

Neural Correlates of the Left-Visual-Field Superiority in Face Perception Appear at Multiple Stages of Face Processing

Galit Yovel^{1,2}, Jerre Levy¹, Marcia Grabowecky², and Ken A. Paller²

Abstract

■ Studies in healthy individuals and split-brain patients have shown that the representation of facial information from the left visual field (LVF) is better than the representation of facial information from the right visual field (RVF). To investigate the neurophysiological basis of this LVF superiority in face perception, we recorded event-related potentials (ERPs) to centrally presented face stimuli in which relevant facial information is present bilaterally (B faces) or only in the left (L faces) or the right (R faces) visual field. Behavioral findings showed best performance for B faces and, in line with the LVF superiority, better performance for L than R faces. Evoked potentials to B, L, and R faces at 100- to 150-msec poststimulus showed no evidence of asymmetric transfer of information between the hemispheres at early stages of visual processing, suggesting that this factor is not

responsible for the LVF superiority. Neural correlates of the LVF superiority, however, were manifested in a shorter latency of the face-specific N170 component to L than R faces and in a larger amplitude to L than R faces at 220–280 and 400–600 msec over both hemispheres. These ERP amplitude differences between L and R faces covaried across subjects with the extent to which the face-specific N170 component was larger over the right than the left hemisphere. We conclude that the two hemispheres exchange information symmetrically at early stages of face processing and together generate a shared facial representation, which is better when facial information is directly presented to the right hemisphere (RH; L faces) than to the left hemisphere (LH; R faces) and best when both hemispheres receive facial information (B faces). ■

INTRODUCTION

The superiority of the right hemisphere (RH) in face perception has been demonstrated in numerous studies (for reviews, see Rhodes, 1985; Ellis, 1983). Hemispheric specialization in face processing is believed to produce a better representation of left visual field (LVF) facial information, which is directly projected to the RH, than of right visual field (RVF) facial information, which is directly projected to the left hemisphere (LH). In particular, studies with normal individuals show faster and more accurate performance for faces presented in the LVF than in the RVF (for reviews, see Rhodes, 1985; Sergent & Bindra, 1981). Levy, Trevarthen, and Sperry (1972) showed that when split-brain patients are asked to match centrally presented chimeric faces (combined left and right halves of two different faces), they perceive a coherent face that is usually a completion of the half face in the LVF, especially with nonverbal matching responses. People with an intact corpus callosum also manifest an LVF superiority in response to briefly presented chimeric faces (e.g., Heller & Levy, 1981; Schwartz & Smith, 1980). For instance, when people

view chimeric faces made from smiling and neutral half faces, the emotional expression presented in the LVF dominates their judgments of facial emotion (Heller & Levy, 1981; Campbell, 1978). These findings suggest that LVF facial information predominates in the mental representation of the complete face. Thus, a better understanding of how faces are processed and represented in the brain requires an investigation of the mechanisms that mediate the LVF superiority.

In an effort to gain further understanding of the LVF superiority in face perception, we examined subjects' behavioral responses and event-related potentials (ERPs) to central facial stimuli. In our task, subjects judged whether a pair of central faces, presented in succession, represent the same or different people. The first face (prime face) was one of three face types: (1) bilaterally symmetric faces (B faces) that project facial information to both hemispheres, (2) left hemifaces (L faces) that project task-relevant facial information to the LVF, and (3) right hemifaces (R faces) that project task-relevant facial information to the RVF. The second face (target) was always a B face (see Figures 1 and 2A). Brain potentials to the three types of prime faces were used to investigate the nature of interhemispheric communication at early stages of visual processing and

¹University of Chicago, ²Northwestern University

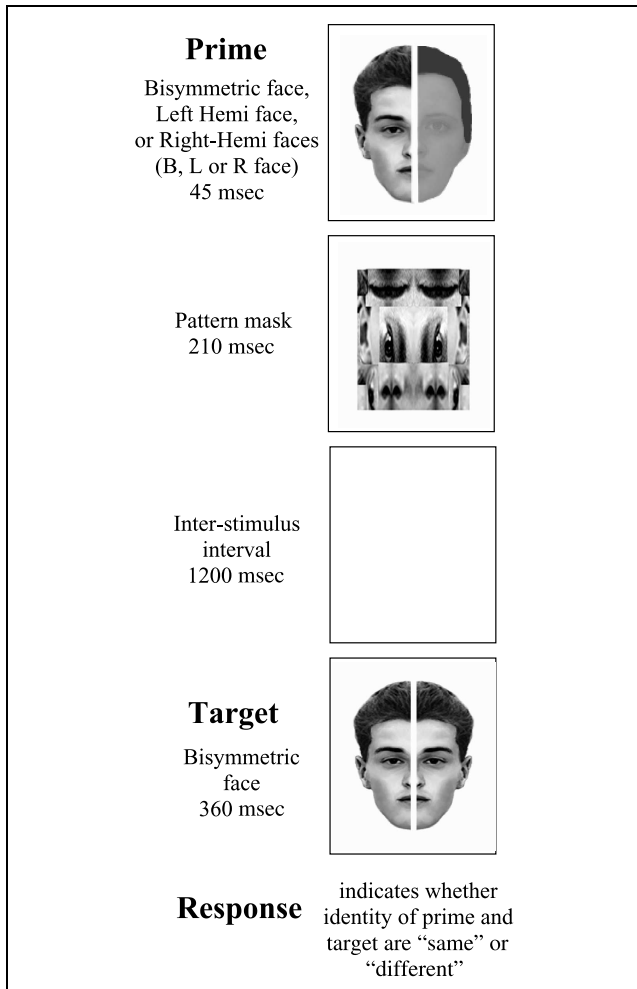


Figure 1. Schematic view of a typical trial sequence with timing parameters shown. Trial sequences began with the presentation of a fixation point, and then a central prime (a B, L, or R face), followed immediately by a pattern mask. The target face was presented after the interstimulus interval and was always a B face. ERPs were recorded time-locked to the prime and the target face.

the stage in face perception at which neural mechanisms that mediate the LVF superiority are manifested. We also measured ERPs to the target face to determine whether the degree of similarity between the representation of B, L or R prime faces and that of a target B face would be manifested in repetition effects on ERPs to the target face.

Interhemispheric Communication and the LVF Advantage

An understanding of the nature of interhemispheric communication in face perception can shed light on mechanisms that mediate the LVF superiority. We suggest two models of interhemispheric communication that may produce a better representation of facial information in the LVF/RH than RVF/LH. According to Model I, the LVF superiority is due to early blocking of information from the inferior LH to the superior RH. This prediction is

based on models of interhemispheric inhibition (for a review, see Chiarello & Maxfield, 1996), which suggest that the superior hemisphere inhibits the inferior one in order to prevent the less efficient processor from interfering with the more competent one. Thus, in the case of face perception, information that the inferior LH encodes directly is not incorporated in the formation of the facial image, which is carried out by the RH.

