

Visual expertise with nonface objects leads to competition with the early perceptual processing of faces in the human occipitotemporal cortex

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Human electrophysiological studies have found that the processing of faces and other objects differs reliably at ≈ 150 ms after stimulus onset, faces giving rise to a larger occipitotemporal field potential on the scalp, termed the N170. We hypothesize that visual expertise with nonface objects leads to the recruitment of early face-related categorization processes in the occipitotemporal cortex, as reflected by the N170. To test this hypothesis, the N170 in response to laterally presented faces was measured while subjects concurrently viewed centrally presented, novel, nonface objects (asymmetric "Greebles"). The task was simply to report the side of the screen on which each face was presented. Five subjects were tested during three event-related potential sessions interspersed throughout a training protocol during which they became experts with Greebles. After expertise training, the N170 in response to faces was substantially decreased ($\approx 20\%$ decrease in signal relative to that when subjects were novices) when concurrently processing a nonface object in the domain of expertise, but not when processing untrained objects of similar complexity. Thus, faces and nonface objects in a domain of expertise compete for early visual categorization processes in the occipitotemporal cortex.

The question of whether faces are processed by qualitatively different mechanisms from other object categories has been debated for more than three decades (1) and has been the focus of numerous studies (for reviews see refs. 2 and 3). Researchers still disagree on whether the neurofunctional mechanisms involved in face processing are domain-specific (4, 5) or are also recruited in identifying members of a visually homogeneous object category for which observers are visual experts (6, 7). Evidence in support of domain-specific face processing comes from the existence of neurons in the inferior temporal cortex of monkeys that respond preferentially to facial patterns. Such "face cells" begin to differentiate between faces and other stimuli between 100 and 200 ms (e.g., see ref. 8). At the systems level, at approximately the same latency, scalp electrophysiological recordings reveal a large occipitotemporal field potential in the lower α range (7–10 Hz), termed the N170 (ref. 9) [termed the M170 in magnetoencephalography (MEG) studies; see ref. 10], that is larger in response to faces than to nonface object categories (9–12). The N170 is thought to originate from a network of regions in the inferior temporal cortex, including the fusiform gyrus and the middle, inferior, and superior temporal gyri (13, 14) (somewhat consistent with the localization of face-sensitive activity in neuroimaging; see refs. 15 and 16).

At the same time, evidence from both behavioral (6, 17) and neuroimaging (18, 19) studies suggests that face-related processes can be recruited for nonface objects when observers are experts (7). However, neuroimaging methods such as functional MRI (fMRI) have poor temporal resolution, on the order of one to several seconds, because of the slowness of the hemodynamic response (20). Thus, results from fMRI do not address whether the face-like effects associated with visual expertise for nonface objects occur during initial visual categorization and in the same time frame as those effects elicited by faces, that is, at ≈ 150 ms after stimulus onset (12, 21, 22). In support of the view that the processing of faces

shares similar temporal characteristics with the processing of nonface objects, it has recently been found that the human scalp N170 is larger in response to birds, dogs, or cars in experts within each of these categories (23, 24) and that the N170 displays a face-like inversion effect after ≈ 10 h of expertise training with novel nonface objects (25).

One criticism of studies comparing the magnitude and/or latency of the N170 for faces and nonface objects is that the N170 in response to faces may present a different spatial distribution, and thus different generators, than does the component observed in response to objects (26, 27). This question is difficult to resolve because of the limited spatial resolution of scalp electroencephalogram (EEG) (28, 29). In other words, the effects of expertise found in previous studies on the N170 may not arise from face-related processes but, rather, from a different potential occurring at approximately the same latency and with an overlapping scalp distribution (26, 27). Thus, the issue of whether other object categories recruit putatively face-specific processes and whether they do so within the same time course (i.e., between 100 and 200 ms after stimulus onset) is still an open question.

To address this question, we recorded event-related potentials (ERPs) in humans during the processing of nonface novel objects, asymmetric "Greebles," before and after expertise training with these objects, as well as during the processing of faces. However, in contrast to previous studies (23, 25), we focused on the N170 in response to faces. We reasoned that if visual expertise with nonface object categories recruits early face-related visual processes, then the N170 in response to faces should be attenuated (i.e., reduced in amplitude) in the presence of another object for which the observer is an expert. Our logic is that the processes normally used for face recognition would either not be available or be only partially available (see ref. 30 for a similar study on the P300 component). In short, we recorded the N170 in response to faces while subjects were visually processing a nonface object. The N170 was recorded to face photographs across the same subjects during three stages of expertise training with a set of visually homogeneous, novel, nonface objects. Our results show that, under conditions of concurrent stimulation, the N170 in response to faces is strongly reduced after expertise training with this set of nonface objects. Such a finding indicates that early face-specific processing as reflected by the N170 may actually arise from an observer's level of visual expertise with faces or other objects rather than the stimulus category *per se*.

