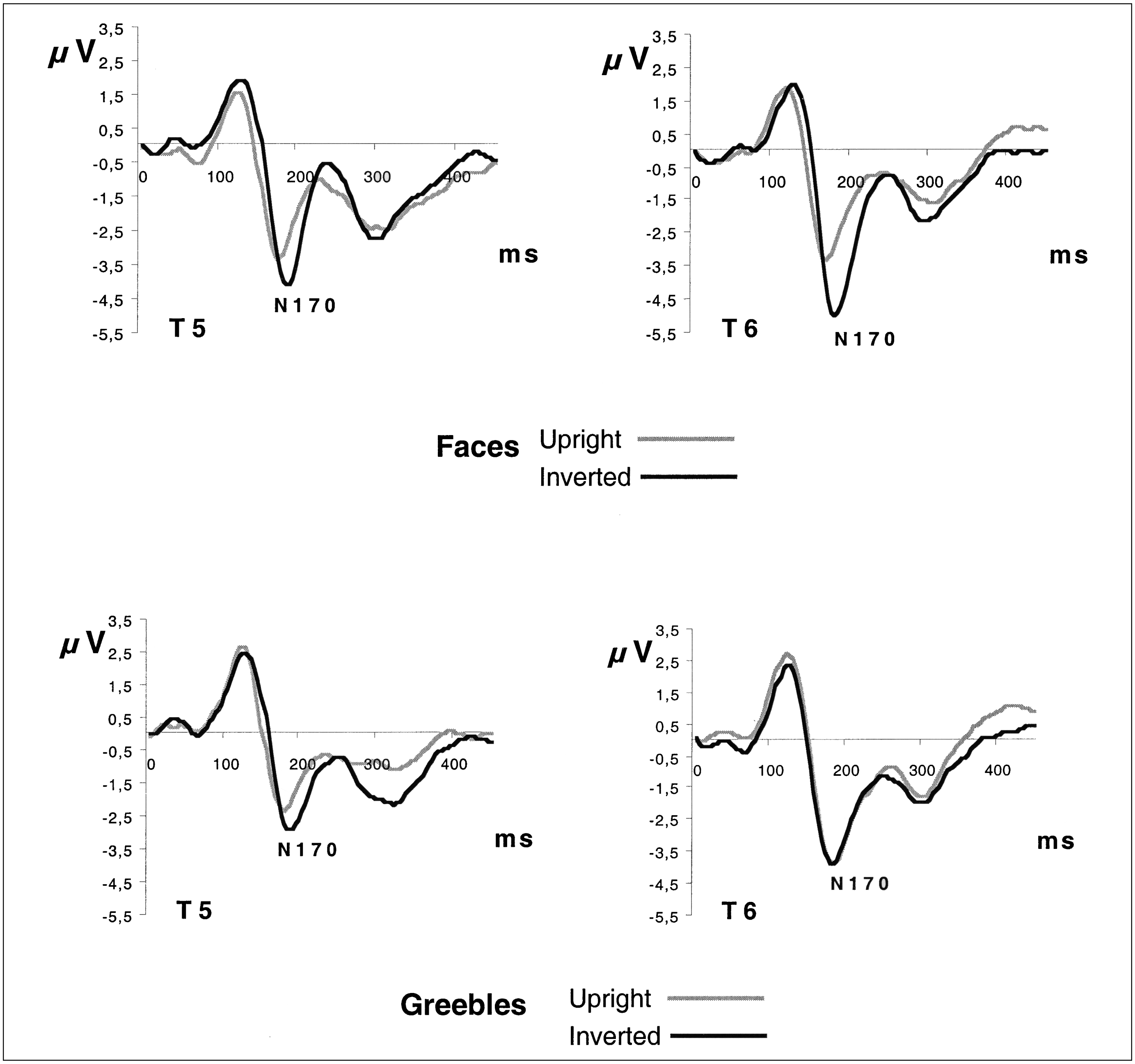

Fig. 3. Waveforms obtained at electrode sites T5 and T6 after expertise training. The graphs at the top show results for faces; those at the bottom show results for Greebles.

nature of these lateralized subcomponents of expert object recognition.