According to Model II, the two hemispheres exchange and utilize information symmetrically at early stages of visual processing. The LVF superiority is due to the superior facial processing mechanisms of the RH, which produce a better facial representation of the visual information it encodes directly rather than indirectly. Thus, Model II posits that the better representation of facial information from the LVF is reflected only at later stages of visual perception, during the formation of the facial representation. Previous reports that perceptual asymmetries are manifested at relatively late stages of information processing (Ivry & Robertson, 1998;

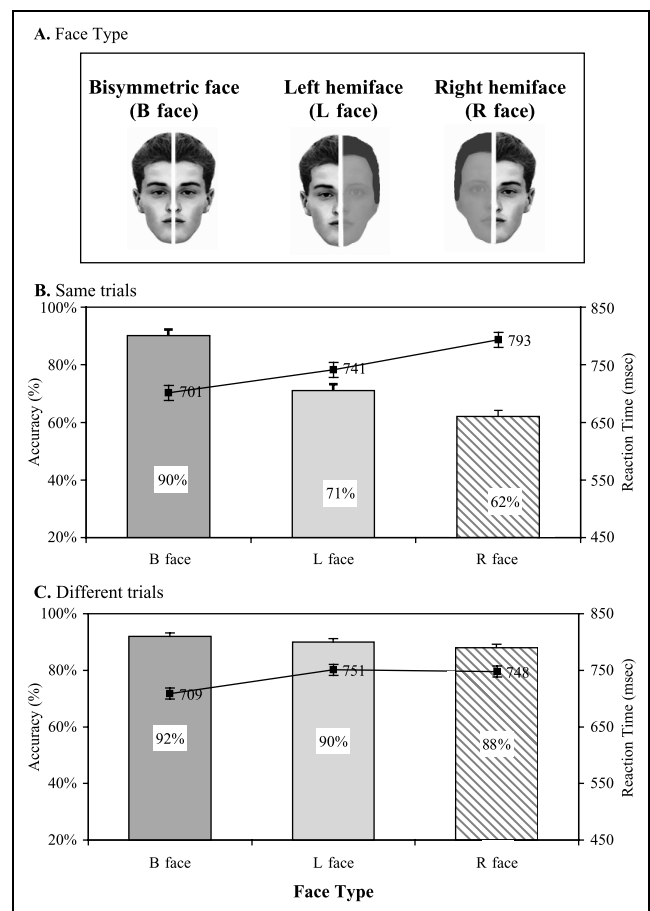


Figure 2. (A) Examples of the three types of prime faces. In order to elicit an illusory percept of a complete, coherent face on all trials, a thin white stripe covered the vertical midline and L and R faces were shown opposite minimal, low-contrast facial information. Accuracy and RT are shown for (B) same and (C) different target faces following B, L, and R face primes. The error bars indicate standard errors averaged across B-L, B-R, and L-R differences.

Moscovitch, Scullion, & Christie, 1976) imply that the LVF superiority does not reflect asymmetric blocking of information at early stages of visual processing, but emerges at later stages of facial processing. Further, the empirical evidence for interhemispheric inhibition in the normal brain is weak (Chiarello & Maxfield, 1996). In light of this evidence, we sought to determine if neural mechanisms mediating the LVF superiority are evident at different stages of face processing.

The Face-Specific N170 Component and the LVF Superiority

ERPs to facial stimuli include a negative peak 170 msec after stimulus onset that is larger over the right than the left temporal lobe (Bentin & Deouell, 2000; Bentin, Allison, Puce, Perez, & McCarthy, 1996). This N170 potential is thought to reflect an early structural encoding stage when a representation of a face is initially formed (Eimer, 2000b; Bentin et al., 1996; Bentin & Deouell, 2000). The N170 is sensitive to the coherence of the facial configuration. Its amplitude is larger and its latency is longer to inverted faces (Eimer, 2000a; Rossion et al., 1999, 2000), faces that deviate from a typical configuration (Halit, de Haan, & Johnson, 2000), eyes only (Eimer, 1998; Bentin et al., 1996), and to faces in which the facial features are positioned in incorrect locations (George, Evans, Fiori, Davidoff, & Renault, 1996). These amplitude and latency effects probably reflect a more effortful processing of poor facial images (Rossion et al., 1999). Neither facial identity (Bentin & Deouell, 2000; Eimer, 2000b; Paller, Gonsalves, Grabowecky, Bozic, & Yamada, 2000) nor the gender of the face (Mouchetant-Rostaing, Giard, Bentin, Aguera, & Pernier, 2000) influence the amplitude or latency of the N170. Interestingly, however, the N170 amplitude is larger to a person's own face than any other face, which suggests some early processing of facial identity (Tanaka & Portfield, 2002).

By measuring the N170 we were able to determine whether neural mechanisms that mediate the LVF superiority in face perception operate at this early face-construction stage or only later, when the particular content of the face is processed. A related question was whether individual differences in the asymmetry of the N170 amplitude are associated with the magnitude of the LVF superiority. Specifically, if the N170 asymmetry reflects the extent to which face processing is lateralized, then it may be associated with the magnitude of behavioral and ERP differences between L and R faces.

Are Complete Faces More Similar to Left Than Right Half Faces?

Previous studies showed that positive ERPs at 300–600 msec were larger for repeated faces than for faces presented for the first time (Paller, Bozic, Ranganath,

Grabowecky, & Yamada, 1999; Schweinberger, Pfutze, & Sommer, 1995; Bentin & McCarthy, 1994). In general, ERP repetition effects are believed to reflect facilitatory processing of a repeated stimulus due to its prior exposure (Rugg, 1995). These findings predict that the greater the similarity between the first and the second presentation of a face, the larger the facilitation and the ERP response to the second face. This effect enables us to assess whether representations of B faces are more similar to those of L faces than R faces, as the LVF superiority predicts. Thus, we compared ERPs to target B faces as a function of the type (B, L, R) of prime face that preceded it. If ERPs to target faces vary as a function of the degree of similarity between the target and preceding prime, then ERPs on correct same-identity trials would be larger to targets that follow B faces than hemifaces. If representations of B faces are more similar to those of L than R faces, ERPs to target B faces would be larger when preceded by L than R hemifaces.

In summary, in order to investigate the neural mechanisms that mediate the LVF superiority, we measured ERPs to B, L, and R prime faces and to subsequent B target faces in a same–different matching task (Figure 1). First, we examined occipital ERPs to prime faces at 100–150 msec to determine the nature of interhemispheric communication at initial stages of visual processing. We predicted symmetric callosal transfer of information at this early stage. Second, we analyzed subsequent ERP responses to prime faces to specify when neural correlates of the LVF superiority for faces are manifested. Third, we measured N170 asymmetries to determine if this measure of functional asymmetry predicts subsequent behavioral and ERP manifestations of the LVF superiority. Finally, we measured ERPs to target faces as a function of the prime that preceded them to assess whether the representation of a B face is more similar to that of an L face or an R face.

RESULTS

Behavioral Results

In debriefing, 10 of 12 subjects reported that they perceived all face stimuli as complete faces and did not notice the degraded information, which was present on L and R face trials. Two subjects reported noticing the degraded half faces, but only during the last few blocks of the experiment. Given that they showed the same pattern of behavioral results as the other 10 subjects, we did not exclude them from statistical analyses.

Reaction Time

We analyzed reaction times (RTs) to target faces for same and different correct responses using a repeated measures ANOVA with similarity (same, different) and prime type (B, L, R) as within-subjects factors. Responses were fastest on B face trials (705 msec), intermediate on

L face trials (746 msec), and slowest on R face trials (770 msec), $F(2,22) = 28.68, p < .001$. There was no difference in RTs between same and different trials, $F(1,11) < 1$. An interaction between similarity and prime type, $F(2,22) = 8.35, p < .005$, indicated different patterns of response on same and different trials.