Methods

Subjects. Five subjects (mean age, 25 years; range, 24–28 years; three females) volunteered for pay (\$10 per h) for this study. Four

Abbreviations: EEG, electroencephalogram; ERP, event-related potential.

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of the subjects were right-handed, and all had normal or corrected-to-normal visual acuity and no known neurological impairments.

Stimuli for the ERP Experiment. Faces. Twenty-four color photographs of faces of undergraduates, all Caucasian, were taken in a full frontal pose. The images were equally divided into 12 males and 12 females, and all faces appeared without glasses, facial hair, or makeup. These images were taken from a larger set of faces used previously in several studies (e.g., see refs. 24, 25, and 29). The face images were edited in PHOTOSHOP VERSION 4.0 (Adobe Systems, San Jose, CA) to remove backgrounds and hair, as well as everything showing below the chin. All faces had a neutral expression. On average, the size of each image was 6 cm wide ($\approx 3^\circ$ when viewed 120 cm from the monitor) and 8.5 cm high. Twelve faces (six male and six female) were presented during the first ERP recording session. In the second and third ERP sessions, six of these faces were used with six new faces added at each stage, resulting in a total of 24 face images being presented.

Greebles. A total of 40 (20 trained and 20 untrained) asymmetric Greebles were used as stimuli. The asymmetric Greebles were created with 3D STUDIO MAX (Discreet, Montreal). These and other Greeble images are available for downloading at www.tarrlab.org/stimuli. Compared with the symmetric Greebles that have been used in several previous studies (e.g., see refs. 17, 25, and 31), the present asymmetric versions were created by shifting the positions of the three attached parts. Thus, the stimuli used here do not have the part configuration associated with human faces. Consequently, many prior arguments regarding “Greebles looking like faces” (which typically appeal to the part arrangement shared between faces and those original Greebles) do not apply to our present study. The Greebles used here can be categorized into five “families” according to the shape of the central part (17); each individual Greeble is visually distinct and has a unique name. Twelve Greebles were used in the first ERP session, six of these being replaced by novel Greebles in each ERP session thereafter. The size of Greebles, when presented on the screen, was approximately the same size as faces (7° high, 5° wide). Despite the different part arrangement, the asymmetric Greebles used here share some properties with faces (rounded parts, smooth surfaces, multiple parts attached to a single larger part with two parts above the others, and a canonical/preferred orientation), but not symmetry or having all attached parts aligned along a common plane (as in previous Greeble studies; e.g., see refs. 17 and 18). Although Greebles do have “little bodies” and their parts can be associated with human body parts (e.g., a head with ears and nose), they do not present the parts and the configuration of a face as commonly construed (two symmetrically placed eyes above a central nose and mouth). There are several lines of reasoning to support this view (see, e.g., ref. 7), the most compelling being that, to those subjects without visual expertise, Greebles do not exhibit face-like behavioral patterns of performance or neural activity.

Control objects (YUFOS). The control stimuli, that is, an object class for which our subjects were not experts, were a set of visually homogeneous 3D objects that had been photorealistically rendered. These objects, dubbed “YUFOS,” share approximately the same spatial configuration on a vertically oriented central part (see ref. 31). Similar to the Greebles, 24 different control objects were used, 12 at the first ERP session and a combination of 6 previously seen and 6 new control objects in each following ERP session. The YUFOS were of roughly the same size as the Greebles, and the two sets were equalized for luminance. These stimuli were used here to provide a baseline condition for the processing of a set of complex stimuli for which subjects were not trained to be experts and thus control for potential general effects of training, that is, generic improvement in the tasks regardless of stimuli or order of ERP recording.

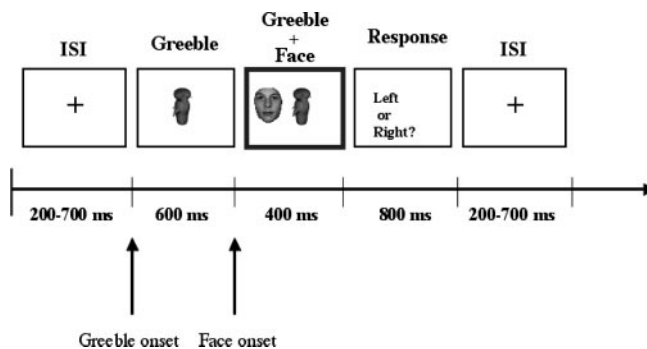


Fig. 1. Time line of the stimulation events. ISI, interstimulus interval.