It is also notable that the expertise effect in ERPs is observed primarily in latencies. We suggest that this latency effect is actually the best candidate for a face-specific visual ERP effect, yet our results argue against a mechanism that is specifically engaged by faces, as measured by ERPs. This is consistent with prior studies using behavioral (Diamond & Carey, 1986; Gauthier & Tarr, 1997; Gauthier et al., 1998) and fMRI (Gauthier et al., 1999, 2000) responses that were once also presumed to be specific to faces but have since been obtained in a variety of experts (e.g., people expert in identifying dogs, birds, cars, and Greebles). Our results are also consistent with a recent report of an expertise effect measured with ERPs (Tanaka & Curran, 2001): N170 amplitude increased (more on the right than the left) for pictures of birds in bird experts and for pictures of dogs in dog experts. Our findings suggest that some components of this expertise effect may arise following a relatively short training procedure (7–10 hr, 2 weeks). In contrast, categories such as birds and dogs are often learned over a lifetime of experience. Regardless of the duration of training, the combination of the present findings with those from

Tanaka and Curran (2001) indicates that expertise can alter an early visual categorization stage for objects and faces that is independent of previous familiarity with specific individuals (Eimer, 2000b; Rossion, Delvenne, et al., 1999).

Do Greebles Look Like Faces?

One oft-raised critique of our research using Greebles is that "Greebles look like faces" and that the effects obtained, including the ERP findings reported here, may be due to their particular facelike geometry. Our response is that multiple findings indicate that Greebles are not treated as facelike until after expertise training (for a more detailed discussion of the following points, see Tarr & Gauthier, 2000). First, Greeble novices do not show Greeble-specific activation in the FFA in fMRI, but Greeble experts do show such activation (Gauthier et al., 1999). Second, Greebles do not elicit facelike behavioral effects in Greeble novices, but do elicit such effects in Greeble experts (Gauthier & Tarr, 1997). Third, C.K., an agnosic patient who has intact face recognition but is dramatically impaired in nonface object recognition (Moscovitch, Winocur, & Behrmann, 1997), cannot recognize Greebles any better than other objects—even when he is told to think of Greebles as faces or little people (Tarr & Gauthier, 2000). Fourth, our previous ERP study (Rossion et al., 2000), as well as the pretraining data here, shows that the supposedly facelike appearance of Greebles is not a sufficient condition for the inversion effect on the N170 to be obtained.

Why Is the N170 Delayed When Objects From an Expertise Domain Are Inverted?

This effect appears related to behavioral measures of expertise. Both faces and Greebles are processed by experts in a holistic-configural[5] manner, but only in their upright orientation (Gauthier & Tarr, 1997; Tanaka & Sengco, 1997); inversion of these stimuli disrupts holistic-configural processing (e.g., Gauthier & Tarr, 1997; Tanaka & Farah, 1993). In ERP studies, other transformations disrupting holistic-configural information—such as presenting isolated face features (Bentin et al., 1996), faces without some features (Eimer, 1998; Jemel, George, Chaby, Fiori, & Renault, 1999), or scrambled faces (George, Evans, Fiori, Davidoff, & Renault, 1996)—lead to a similar delay of the N170. The same effect is obtained when observers focus their attention on the eyes rather than on the entire face (Jemel et al., 1999). Thus, the latency delay observed with face inversion for Greebles following expertise training may be due to the disruption of holistic-configural sensitivity in experts. In line with this observation, other ERP results suggest that holistic-configural or global information is processed earlier than local features for both hierarchical stimuli (Han, Fan, Chen, & Zhuo, 1997) and faces (Jemel et al., 1999).