For same responses, RTs were faster on B face trials than on L face trials, $F(1,11) = 9.15, p = .01$, which were faster than R face trials, $F(1,11) = 15.74, p < .005$, (Figure 2B). On different trials, RTs were faster on B face trials than on L face trials, $F(1,11) = 18.73, p < .005$, or R face trials, $F(1,11) = 16.55, p < .002$, whereas L and R face trials did not differ, $F(1,11) < 1$ (Figure 2C).

Accuracy

Accuracies were consistent with RTs. Accuracy was best on B face trials (91.2%), intermediate on L face trials (80.2%), and poorest on R face trials (74.9%), $F(2,22) = 83.58, p < .0001$. Accuracy was higher on different than same trials, $F(1,11) = 18.49, p < .005$. An interaction between similarity and prime type, $F(2,22) = 44.46, p < .0001$, reflects a stronger difference between the three types of faces for same than different trials.

For same trials, the proportion of correct responses was the highest on B face trials, intermediate on L face trials, and lowest on R face trials, $F(2,22) = 80.26, p < .0001$ (Figure 2B). The higher accuracy on B than L face trials was reliable, $F(1,11) = 153.38, p < .0001$, as was the higher accuracy on L than R face trials, $F(1,11) = 15.08, p < .01$. For different trials, a main effect of prime type, $F(2,22) = 6.95, p < .005$, reflects higher accuracy on B face trials than on L face, $F(1,11) = 4.98, p < .05$, or R face trials, $F(1,11) = 14.02, p < .005$, but no difference between L face and R face trials, $F(1,11) = 2.36, p = .15$.

ERPs to Prime Faces

Lateralized Early Visual Processing and Interhemispheric Communication

The three types of prime faces project different kinds of visual information to the two hemispheres. This difference was manifested in lateralized ERP responses over the occipital cortex 100–150 msec after face onset at early stages of visual processing (Figure 3). A repeated measures ANOVA on mean amplitude at occipital and occipito-temporal regions within the 100- to 150-msec interval, with face information (bilateral, contralateral, ipsilateral),¹ hemisphere, and area (occipital, occipito-temporal) as repeated measures, revealed lower amplitudes over the RH than LH, $F(1,11) = 5.96, p < .04$. In addition, a main effect of face information, $F(2,22) = 14.16, p < .0001$, reflects a lower amplitude to bilateral than contralateral face information, $F(1,11) = 18.13, p < .005$, and to contralateral than ipsilateral face information, $F(1,11) = 5.56, p < .05$. Importantly, neither the interaction of face information and hemi-

sphere, $F(1,11) < 1$, nor the interaction of face information, hemisphere, and area, $F(1,11) < 1$, were significant, which suggests symmetric transfer of information between the hemispheres. An interaction of face information and area, $F(2,22) = 10.82, p < .001$, reflects a larger difference among the three face types over occipital than occipito-temporal regions, $F(1,11) = 18.92, p < .005$ occipital; $F(1,11) = 9.14, p < .02$ occipito-temporal.

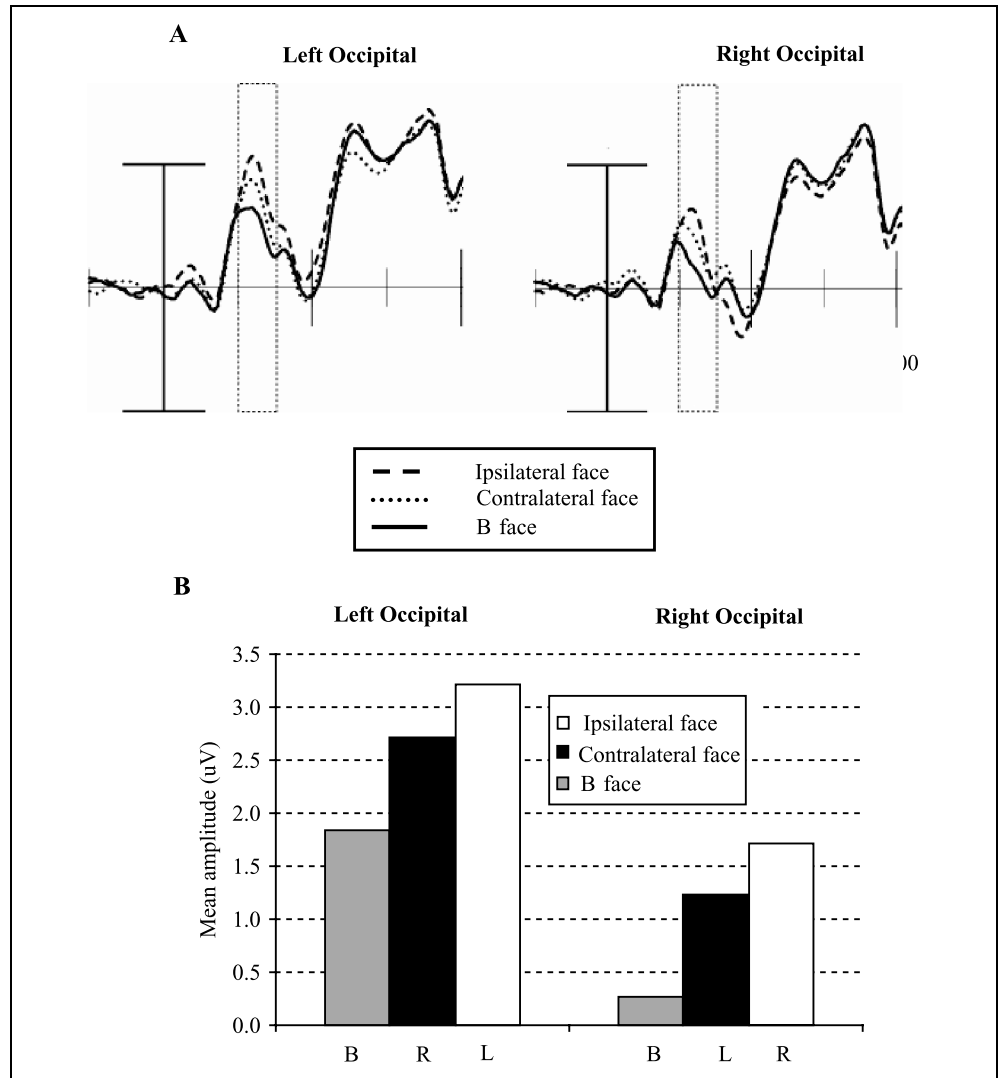
The difference in ERP amplitudes between contralateral and ipsilateral hemifaces, which was equal over the left and right hemispheres, $F(1,11) < 1$, suggests that occipital responses over the RH or the LH mainly reflect processes that are carried out by that hemisphere (see also Rugg, Milner, & Lines, 1985, for evidence from callosal agenesis patients and Steger et al., 2001, for source localization of early components to unilateral stimuli in normal subjects). Given that B faces and contralateral hemifaces project the same information to the contralateral hemisphere but different information to the ipsilateral hemisphere, the different brain potentials they elicit are likely to reflect the influence of transcallosal data. The absence of an interaction between face and hemisphere, which shows that the difference between B faces and the contralateral hemiface was the same over the two hemispheres, provides evidence for symmetric interhemispheric communication at this early visual perception stage.