Procedure. Expertise training. Expertise training and EEG recording took place over 2 weeks for each subject. Subjects were first recorded in EEG and then underwent training during a single week (sessions 1–4), after which a second EEG recording session was run. Subsequent to session 2, expertise training was carried out until subjects reached the expertise criterion defined in previous studies (e.g., see refs. 17, 25, and 31): that is, subjects should be as fast at classifying Greebles correctly at the individual level as at the family level. This criterion was reached in sessions 7 (one subject), 8 (two subjects), 9 (one subject), and 11 (one subject). The overall training procedure was similar to the paradigm used by Gauthier *et al.* (32): each training session consisted of a naming task and a verification task. In the naming task, a Greeble was presented, and subjects pressed the 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 subjects pressed a “yes” or “no” key depending on the match between the name and the picture. Five new Greebles were learned during each session (sessions 1–4), one from each family, for a total of 20 Greebles learned over the course of training. In the remaining sessions, subjects were encouraged to respond as quickly as possible while keeping accuracy high. Training performance reflected the typical pattern obtained in previous studies (17, 18, 30), namely, reduced response times across correct trials (overall accuracy was 95% throughout the eight training sessions) for both the naming and verification tasks. In the first expertise training session, the average response times (t) in the verification task were 864 ms for family level and 1,267 ms for individual level [$t(4) = 2.73$ s; $P < 0.05$]. After expertise training, the average response times in the verification task were 471 ms for family level and 492 ms for individual level [$t(4) = 0.548$ ns].

EEG recording. Subjects were seated in a comfortable chair in a dimly lit room, 114 cm from the stimulation monitor [a 17-in (1 in = 2.54 cm) flat-screen cathode ray tube (CRT)] controlled by a personal computer (PC). They were instructed to fixate on the center of the screen during the presentation of two consecutive blocks (with a 1-minute pause between blocks) of 120 trials each. Stimuli were presented by using ERTS (Berisoft Cooperation, Frankfurt). A trial was composed of the presentation of a novel object (Greeble or YUFO) for 1,000 ms in the center of the screen. Six-hundred milliseconds after the object appeared, a face photograph was presented for 400 ms, either on the left or right of the object (Fig. 1). A relatively long (600-ms) duration between the onset of the first and the second stimulus was used to allow a return to the baseline level of activity recorded on the scalp before the onset of the second stimulus (i.e., to avoid contamination by the ERPs evoked by the first stimulus). The duration of 400 ms for the second stimulus was chosen to avoid contamination of the signal by visual offset potentials, which may occur in temporal contiguity with the N170 component when using shorter durations. Although this 400-ms stimulus duration for lateralized pictures may have led to eye

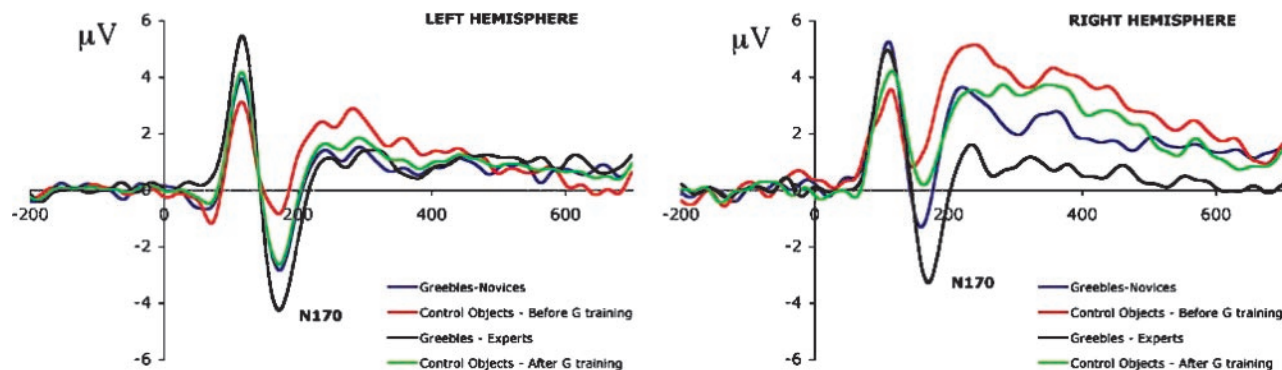


Fig. 2. Response to the first stimulus. ERPs time-locked to the first stimulus (nonface object), before and after expertise training (G training). Three occipitotemporal channels in each hemisphere are pooled together.

movements, there were few lateral eye movements recorded by electrooculogram (EOG) during the experiments, and these trials were excluded from the analyses.