The interpretation of the amplitude enhancement of the N170 to inverted stimuli, which was substantial although not statistically significant for Greebles following training, is less straightforward for several reasons. First, this effect is less robust for faces than the latency delay (Rossion et al., 2000). Second, recent findings on the effect of attention on the N170 suggest that the amplitude effect may reflect a larger attentional demand (Eimer, 2000a) for inverted faces and inverted Greebles than for upright stimuli in experts. However, such an attentional modulation cannot account for the latency delay observed for inverted faces, for two reasons: (a) Spatial attention does not appear to modulate the latency of visual components (Luck, Woodman, & Vogel, 2000). (b) A recent study indicates that if object-based selective attention modulates the latency of the N170, a delay of this component is observed when the stimulus is *not* the object of attention (i.e., when a concurrent highly demanding task is performed; see Eimer, 2000b). An alternative interpretation based on fMRI findings is that inverted faces may recruit both face-selective and general object recognition areas (Haxby et al., 1999). Because the N170 as a whole is unlikely to reflect only the activity of the FFA (Liu et al., 2000; Rossion et al., 2000), the additional contribution of activity from other areas might increase the N170 to inverted faces.

CONCLUSIONS

This study demonstrated an electrophysiological inversion effect on the N170 for a visually homogeneous nonface stimulus class—Greebles—following expertise training. We interpret these results as evidence that visual expertise—independent of object category—plays a role in shaping the N170 inversion effect typically associated with face processing. One caveat is that this effect was limited to the left hemisphere, whereas the analogous effect for faces is typically bilateral. Thus, there remains some question as to whether early face and object mechanisms differ with regard to their localization in the brain. This question should be the subject of future ERP studies.

Acknowledgments—B.R. was supported by the Belgian National Fund for Scientific Research (FNRS). B.R., I.G., and M.J.T. were supported by a James S. McDonnell Foundation Collaborative Research Award. M.J.T. was supported by National Science Foundation Award SBR-9615819. We thank David Pirenne, Sylvie Linotte, and Gilles Pourtois for their help in data recording and processing.

REFERENCES

Bentin, S., Allison, T., Puce, A., Perez, A., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience*, *8*, 551–565.

Bötzel, K., Schulze, S., & Stodieck, R.G. (1995). Scalp topography and analysis of intracranial sources of face-evoked potentials. *Experimental Brain Research*, *104*, 135–143.

Diamond, R., & Carey, S. (1986). Why faces are and are not special: An effect of expertise. *Journal of Experimental Psychology: General*, *115*, 107–117.

Eimer, M. (1998). Does the face-specific N170 component reflect the activity of a specialized eye detector? *NeuroReport*, *9*, 2945–2948.

Eimer, M. (2000a). Attentional modulations of event-related brain potentials sensitive to faces. *Cognitive Neuropsychology*, *17*, 103–116.

Eimer, M. (2000b). Effects of face inversion on the structural encoding and recognition of faces: Evidence from event-related brain potentials. *Cognitive Brain Research*, *10*, 145–158.

Gauthier, I., Anderson, A., Skudlarski, P., & Gore, J.C. (2000). Expertise for cars and birds recruits middle fusiform face-selective areas. *Nature Neuroscience*, *3*, 191–197.

Gauthier, I., & Tarr, M.J. (1997). Becoming a "Greeble" expert: Exploring the face recognition mechanism. *Vision Research*, *37*, 1673–1682.

Gauthier, I., & Tarr, M.J. (in press). Unraveling neural mechanisms for expert object recognition: Bridging brain activity and behavior. *Journal of Experimental Psychology: Human Perception and Performance*.

Gauthier, I., Tarr, M.J., Anderson, A.W., Skudlarski, P., & Gore, J.C. (1999). Activation of the middle fusiform area increases with expertise in recognizing novel objects. *Nature Neuroscience*, *6*, 568–573.

---

[5] We use "holistic-configural" in contrast to "holistic-contextual" and "holistic-attentional" to distinguish among three different senses of "holistic" or "configural" that are used inconsistently in the literature. Holistic-configural processing means an object part is better recognized in the context of the other original parts of the object in their original configuration than in the context of the same parts in a new configuration. See Gauthier and Tarr (in press) for further discussion.