Despite the fact that B faces project high-contrast visual information to both hemispheres, they elicited lower amplitudes than did the hemifaces, which contain low-contrast visual information on one side. The reason for the lower amplitude to B faces is unclear, but may reflect overlapping negative components that are larger for bilateral facial input than for unilateral high-contrast visual input (i.e., contralateral hemiface) and for contralateral high-contrast than low-contrast visual input (i.e., ipsilateral hemiface). Another possibility is that early negative evoked responses to the mask, which is presented 60 msec after face onset, were modulated by the contrast level of the previous face stimulus. Whatever the mechanism that elicits the lowest amplitude to B faces, the difference in responses to B faces and the contralateral hemiface over the hemisphere that receives identical information from those stimuli (B and L face over the RH and B and R faces over the LH) plausibly reflects the influence of transcallosal codes from the ipsilateral hemisphere.

Early Stages of Face Processing (N170) and the LVF Superiority

Peak amplitude. We measured the peak amplitude of the face-specific N170 component in response to the three types of prime faces (B, L, R) over left (PO7,

Figure 3. (A) ERP responses and (B) mean amplitudes to the three prime faces at the left and right occipital electrodes (O1 and O2). Responses at 100–150 msec reflect symmetric interhemispheric transfer of visual information.

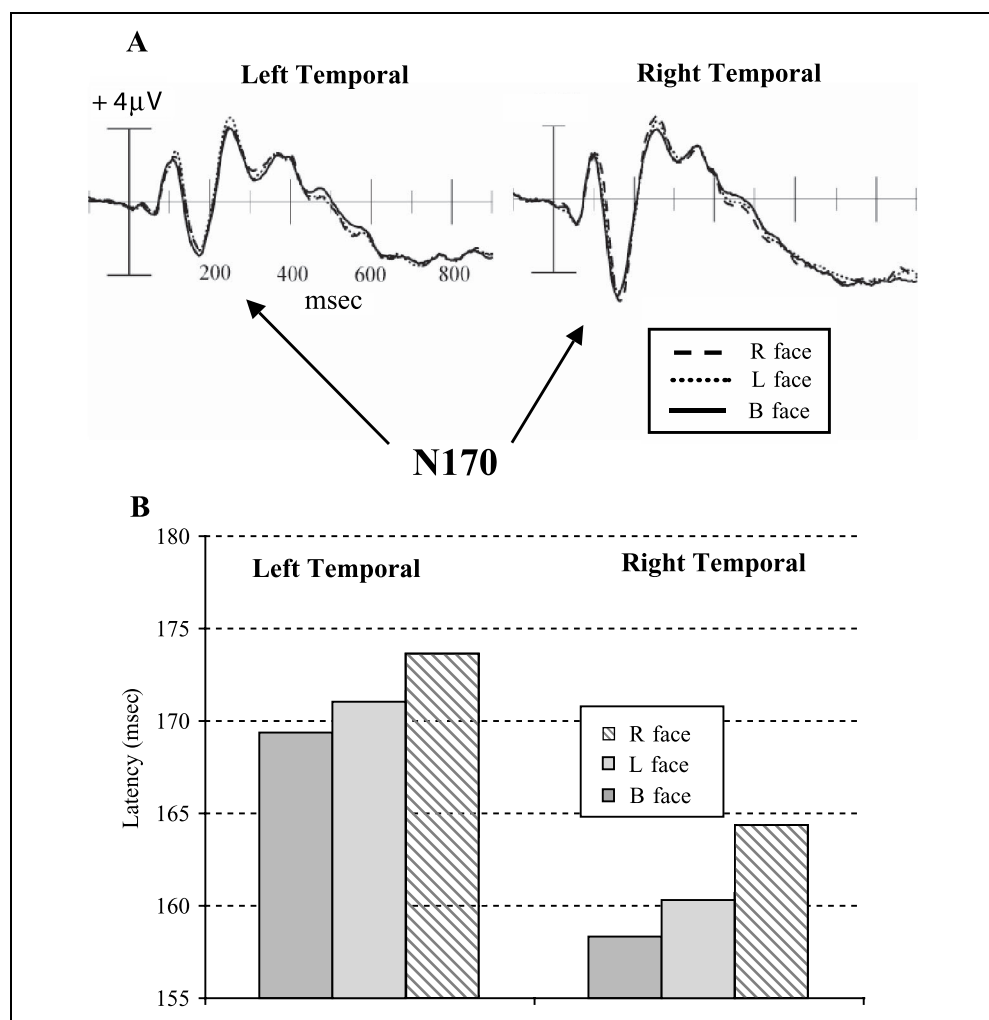


PO9, P7) and right (PO8, PO10, P8) occipito-temporal electrodes (see Figure 4A for PO7 and PO8). We performed an ANOVA with face type (B, L, R), hemisphere (LH, RH), and electrode site (PO7-8, PO9-10, P7-8) as repeated measures. Consistent with previous reports, N170 peak amplitude was larger over the RH than over the LH, $F(1,11) = 5.14$, $p < .05$, for all temporal sites (see Table 1). We found neither a main effect of face type nor an interaction of face type with hemisphere, electrode site, or both together. Thus, N170 was equally large and asymmetric when high contrast facial information was projected to both hemispheres (B faces), only to the RH (L faces), or only to the LH (R faces).

Latency. N170 peak latency was shorter over the RH than the LH (Tables 1 and 2). Figure 4B shows the latencies at PO7 and PO8 to the three types of faces. This finding was confirmed by an ANOVA with face type, hemisphere, and electrode site as repeated measures, which showed a main effect of hemisphere, $F(1,11) = 6.05$, $p < .05$, and no interaction of hemisphere and site.

An interaction of face type and site, $F(4,44) = 3.80$, $p < .01$, indicated no effect of face type at P7 and P8, but a main effect of face type at PO7, PO8, $F(2,22) = 7.13$, $p < .01$, and PO9, PO10, $F(2,22) = 6.98$, $p < .01$. The N170 latency to B faces was shorter than to L faces, PO7, PO8: $F(1,11) = 10.11$, $p < .01$; PO9, PO10: $F(1,11) = 24.21$, $p < .001$, and R faces, PO7, PO8: $F(1,11) = 9.67$, $p < .01$; PO9, PO10: $F(1,11) = 7.84$, $p < .02$. Although Table 2 shows a shorter latency to L than R faces at four of six electrode sites, with no difference at the other two, the difference does not reach a conventional level of significance at any site. Nonetheless, given the sampling rate used, a trend toward a reliable difference at PO7, PO8, $F(1,11) = 4.12$, $p = .07$, suggests that the power of statistical tests may have been too weak to detect a real difference. In fact, only one subject showed an opposite effect of a shorter latency to R than L faces. The three-way interaction of face type, electrode site, and hemisphere was not significant, which indicates the same pattern of differences among the face types over the two hemispheres.

Figure 4. (A) N170 to the three types of prime faces at left and right posterior occipital electrodes (PO7 and PO8). (B) N170 latency at PO7 and PO8 (Tables 1 and 2 show amplitude and other latency measures). Average scalp amplitude was used as a reference for this analysis. Because late ERP differences among the three faces appeared at all electrode sites, they were reduced when the average scalp amplitude was used as a reference.



Late Stages of Face Perception and the LVF Superiority
 220–280 msec. Later brain potentials at frontal, central, and parietal electrodes showed a negative component, with a peak approximately 250 msec after stimulus onset (Figure 5). An ANOVA on mean amplitude in the 220- to 280-msec interval with face type (B, L, R), area (frontal, central, parietal), and hemisphere as repeated measures revealed a main effect of face type, $F(2,22) = 6.49, p < .001$, which reflects smaller amplitudes to R than L faces, $F(1,11) = 5.76, p < .04$, or B faces, $F(1,11) = 12.42, p < .05$, but no difference between B and L faces, $F(1,11) = 1.26, p = .29$. There

was no interaction of face type with area, hemisphere or both, which implies the same patterns of response over the two hemispheres and three areas. An analysis of data from the midline electrodes with face type and electrode site (Fz, Cz, Pz) as repeated measures showed a similar pattern. A main effect of face type, $F(2,22) = 8.89, p < .005$, reflects a lower amplitude to R than L faces, $F(1,11) = 7.32, p < .02$, or B faces, $F(1,11) = 17.24, p < .005$, but no difference between B and L faces, $F(1,11) = 2.09, p = .17$. There was no interaction of face type and electrode site.