The center of the face stimulus appeared 7.5 cm from the center of the screen (3.75°). The offset of the two stimuli was simultaneous, and a blank screen was then presented for $\approx 1,250$ ms (the actual time being a randomized delay of 1,000–1,500 ms). Half of the 240 trials were composed of a Greeble plus Face sequence, and the other half of the trials were composed of a YUFO plus Face sequence. The face appeared 50% of the time on each side (left or right) of the screen, resulting in 60 trials per condition for ERP averages. The order of all trials was fully randomized so that subjects could not anticipate whether a Greeble or a YUFO would be presented in the next trial, or whether the face would appear in the left or right visual field. The subject's task was to press a key corresponding to whether the face appeared on the left or right of the nonface object as accurately and as quickly as possible. Critically, we used a task that was irrelevant to our hypothesis to avoid any attentional bias in favor of one of the object categories (trained or novel) throughout the experiment.

Subjects were instructed to keep their gaze and attention on the center of the screen. Vertical and horizontal eye movements [electrooculogram (EOG)] were recorded by bipolar electrodes placed on the external canthi of the eyes (horizontal movements) and in the inferior and superior areas of the ocular orbit (vertical movements). Scalp electrical activity (EEG) was recorded by 64 electrodes mounted in an electrode cap (Quik-Cap, Neuromedical Supplies, Sterling, VA). Electrode positions included the standard 10–20 system locations and additional intermediate positions as well as a row of low occipitotemporal electrodes for a better sample of visual evoked potentials (VEPs) related to face perception and recognition (Fig. 4). EEG recordings were performed with linked earlobes and referenced offline to a common average reference. The EEG was amplified by battery-operated amplifiers with a gain (K) of 4.6 through a bandpass of 0.01–100 Hz. Electrode impedances were kept below 5 k Ω during EEG recording. EEG was continuously acquired at a 512-Hz analog/digital (A/D) rate and stored on a disk for offline analysis.

EEG/ERP analyses. EEG data were analyzed by using EEPROBE VERSION 3.0 (Ant Software, Enschede, The Netherlands) running on LINUX VERSION 7.0 (Red Hat, Raleigh, NC). After filtering of the EEG with a 1- to 30-Hz bandpass filter, EEG and electrooculogram (EOG) artifacts were removed by using a $[-35; +35 \mu\text{V}]$ deviation over 200-ms intervals on all electrodes. One-hertz high-pass filtering was used to reduce the effect of stimulus anticipation on the EEG preceding the presentation of the face photograph. In the case of too many blink artifacts (two subjects across a total of three recording sessions), data were corrected by a subtraction of vertical EOG propagation factors, based on principal component analysis (PCA)-transformed EOG components (33). Epochs beginning 200 ms before stimulus onset and continuing for 700 ms were computerized, corrected from baseline deviations from 0 by using a 200-ms prestimulus window, and averaged for each condition separately. Only correct response trials were averaged. The number of remaining trials was not different between conditions across sessions (between 92.5% and 96.6% of trials).

Statistical analyses. ERPs were measured and analyzed separately for the first (Greeble or YUFO) and the second (face) stimuli. After visual inspection of the topographies, the N170 amplitude was measured at three occipitotemporal locations where it was the largest in response to objects and faces in the two hemispheres (PO7/PO8, P9/P10, and PO10/PO9). Grand-averages analyses revealed that the N170 peaked at approximately the same latency for Greebles and YUFOs (≈ 160 ms; Fig. 2 and Table 1). Latency did not differ for faces whether they were preceded by Greebles or YUFOs (Table 1). To account for the latency differences in response to ipsi- and contralateral presentations of the faces, mean amplitude was calculated within 40-ms temporal windows that were centered around these mean latencies: 140–180 ms (contralateral) and 160–200 ms (ipsilateral). For the first stimulus, amplitudes were averaged over 140–180 ms, and ANOVA included the factors “Category” (Greebles vs. YUFOs), “Expertise Level” (before, during, and after expertise training), “Hemisphere” (left vs. right), and “Electrode Site” (3). The factor “Visual Field Stimulated” (left vs. right) was added in the analyses on the second (face) stimulus, for which the three electrodes were pooled together.