Gauthier, I., Williams, P., Tarr, M.J., & Tanaka, J. (1998). Training “Greeble” experts: A framework for studying expert object recognition processes. *Vision Research*, *38*, 2401–2428.

George, N., Evans, J., Fiori, N., Davidoff, J., & Renault, B. (1996). Brain events related to normal and moderately scrambled faces. *Cognitive Brain Research*, *4*, 65–76.

Han, S.H., Fan, S.L., Chen, L., & Zhuo, Y. (1997). On the different processing of wholes and parts: A psychophysiological analysis. *Journal of Cognitive Neuroscience*, *9*, 687–698.

Haxby, J.V., Ungerleider, L.G., Clark, V.P., Schouten, J.L., Hoffman, E.A., & Martin, A. (1999). The effect of face inversion on activity in human neural systems for face and object perception. *Neuron*, *22*, 189–199.

Jemel, B., George, N., Chaby, L., Fiori, N., & Renault, B. (1999). Differential processing of part-to-whole and part-to-part face priming: An ERP study. *NeuroReport*, *10*, 1069–1075.

Kanwisher, N. (2000). Domain-specificity in face perception. *Nature Neuroscience*, *3*, 759–763.

Liu, J., Higuchi, M., Marantz, A., & Kanwisher, N. (2000). The selectivity of the occipitotemporal M170 for faces. *NeuroReport*, *11*, 337–341.

Luck, S.J., Woodman, G.F., & Vogel, E.K. (2000). Event-related potential studies of attention. *Trends in Cognitive Sciences*, *4*, 432–440.

Moscovitch, M., Winocur, G., & Behrmann, M. (1997). What is special about face recognition? Nineteen experiments on a person with visual object agnosia and dyslexia but normal face recognition. *Journal of Cognitive Neuroscience*, *9*, 555–604.

Rossion, B., Delvenne, J.-F., Debatisse, D., Goffaux, V., Bruyer, R., Crommelinck, M., & Guérit, J.M. (1999). Spatio-temporal localization of the face inversion effect: An event-related potentials study. *Biological Psychology*, *50*, 173–189.

Rossion, B., Gauthier, I., Delvenne, J.-F., Tarr, M.J., Bruyer, R., & Crommelinck, M. (1999, November). *Does the N170 occipito-temporal component reflect a face-specific structural encoding stage?* Paper presented at Object Perception and Memory 99, Los Angeles.

Rossion, B., Gauthier, I., Tarr, M.J., Despland, P.A., Bruyer, R., Linotte, S., & Crommelinck, M. (2000). The N170 occipito-temporal component is delayed and enhanced to inverted faces but not to inverted objects: An electrophysiological account of face-specific processes in the human brain. *NeuroReport*, *11*, 69–74.

Tanaka, J.W., & Curran, T. (2001). A neural basis for expert object recognition. *Psychological Science*, *12*, 43–47.

Tanaka, J.W., & Farah, M.J. (1993). Parts and wholes in face recognition. *Quarterly Journal of Experimental Psychology*, *46A*, 225–245.

Tanaka, J.W., & Sengco, J.A. (1997). Features and their configuration in face recognition. *Memory & Cognition*, *25*, 583–592.

Tanaka, J.W., & Taylor, M. (1991). Object categories and expertise: Is the basic level in the eye of the beholder? *Cognitive Psychology*, *23*, 457–482.

Tarr, M.J., & Gauthier, I. (2000). FFA: A Flexible Fusiform Area for subordinate-level visual processing automatized by expertise. *Nature Neuroscience*, *3*, 764–769.

Taylor, M.J., McCarthy, G., Saliba, E., & Degiovanni, E. (1999). ERP evidence of developmental changes in processing of faces. *Clinical Neurophysiology*, *110*, 910–915.

(RECEIVED 10/20/00; REVISION ACCEPTED 7/20/01)