Table 1. N170 Peak Amplitude at Three Left and Right Occipito-temporal Electrodes

	LH			RH		
	PO9	PO7	P7	PO10	PO8	P8
Amplitude (μV)	-6.7	-3.7	-3.7	-9.4	-6.3	-5.6
Latency (msec)	175.7	171.3	169.6	164.4	161.0	161.8

Table 2. N170 Latency (msec) to B, L, and R Faces at Three Left and Right Occipito-temporal Electrodes

Face	LH			RH		
	PO9	PO7	P7	PO10	PO8	P8
B	167	169	178	160	158	164
L	171	171	174	161	160	165
R	171	174	175	164	164	165

400–600 msec. Brain potentials to the three faces diverged from each other at all electrode sites approximately 400–500 msec after stimulus onset (Figure 5). We first analyzed the mean amplitude to the three faces during the 400- to 600-msec interval using an ANOVA with hemisphere, area (frontal, central, occipito-parietal, occipito-temporal, occipital), and face type (B, L, R) as repeated measures. We then measured the mean amplitude at 50-msec intervals between 350 and 750 msec to determine when responses to the different face stimuli diverged.

A main effect of face type, $F(2,22) = 16.09, p < .0001$, but no interaction of face type and hemisphere, reflects a larger amplitude to B faces than to L faces, $F(1,11) = 10.55, p < .001$, or R faces, $F(1,11) = 31.72, p < .0001$, and a larger amplitude to L than R faces, $F(1,11) = 5.68, p < .04$, over both hemispheres. An interaction of face type and area, $F(8,88) = 2.76, p < .01$, indicates a smaller difference among the three face types over frontal regions than other regions.

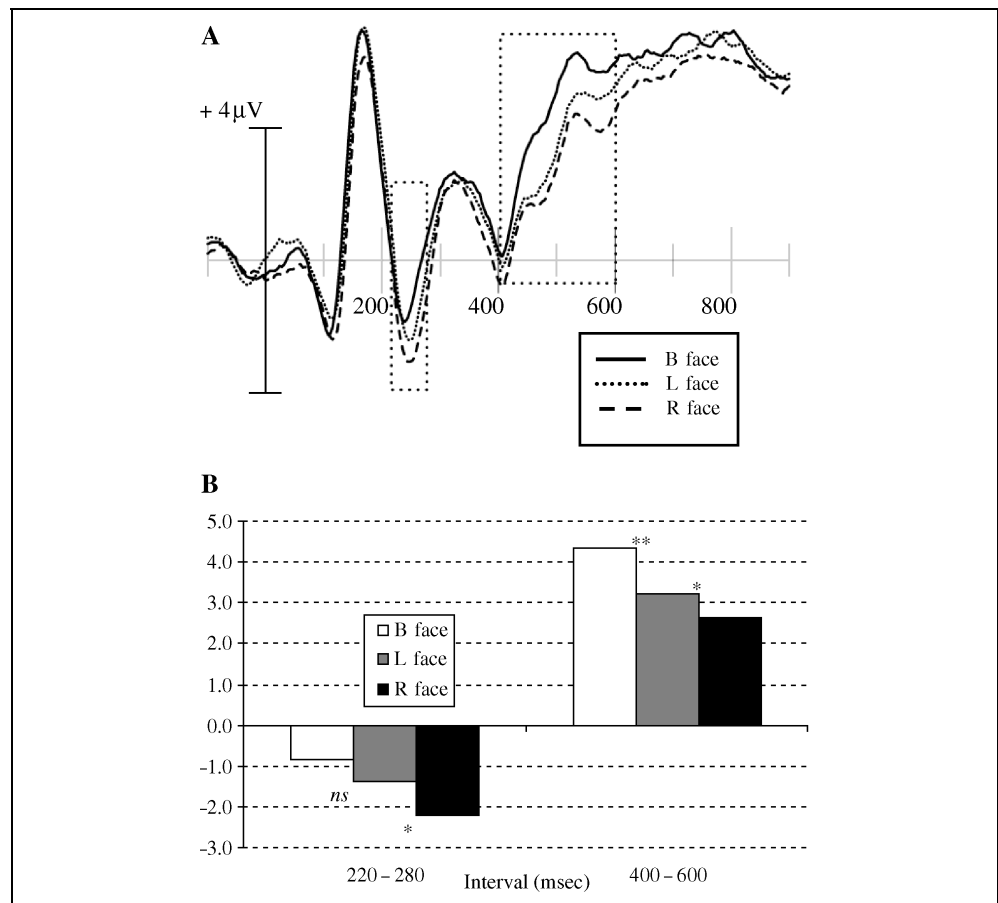
An analysis of amplitudes at the midline electrodes with face type (B, L, R) and electrode site (Fz, Cz, Pz, Oz, Iz) as repeated measures revealed similar findings. Figure 5 shows results from the Cz electrode. The main effect of face type, $F(2,22) = 14.41, p < .0001$, reflected a larger amplitude to B than L faces, $F(1,11) = 10.288, p < .01$, and to L than R faces, $F(1,11) = 4.51, p = .05$.

A more detailed analysis, restricted to the midline electrodes, in which we measured the mean amplitude during 50-msec intervals between 350 and 750 msec, showed that ERPs to B faces first diverged from ERPs to R faces, $F(1,11) = 18.11, p < .001$, and L faces, $F(1,11) = 23.99, p < .001$, at the 450- to 500-msec interval. A significant difference between L and R face ERPs first emerged at the 500- to 550-msec interval, $F(1,11) = 6.26, p < .05$. Thus, a difference between L and R faces, which reflects the different qualities of their representations, first appeared at about 250 msec, disappeared, and then reappeared by 500 msec. Similarly, a difference between B and R faces first emerged around 250 msec, disappeared, and reappeared by 450 msec. The difference among the three face stimuli was not significant beyond 600 msec.

The N170 Asymmetry and the LVF Superiority

The degree of asymmetry of the N170 amplitude (LH–RH) was positively associated with the difference in ERP responses to L and R faces at the 220- to 280-msec interval and at the 400- to 600-msec interval (see Figure 6 for correlations with parietal electrodes at 220–280 msec, $r(10) = .68$, and 400–600 msec, $r(10) = .68$). The correlation at the 220- to 280-msec interval averaged across all areas was $r(10) = .67 (p < .02)$ and at the

Figure 5. (A) ERP responses and (B) mean amplitude at 220–280 and 400- to 600-msec intervals at the central midline electrode (Cz). These results show that ERPs to B faces diverged from ERPs to R faces earlier than from ERPs to L faces. The difference between the faces in the 400- to 600-msec interval parallels behavioral findings (see Figure 2). *ns* = not significant; * = $p < .05$, ** = $p < .01$.



400- to 600-msec interval was $r(10) = .66$ ($p < .02$). Neither the N170 asymmetry nor the L–R difference in ERP responses was associated with the difference between L and R faces in behavioral measures.