Table 1. Grand-average latency and peak amplitude values for the N170 response to Greebles and YUFOs

| N170 | Greebles | | | | | | YUFOs | | | | | |
|--------------------------|----------|-------|---------|-------|---------|-------|---------|------|---------|-----|---------|-----|
| | Stage 1 | | Stage 2 | | Stage 3 | | Stage 1 | | Stage 2 | | Stage 3 | |
| Hemisphere | L | R | L | R | L | R | L | R | L | R | L | R |
| Latency, ms | 173 | 159 | 174 | 171 | 173 | 170 | 171 | 150 | 175 | 165 | 173 | 164 |
| Amplitude, μV | -2.98 | -1.53 | -3.16 | -2.41 | -4.38 | -3.36 | -1.07 | 0.72 | -0.826 | 0.3 | -0.98 | 0.1 |

L, left; R, right.

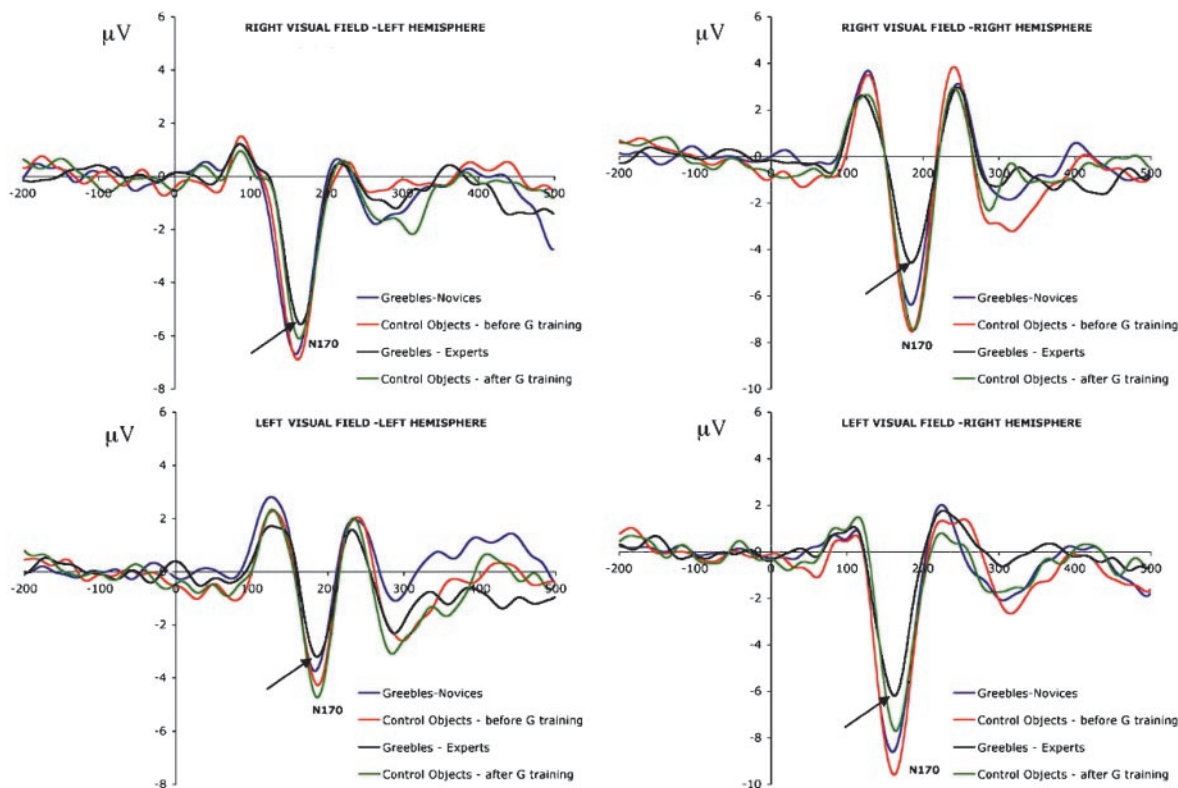


Fig. 3. Response to face stimulus. ERPs time-locked to the second stimulus (face), before and after expertise training (G training). The arrows indicate the condition for which the largest decrease of amplitude is expected (Greebles, after training). Three occipitotemporal channels in each hemisphere are pooled together.

Results

During the EEG recording, each subject's level of attention was monitored by requiring that each detect the occurrence of the face stimulus appearing in the right or left visual field. The subject then indicated whether the face appeared in the left or right field by pressing one of two keys corresponding to the two fields. Subjects all responded with their right hand. Subjects performed at a near-ceiling level in this task (98–100%), in all conditions (three sessions \times two visual fields \times two preceding object types). Response times ranged from 250 to 280 ms, with no significant effects of condition, nor any significant interactions ($P > 0.3$ for all). In short, subjects were accurate and fast in performing the lateralized detection task during all sessions, and this was true whether the faces were preceded by objects of expertise or by control objects.