The absence of reliable correlations between ERP measures and the L–R difference in accuracy may reflect the low reliability of the behavioral measure. The reliability (α coefficient) of the accuracy difference (L–R) is only 0.43 for same responses, and 0.32 for same and different responses, which puts stringent limits on its correlation with other measures. Indeed, in a face-matching task with the same three face types (B, L, R) but six response choices, which yielded an alpha coefficient of .89 for the accuracy measure, we have found a highly significant correlation between the L–R difference in late ERP responses (400–600 msec) and behavioral measures (Yovel, Levy, Grabowecky, & Paller, unpublished data).

ERPs to Target Faces—Repetition Effects

ERPs to targets showed a typical ERP repetition effect, with greater positive amplitudes for same- than different-identity target faces. We compared amplitudes in the 300- to 500-msec interval on correct trials according to whether the identity of the target was the same as or different from the prime. An ANOVA with similarity to prime (same, different), prime type (B, L, R), and electrode site (Fz, Cz, Pz, Oz, Iz) as repeated measures revealed larger ERPs to targets preceded by same-identity than different-identity primes, $F(1,11) = 29.27$, $p < .0005$. There was no interaction of similarity with prime type, $F(2,22) = 1.64$, $p = .217$. Despite a three-way interaction of similarity, prime type, and electrode site, $F(1,11) = 2.34$, $p = .023$, there were no significant interactions between prime type and similarity at any electrode site.

A second question was whether ERPs to target faces on correct same trials varied in magnitude depending on the prime type (B, L, R). If the representational similarity between primes and targets of the same identity is greatest for B face primes, intermediate for L face primes and least for R face primes, then based on the repetition effect, ERPs to correct same targets would be largest when preceded by B primes and least when preceded by R primes.

An analysis restricted to correct same responses with prime type (B, L, R) and electrode site (Fz, Cz, Pz, Oz, Iz) as repeated measures revealed a main effect of prime type, $F(2,44) = 7.05$, $p < .005$, which reflects the larger amplitude to targets on B face trials than on hemiface trials, L face: $F(1,11) = 22.86$, $p < .001$; R face: $F(1,11) = 39.42$, $p < .0001$. There was no difference in ERP amplitudes to target faces on L and R trials at any electrode site (see Figure 7 for Cz). Thus, repetition effects were larger to targets preceded by identical primes (B primes) than to targets preceded by primes

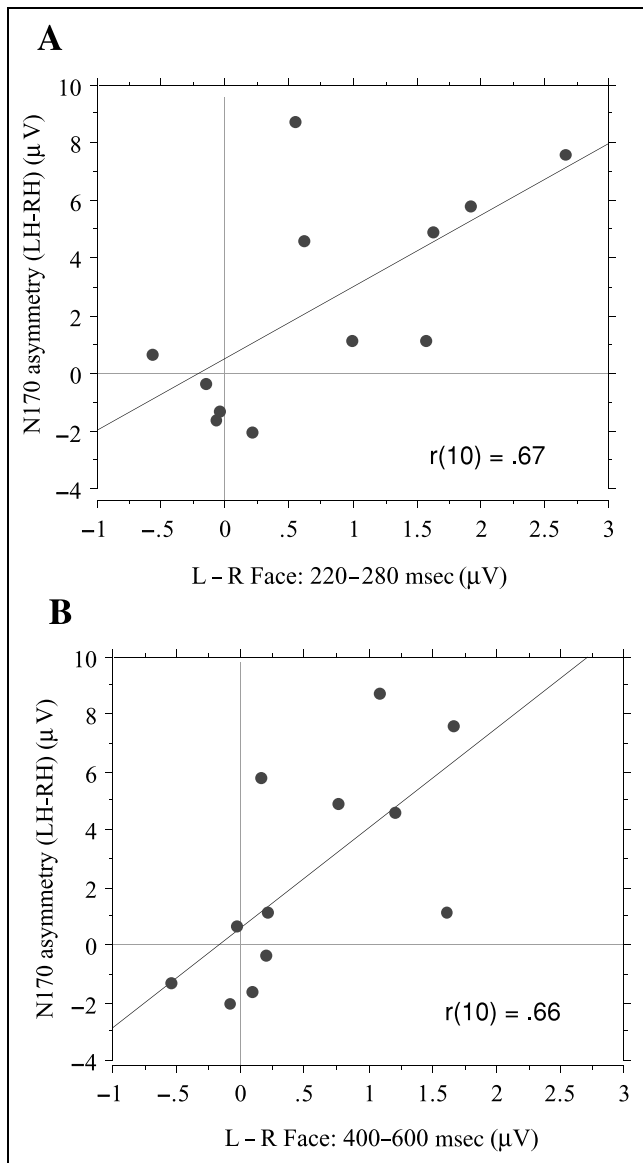


Figure 6. Positive correlations between the asymmetry of N170 amplitude (LH–RH) and the L–R difference at intervals from (A) 220–280 msec and (B) 400–600 msec. Larger RH activity at early stages of face processing was associated with a larger difference in later ERPs between L and R faces.

that are only half-identical to targets (L and R primes). Contrary to our hypothesis, however, ERPs to targets on L prime trials did not differ from those to targets on R prime trials (Figure 7).

In order to determine whether this pattern of response to target faces was different over the two hemispheres, we performed a repeated measures ANOVA with prime type (B, L, R), hemisphere (LH, RH) and area (central, frontal, parieto-occipital, temporal-occipital, occipital) as repeated measures. A main effect of prime type, $F(2,22) = 6.90$, $p < .005$, reflects larger potentials to targets on B face trials than on L face, $F(1,11) = 21.97$, $p < .001$, or R face, $F(1,11) = 35.75$, $p < .001$, trials. The absence of an interaction of prime

type and hemisphere, $F(2,22) = 1.32, p = .28$, reveals that there is no difference between the right and left hemispheres in the effects of prime types on ERPs to targets.

DISCUSSION

The goal of the present study was to explore the neurophysiology of the LVF advantage in face perception by examining ERPs to faces that project task-relevant facial information to both hemispheres (B faces), only to the RH (L faces), or only to the LH (R faces). As shown in Figure 2, we found the best performance for B faces and, in line with the LVF superiority in face perception, better performance for L than R faces. These findings imply that the quality of the facial representation is best for B faces and poorest for R faces. It should be noted that although hemiface stimuli contain low-contrast facial information on one side, they were generally perceived as complete faces.