Group averages of the ERPs after the first stimulus show an occipitotemporal N170 component peaking at approximately the same latency for trained and untrained objects (≈ 160 ms; Fig. 2 and Table 1) but are larger for Greebles relative to control objects, as confirmed by a main effect of Category [$F(1, 4) = 10.5, P < 0.05$]. There was also a specific increase of the N170 for Greebles after expertise training (Fig. 2 and Table 1), reflected by a Category \times Expertise Level \times Electrode Interaction [$F(4, 16) = 3.8, P < 0.05$]. Post hoc t tests showed that Greebles and control objects did not differ significantly at any electrode sites before training ($P > 0.2$ for both), but a larger N170 in response to Greebles than to control objects was recorded midway through and after expertise training at lower electrode sites (PO10/PO9 and P10/P9; $P < 0.05$ for both sites), with a nonsignificant trend at electrode sites PO8/PO7 after training ($P = 0.09$). Thus, there was a significant increase of N170 amplitude in response to Greebles relative to control objects after expertise training with Greebles (Fig. 2).

On average, the N170 in response to lateralized faces took place at ≈ 160 ms when the stimuli were presented in the contralateral

hemisphere and was delayed ≈ 20 ms in the ipsilateral hemisphere, taking place at ≈ 180 ms (34). The N170 latency did not differ whether preceded by trained or untrained objects (Fig. 3 and Table 2). The N170 was also larger in the contralateral hemisphere [Fig. 3, Visual Field \times Hemisphere, $F(1, 4) = 12.6, P < 0.01$]. Most pertinent to the present study was a significant Category \times Expertise Level interaction [$F(2, 8) = 7.1, P < 0.01$], reflecting the decrease of the N170 in response to faces preceded by Greebles compared with the N170 evoked by the same face stimuli but preceded by control objects (Figs. 3 and 4 and Table 2). This effect was significant only after expertise training (Expertise Level 3; $P < 0.05$). No other effect was significant.

In summary, the N170 in response to a lateralized face image undergoes a major decrease in amplitude after expertise training with nonface objects, but only when the face is preceded by an object from a category of expertise and not when preceded by an object from an untrained category (Figs. 3 and 4 and Table 1).

Discussion

Over the course of 2 weeks of expertise training with a novel object category, we observed an increase of the occipitotemporal N170 in response to members of this category. This finding replicates previous observations relying on long-term “naturally developed” expertise with real-life object categories (23, 24), as well as neuroimaging findings of increased activation in the mid-fusiform gyrus concurrent with expertise training with previously novel objects (18).

Most importantly, given the question of whether the electrophysiological changes reflect the recruitment of face-related processes at the perceptual level (26, 27), we find that the face-sensitive N170 is modulated by the level of expertise of our subjects with the trained nonface object category. More specifically, we presented face stimuli together with the nonface objects, identifying the field

Table 2. Grand-average latency and peak amplitude values for the N170 response to faces preceded by Greebles or YUFOs

| N170 | Greebles | | | | | | YUFOs | | | | | |
|--------------------|--------------------------------|-------|---------|-------|---------|-------|---------|-------|---------|-------|---------|-------|
| | Stage 1 | | Stage 2 | | Stage 3 | | Stage 1 | | Stage 2 | | Stage 3 | |
| | Left visual field stimulation | | | | | | | | | | | |
| Hemisphere | L | R | L | R | L | R | L | R | L | R | L | R |
| Latency, ms | 183 | 160 | 184 | 163 | 186 | 163 | 188 | 163 | 183 | 161 | 187 | 161 |
| Amplitude, μ V | -3.76 | -8.70 | -3.43 | -7.20 | -3.22 | -6.23 | -4.29 | -9.64 | -4.39 | -8.28 | -4.75 | -8.29 |
| | Right visual field stimulation | | | | | | | | | | | |
| Hemisphere | L | R | L | R | L | R | L | R | L | R | L | R |
| Latency, ms | 159 | 185 | 163 | 186 | 167 | 185 | 162 | 186 | 160 | 188 | 165 | 189 |
| Amplitude, μ V | -6.73 | -6.41 | -5.35 | -4.86 | -5.66 | -4.64 | -6.97 | -7.55 | -6.18 | -6.80 | -6.15 | -7.48 |

L, left; R, right.

potentials in response to the two categories by presenting the face stimulus after the nonface object to avoid an overlap of ERP components between the two visual stimulations (Fig. 1). Under these conditions, after expertise training with the nonface object category, we saw a substantial reduction in the face-sensitive N170 amplitude ($\approx 20\%$ of signal) at occipitotemporal sites where the response to faces was maximal. Thus, the N170 amplitude in response to faces can be strongly modulated as a consequence of expertise training with novel nonface objects. This finding indicates that the additional neurofunctional processes involved in processing objects of visual expertise compete with those recruited to process faces.

One might expect the reduction of amplitude to work both ways (24): the N170 in response to the detection of nonface objects of expertise might be substantially reduced when presented in competition with a face stimulus. However, given the current debate about the specificity of the face N170 response (25–28), our goal was to study the mechanisms involved in processing faces that could be recruited by visual expertise. Furthermore, any effect on N170 in response to objects of expertise under the conditions of concurrent stimulation created here may be difficult to interpret. In fact, it is likely that two opposite effects would cancel each other: the N170 in response to objects of expertise would normally increase as a result of the additional recruitment of face-related mechanisms, but during the processing of a face stimulus these mechanisms would be suppressed. Here, the development of visual expertise with Greebles had a specific effect on the N170 in response to faces, which was not reduced in amplitude after the control objects. Similarly, outside the conditions of competition between two visual stimuli in this paradigm, we do not expect any reduction of the N170 in response to faces after visual expertise training with nonface objects (see refs. 24 and 25).

Our interpretation is that visual processes involved in face recognition are recruited progressively for nonface objects during the acquisition of visual expertise with these objects. That is, mechanisms that are engaged during the sustained presentation of the nonface objects for which subjects are experts cannot be

recruited in their entirety when a face stimulus is presented. This result and its interpretation are in agreement with the findings of Gauthier *et al.* (24) of a behavioral and electrophysiological interference between the processing of faces and cars in car experts. Although also observed at the level of the N170, our results and theoretical implications differ in several ways from this work (24). First, in that study, the N170 in response to faces was not reduced in amplitude when cars were presented to car experts. Second, Gauthier *et al.* (24) used a delayed matching task, with one stimulus (face or car) presented at a time and then needing to be held in short-term visual memory in order to perform the task. The smaller modulation observed at the face-sensitive N170 in this latter case may be due to interference between maintenance of short-term visual memory and perceptual processing of the incoming face stimulus. In contrast, in our present study, our goal was to create competition within the visual domain, that is, to test directly whether the visual processes (as opposed to possibly short-term memories) recruited for two object categories overlap. Our interpretation is that the visual processing of the incoming face stimulus recruited at least some of the same processes still actively engaged by the objects of expertise. Thus, we observed a smaller transient increase of activity at ≈ 150 ms, relative to the same response without expertise-related competition. Finally, compared with the previous work with familiar objects (24), our present results demonstrate that a short (8–10 h) training with novel objects is sufficient to lead to large expertise effects at the perceptual level. Thus, the N170 in response to faces in human adults appears to reflect flexible categorization processes that can be recruited for other domains over the course of a few hours of training.

The same concurrent stimulation paradigm may potentially be used to address other theoretical issues related to the dissociation of high-level visual representations, within or between object domains. However, an alternative explanation of results based on our paradigm may be that experts pay more attention to the central stimulus posttraining, thus allocating fewer general resources for forthcoming events and leading to a decrease in the electrophysiological response to the second, i.e., face, stimulus. Several pieces

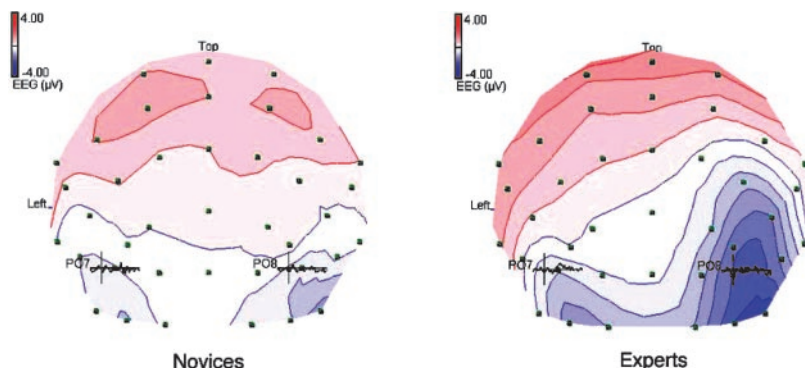


Fig. 4. Effect of training on the N170 evoked by faces. Topographical mapping of the specific effect of expertise training. N170 evoked by faces when preceded by Control objects and Greebles in novices and experts. (Right) After expertise training, the N170 in response to faces is reduced when preceded by objects of expertise (Greebles), thus leading to a large N170 difference at occipitotemporal sites. Left and right visual field presentations are averaged together, and the mapping is at 180 ms after stimulus onset. Note that the effect of expertise appears larger in the right hemisphere, but the Expertise Level \times Hemisphere interaction did not reach significance.