Interhemispheric Communication in Early Visual Processing

Unilateral stimuli do not elicit ipsilateral visual evoked responses (P1 and N1) in split-brain and callosal agenesis patients (Brown, Jeeves, Dietrich, & Burnison, 1999; Rugg et al., 1985). This finding suggests that early occipital components over a given hemisphere mainly reflect processes carried out by that hemisphere and not

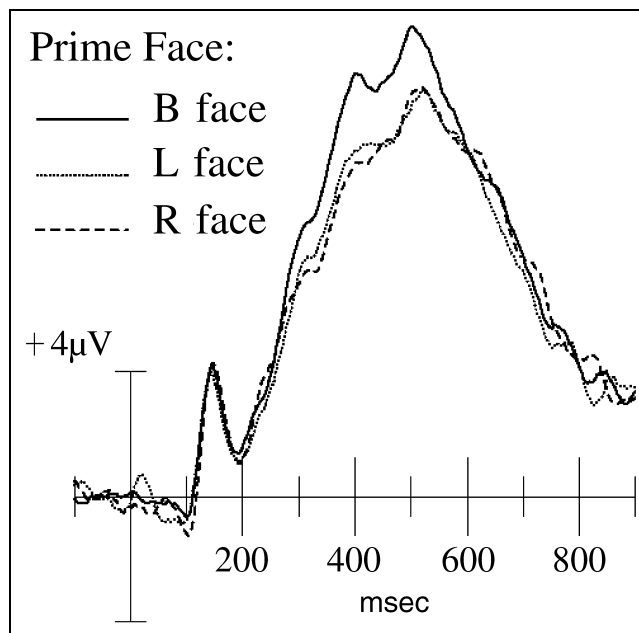


Figure 7. ERPs to correct responses to target faces from the central midline electrode (Cz). Responses are shown to target B faces that followed B, L, and R prime faces of the same identity. Responses to target faces that followed B face primes were larger than to target faces that followed hemiface primes.

by the opposite hemisphere (see also Steger et al., 2001, for a source localization analysis of occipital potentials to unilateral stimuli). Thus, the difference we observed between potentials to B and L faces over the RH, which project the same information to the RH but different information to the LH, reflects the influence of transcallosal data from the LH.

Contrary to predictions of interhemispheric inhibition models, we found no evidence that the LVF superiority is due to early blocking of transcallosal input from the inferior LH to the superior RH. In particular, the difference between ERPs to B and L faces over the RH, which reflects the influence of transcallosal input from the LH, was the same as the difference between ERPs to B and R faces over the LH, which reflects the influence of transcallosal input from the RH (Figure 3). We conclude that interhemispheric transfer of visual information between the hemispheres is symmetric and that the LVF advantage for faces is mediated by later face-perception mechanisms that are more efficient in the RH than the LH.

Neural Correlates of the LVF Superiority at Multiple Stages of Face Perception

Consistent with prior findings, the N170, which reflects early structural face processing (Bentin et al., 1996), was larger over the right than the left occipito-temporal region for all face types. Neither N170 amplitude nor its asymmetry differed across B, L, and R faces. N170 peak latency, however, varied slightly but significantly as a function of facial type at occipito-temporal sites. Latencies to B faces were shorter than to L or R faces and there was a trend ($p = .07$) at PO7/PO8 for a shorter latency for L than R faces (see Table 2 and Figure 4B). Longer N170 latencies are thought to reflect a more difficult construction of the face image (Rossion et al., 1999). Thus, our findings suggest easier construction of B faces than hemifaces and possibly easier construction of L than R faces.

The LVF superiority predicts that the representations of B faces are more similar to those of L than R faces. Indeed, ERPs to B faces first diverged from R faces at the 220- to 280-msec interval but not from L faces until the 450- to 500-msec interval. At about 450 msec after stimulus onset, ERP responses were largest to B faces and smallest to R faces (see Figure 5). Previous studies revealed an RH-LVF advantage in face-perception tasks that entailed low levels of processing, such as face/no-face categorization (e.g., Young, Hay, & McWeeny, 1985), intermediate levels of processing, such as same-different matching decisions (e.g., Hellige, Jonsson, & Michimata, 1988), and higher levels of processing, such as face recognition (e.g., Levine, Banich, & Koch-Weser, 1988). Given that the difference between ERPs to same and different target faces (i.e., congruency effect) emerges at about 250–300 msec (Schweinberger et al.,

1995), we believe that the difference between prime L and R faces at about the same interval (220–280 msec) reflects intermediate stages of face processing, in which the facial representation is elaborated enough for a matching judgment. Based on previous reports that ERP differences between known and unknown faces emerge at about 400 msec (Bentin & Deouell, 2000; Eimer, 2000b; Paller et al., 2000), we suggest that the difference in the later component (400–600 msec) reflects evaluation of facial identity.

Asymmetries of the N170 (LH–RH) correlated positively with differences in responses to L and R faces at the 220- to 280-msec and 400- to 600-msec intervals (Figure 6). These findings suggest that a greater hemispheric asymmetry in early responses to faces is associated with a larger LVF advantage in later stages of face processing. The fact that we found no correlations with behavioral measures might reflect the low reliability of the accuracy measure ($R = .32$) and different neural mechanisms that mediate individual differences in the amplitudes of ERPs and in RTs. In fact, on a face matching task, in which accuracy had a high reliability ($R = .89$), Yovel et al. (unpublished data) observed substantial correlations between the L–R face difference in accuracy and ERPs.

Finally, despite the RH superiority in face perception and the variations in facial data projected to each hemisphere by B, L, and R faces, by 200 msec there were no hemispheric differences in the pattern of ERPs to the three prime faces ($B > L > R$). Thus, our findings suggest that the two hemispheres exchange facial information early in visual processing and collaboratively generate a joint facial representation, which is best for B faces and better for L than R faces.

The LVF Superiority and Repetition Effects

Previous studies have shown that repeated faces elicit larger ERP amplitudes at 300–600 msec than do non-repeated faces, an ERP repetition effect (e.g., Paller et al., 1999; Schweinberger et al., 1995; Bentin & McCarthy, 1994). Similarly, we found larger ERPs to target faces on same than on different trials for all three types of prime faces. If ERP repetition effects reflect facilitation due to prior exposure to the same stimulus (Rugg, 1995), the greater the degree of similarity between a prime and a target, the larger the ERP to the target. This hypothesis predicts the largest amplitude in response to targets following same B primes, where the prime and target are perfectly identical. If representations of B faces are more similar to those of L than R faces, ERPs to targets following same L face primes would be larger than to those following same R face primes. The latter prediction is based on the better representation of L than R faces as manifested in accuracy and RT, which implies that representations of targets (B faces) are more similar to those of L primes than R primes. Although we found

that ERPs were largest to targets that followed same B primes, we observed no difference in ERPs to targets that followed same L and R primes. It may be that the representational qualities of L and R primes are not sufficiently different to generate a detectable difference in facilitation of target responses.

Conclusions

In summary, examination of the nature of inter-hemispheric communication at a very early period (100–150 msec) of visual processing suggests that the LVF superiority is not due to early blocking of trans-callosal information from the LH to the RH, as models of interhemispheric inhibitions would predict (Chiarello & Maxfield, 1996). The higher fidelity of the representation of L than R faces, which is evident in behavioral measures (Figure 2), is first manifested electrophysiologically in several ways. First, there was a trend towards a shorter latency of the early face-construction component (N170) to L than R faces (Figure 4), which may indicate easier face construction for L than R faces. Later ERP responses that probably reflect intermediate (220–280 msec) and high-level (400–600 msec) face processing also differed between L and R faces (Figure 5). The covariation between N170 asymmetry and later responses to L and R faces (Figure 6) suggests that people with a greater relative reliance on the RH for early processing of facial structure also show a greater advantage for LVF facial information. Overall, our findings show that neural correlates of the LVF superiority are reflected at multiple stages of face perception and are associated with the asymmetry of early face processing reflected by the N170. Notably, by 200 msec both hemispheres share the same facial representation, as suggested by the absence of asymmetry in the pattern of ERPs. We propose that the two hemispheres symmetrically exchange facial information early in visual processing and generate in collaboration a shared facial representation, in which facial information that is directly projected to the RH is of a higher fidelity than facial information that is directly presented to the LH.

METHODS

Participants

Twelve individuals (5 men, aged 18–27 years) volunteered to participate in the experiment. They each gave informed consent in advance and were paid for their participation. All participants completed a 9-item handedness questionnaire and indicated that they preferred their right hand on each of its items.