of evidence argue against this possibility. First, a hypothesis based on such a “general attention” theory may equally well predict the opposite effect, given that novices might actually be expected to engage attention to a greater degree than experts, because they are less familiar with the objects presented (and, presumably, less able to process them efficiently). Second, the lateralized detection task was irrelevant to the hypothesis tested and required subjects to pay attention to only the second, not the first, stimulus. Third, subjects were at a ceiling level and quite fast in performing our task, with no difference between conditions in response times. Thus, there is no evidence that subjects paid less attention to faces preceded by an object of expertise. Indeed, half of the trained objects used during each EEG recording session were novel exemplars of the expert category (see *Methods*), yet there was no difference in the decrease of the face-evoked N170 regardless of whether it was preceded by a familiar or an unfamiliar individual from the domain of expertise. Fourth and most importantly, the effect found here occurs in a very narrow time window, between 130 and 180 ms after stimulus onset, whereas effects of attention on early visual components typically start at ≈ 90 ms, at the level of the P1, and are generally sustained (see, e.g., ref. 35). Finally, the large reductions of the face-sensitive N170 amplitude measured in our study are inconsistent with the relatively small or null effects of spatial and/or selective attention on the N170 amplitude in response to faces in general (36, 37), suggesting that the reductions observed here do not merely reflect a modulation of the level of attention for faces.

At the same time, there are several possible physiological mechanisms underlying the competition effects observed when using scalp electrodes. The N170 is thought to originate from brain areas located in the inferior occipitotemporal cortex, including the fusiform gyrus, the superior temporal sulcus, and the middle and inferior temporal gyri (9, 13, 14, 16, 29), where cortical surface potentials in response to faces, N200s, have been observed at roughly the same latency (13). Single-cell recordings from the monkey temporal lobe show that cells in these regions are organized in columns that may be highly selective for faces or other complex stimuli (e.g., see refs. 38–40). One possible account of the present results is that visual expertise with nonface objects leads to the recruitment of the very same neurons involved in processing faces. This hypothesis may be measuring the neural responses of neurons in the inferotemporal (IT) cortex for the two categories of stimuli, after expertise training in monkeys.

Another plausible explanation of the present observations at the physiological level is that, as a result of expertise, neighbor populations of cells in the same cortical areas enter into competition for the two stimuli. After expertise training, the presentation of the nonface salient stimulus is associated with a sustained response in

subpopulations of cells in the inferotemporal cortex (IT), possibly causing a suppression or reduction of the activity of “face cells” through local lateral inhibitory connections, when the two items are presented concurrently in the visual field (41, 42). In monkey IT, such competitive inhibitory connections between neighboring populations of neurons coding for different stimuli have been associated with an increase of stimulus selectivity (43). These same inhibitory mechanisms appear to be at work in the human extrastriate cortex, as suggested by the observation of polarity reversal of the N200 cortical surface potential recordings in the same site, in response to different stimuli (44). Note that from a functional perspective it is not clear that these two alternatives are really all that different. Whether the obtained competition effects arise from recruitment of literally the same neurons or from interactions between intermingled neurons in a relatively small and functionally homogeneous brain region, it is implied that the same mechanisms are used in the processing of both object classes.

Overall, our results support the hypothesis that the visual mechanisms engaged by faces remain sufficiently flexible through adulthood to become recruited by nonface objects after the acquisition of visual expertise with a visually homogeneous category. Indeed, it appears that a relatively small amount of training with distinguishing members of nonface categories may lead to considerable recruitment of visual face-related processes. It is also worth noting that the particular nonface object category used here, asymmetric Greebles, has only a limited number of characteristics in common with faces, but, critically, not symmetry or coplanar parts (as in previous Greeble studies; see, e.g., refs. 17, 18, and 31). Taken together with other sources of evidence (for a review see ref. 7), our present results indicate that these properties alone, without face expertise, do not produce or account for face-like effects. It may be that no particular geometric or image properties of objects are necessary to obtain such effects, but at most it appears to be a combination of some or all of this set of geometric properties concatenated with visual expertise processes. Future work will not only have to clarify the nature of the visual processes used for both faces and domains of expertise, most likely related to the ability to process images in a configural/holistic manner (17, 24, 45), but also to determine the extent to which any of these properties are obligatory for the recruitment of these overlapping visual processes.

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