Stimuli and Apparatus

Frontal views of faces of six young males were selected from the University of Stirling face database

(<http://pics.psych.stir.ac.uk>). Only the left or only the right hemiface of each face was used. Six bisymmetric (B) faces were made from the combination of a half face and its mirror image. Six right (R) and six left (L) hemiface stimuli were made by combining a half face or its mirror image with a standard task-irrelevant female half face, which was reduced to 33% contrast of the original face (see Figure 2A). The R and L faces presented the experimental hemiface in the RVF and LVF, respectively. Our pilot studies showed that when such hemifaces are presented for 60 msec or less followed by a pattern mask, the majority of subjects do not notice that they are presented with only half high-contrast faces, but perceive all face stimuli as bilaterally complete. Furthermore, Yovel, Paller, and Levy (submitted) showed that performance level does not differ between half faces, which present information only in one visual field, and hemifaces, which present low-contrast neutral information in the opposite visual field. This finding suggests that the low-contrast information does not interfere with the perception of the experimental hemiface. Prime faces were one of the 18 B, L, or R faces. Targets were one of the six B faces. The low-contrast standard female face was never a target. Each face subtended 2.64° of visual angle horizontally. A thin white stripe (0.17° wide) covered the vertical midline of all faces. All faces were equated for luminance, length, and width. The stimuli were presented on a 15-in. monitor (832×624 , 67 Hz, Mac Std Gamma) and viewed from a distance of 65 cm.

Procedure

Participants were introduced to the experiment and prepared for the ERP recordings, as described below. They were then seated in a recording chamber and communicated with the experimenter over an intercom. Subjects read the task instructions and completed two example trials to make sure that they understood the task. The instructions did not inform the subjects that some of the stimuli were hemifaces. All example trials presented only B faces. Subjects then completed a practice run of 24 B face trials. Following the practice run, subjects were told that faces in subsequent runs would be masked in order to make the task more difficult. They then viewed two example trials that showed the sequence of a masked trial. At the end of the experiment, subjects were queried about whether they noticed the low-contrast side of hemifaces, starting with indirect questions (i.e., Did you notice anything unusual about the prime faces?) and progressing to more direct questions (i.e., Did you notice that some faces consisted of only the right or the left side of the face?).

A trial sequence began with the appearance of a central fixation cross for 1000 msec followed by a circle that replaced the cross for 500 msec (warning cue), a 30-msec interstimulus interval, a central prime face for

45 msec, and a symmetrical rectangular pattern mask of scrambled facial features (3.9° high by 2.9° wide) for 210 msec. The target B face appeared 1455 msec after the onset of the prime and was presented for 360 msec (see Figure 1). Prime and target faces were the same individual on half the trials and different individuals on the other half. The participant's task was to press one key if the prime and the target were the same person and another key if they were different. The next trial began 2000 msec after the participant's response.

There were a total of 540 trials, which included 180 prime faces of each type (B, L, R) in a random order. Trials were subdivided into 15 runs separated by rest periods of 1 min. Each run included 12 B face trials, 12 L face trials, and 12 R face trials. For each set of 12 trials, the primes were made using each of the six stimulus faces twice, and the targets were made using each stimulus face once as a "same" face and once as a "different" face. The experimental task lasted approximately 1 hr.

ERP Procedure

ERPs were recorded using 29 tin electrodes on an elastic cap (Fz, Cz, Pz, Oz, Iz, Fp1, Fp2, F3, F4, F7, F8, C3, C4, T3, T4, P3, P4, P7, P8, PO3, PO4, PO7, PO8, PO9, PO10, O1, O2, O9, O10) and right and left mastoid electrodes. Scalp recording locations are shown in Pivik et al. (1993). Electrooculographic (EOG) recordings were made using 3 tin electrodes, one located below the right eye (vertical EOG) and two lateral to the right and left eye (horizontal EOG). Impedance was reduced to 5 k Ω for scalp electrodes and 3 k Ω for mastoid electrodes. EEG signals were amplified with a 0.1- to 100-Hz band pass and were digitized on-line with a sampling rate of 250 Hz. For ERP averaging, the EEG was segmented into epochs of 1024 msec, starting 100 msec before stimulus onset. Trials with artifacts due to blinks or eye movements were excluded prior to averaging. All recordings, except horizontal EOG, were referenced to a left mastoid electrode, which was changed offline to the average of the two mastoid recordings.

The two conventional ways to measure the N170 use either a reference electrode on the nose (e.g., Eimer, 1998; Bentin et al., 1996) or the average amplitude over all scalp electrodes as a reference (e.g., Rossion et al., 2000). The two methods yield comparable results (C. I. Hooker, A. R. Miller, & K. A. Paller, unpublished data). Here we used a common average as a reference to measure N170 amplitude and latency. The average mastoid amplitude was used as a reference for all other components.

Data Analysis

We calculated averaged ERPs for each scalp electrode for prime stimuli and for target stimuli. Although there was a fixed time interval between prime and target stimuli, ERPs to B, L, and R prime stimuli were no longer

different by 700 msec after prime onset and remained undifferentiated until the target stimulus appeared. Separate averaging was performed for each of the three types of prime faces (B, L, R) and for same and different B target faces as a function of the type of prime face that preceded them.

The difference among the three prime faces was examined by computing mean ERP amplitudes to the prime faces at selected intervals. We first performed an omnibus ANOVA with face type (B, L, R) as a repeated measure followed by planned comparisons of each pair (BL, BR, LR). We used the averaged mean square error of the three comparisons as a common error term for the paired comparisons.

Evoked responses at occipital electrodes did not elicit a clear P100 peak in each individual, although across subjects there was a positive component 100–150 msec after stimulus onset. The P100 was thus measured as the mean amplitude in the interval 100–150 msec at occipito-temporal (P7, PO7, PO9, P8, PO8, PO9) and occipital (O1, O2, O9, O10) sites.

The peak amplitude of N170 and its latency were measured at the left and right occipito-temporal electrodes (P7, PO7, PO9, P8, PO8, PO9), using a common average as a reference. For each subject, the most negative point within the 140- to 200-msec interval was identified as the peak amplitude. Latency was defined as the time from stimulus onset to the peak point.

ERP responses to target faces were analyzed within the interval of 300–500 msec after stimulus onset, where repetition effects have been reported previously. To reduce the complexity of the analysis we divided the scalp into five areas: frontal (Fp1, Fp2, F3, F4, F7, F8), central (C3, C4, T3, T4), occipito-parietal (P3, P4, PO3, PO4) occipito-temporal (P7, PO7, PO9, P8, PO8, PO9), and occipital (O1, O2, O9, O10). Data from the midline electrodes (Fz, Cz, Pz, Oz, Iz) were analyzed separately. Sphericity was not violated in any of the ANOVAs included in this report and therefore there was no need to apply the Geisser–Greenhouse correction.

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Reprint requests should be sent to Galit Yovel, Department of Brain and Cognitive Sciences, Massachusetts Institute of Technology, 77 Massachusetts Avenue, NE20-443, Cambridge, MA 02139, USA, or via e-mail: galit@mit.edu.

Note

1. For the analyses of early occipital evoked responses, hemifaces were classified as contralateral and ipsilateral faces: contralateral faces = L face over the RH and R face over the LH; ipsilateral faces = R faces over the RH and L faces over the LH. For analyses of later components, hemifaces were

defined according to the characteristics of the face stimulus (L face; R face).

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