Research Report

PRIMING VISUAL FACE-PROCESSING MECHANISMS:
Electrophysiological Evidence

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Abstract—*Accumulated evidence from electrophysiology and neuroimaging suggests that face perception involves extrastriate visual mechanisms specialized in processing physiognomic features and building a perceptual representation that is categorically distinct and can be identified by face-recognition units. In the present experiment, we recorded event-related brain potentials in order to explore possible contextual influences on the activity of this perceptual mechanism. Subjects were first exposed to pairs of small shapes, which did not elicit any face-specific brain activity. The same stimuli, however, elicited face-specific brain activity after subjects saw them embedded in schematic faces, which probably primed the subjects to interpret the shapes as schematic eyes. No face-specific activity was observed when objects rather than faces were used to form the context. We conclude that the activity of face-specific extrastriate perceptual mechanisms can be modulated by contextual constraints that determine the significance of the visual input.*

Single-unit recordings in animals (Bruce, Desimone, & Gross, 1981; Desimone, Albright, Gross, & Bruce, 1984; Perrett, Rolls, & Caan, 1982; Young & Yamane, 1992), neuroimaging studies using positron emission tomography (PET; Sergent, Ohta, & MacDonald, 1992) or functional magnetic resonance imaging (fMRI; Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997), and intracranial recordings of event-related potentials (ERPs) in humans (Allison, Puce, Spencer, & McCarthy, 1999; McCarthy, Puce, Belger, & Allison, 1999; Puce, Allison, & McCarthy, 1999) have shown that faces elicit specific brain responses from relatively well-defined areas in the extrastriate regions of the visual cortex. Scalp-recorded ERPs in humans have extended the electrophysiological findings, revealing a face-specific negative component that peaks between 150 and 180 ms from stimulus onset (N170), is distributed over posterior temporal regions, and is larger at right- than at left-hemisphere sites (Bentin, Allison, Puce, Perez, & McCarthy, 1996; George, Evans, Fiori, Davidoff, & Renault, 1996). Because the N170 is not sensitive to face familiarity (Bentin & Deouell, 2000), it is probably associated with a precategorical structural-encoding mechanism responsible for the formation of the visual representation of a face, prior to its within-category identification.

Although this structural mechanism is selectively triggered by faces or face components,[1] recent studies have suggested that the scope of this specificity is quite wide: Schematically drawn human faces (such as a "smiley" face) are sufficient to elicit the face-specific N170 at the scalp (Sagiv & Bentin, 2001), as well as its intracranially recorded analogue, the N200 (Allison et al., 1999). A similar trend has been observed in neuroimaging studies: fMRI has identified regions in the middle fusiform gyrus in which the activity elicited by schematic faces (contrasted with the activity elicited by drawings of objects) overlaps with the activity elicited by photographs of natural faces (contrasted with the activity elicited by photographs of objects; Bentin, Mecklinger, Bosch, Sagiv, & von Cramon, 1999). These data suggest that the face-specific structural-encoding mechanism can adapt itself to process novel stimuli if they convey physiognomic information. How flexible is this adaptation ability? Can a face-specific structural-encoding process be induced by contextual information?

One way of addressing these questions is to teach the visual system to detect physiognomic features in stimuli that do not normally (or easily) convey such information. For instance, Dolan et al. (1997) showed that visual stimuli did, or did not, activate face-specific areas in the fusiform gyrus depending on whether the subject was, or was not, trained to detect a face in a visually masked display. These results suggest that perceptual learning involves a direct interaction between content-specific visual mechanisms, spatial-attention and feature-binding mechanisms. However, because the faces had actually been presented in that study, these results cannot tell whether priming can induce face-specific structural encoding of stimuli that normally do not activate face areas. We examined the latter question by recording ERPs elicited by visual symbols that, primed by a face context, could be interpreted as portraying eyes.

Previous studies have demonstrated that a robust N170 can be elicited by eyes isolated from photographs of natural faces (Bentin et al., 1996). However, whereas natural eyes are unequivocally perceived as a face component, even in isolation, sketched schematic eyes (e.g., two "+" symbols presented slightly apart on a horizontal axis) bear no physiognomic information outside the schematic face context. Indeed, subjects did not recognize schematic eyes as face components when these stimuli were presented outside the context of a schematic face. In the present study, we used this difference between the perception of schematic and natural eyes to examine whether induction of a face context may trigger face-specific activity during processing of stimuli that are not normally perceived as face components.

METHOD

Participants

The participants were 36 undergraduates from the Hebrew University, Jerusalem, Israel, who participated for payment or credit toward a course requirement. Among them, 18 participated in the experimental

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1. Several authors have demonstrated that the face-specific brain areas can be invoked to process other stimulus categories for which the viewer has acquired expertise with within-category item discrimination (e.g., Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Tanaka & Curran, 2001). Such findings, however, are not evidence against the hypothesis that domain-specificity in processing faces is a natural characteristic of the visual system.

group and 18 in a control group. They were all right-handed and had normal or corrected-to-normal vision.
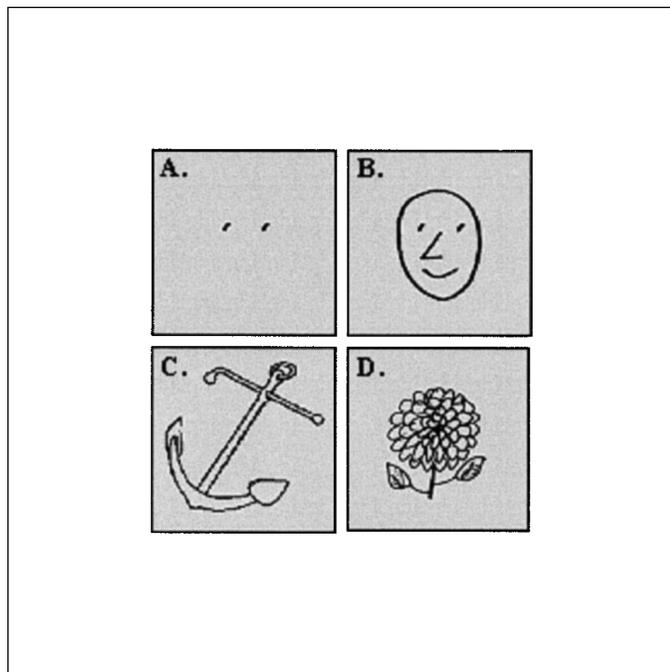
Stimuli

The stimuli were schematic black-and-white drawings of 64 faces, 64 objects (Snodgrass & Vanderwart, 1980), 64 pairs of small undefined unidimensional shapes (the "eyes" used in the schematic faces), and 36 schematic drawings of flowers (see examples of the stimuli in Fig. 1).

Task and Design

ERPs were recorded in four successive experimental blocks. A block comprised 8 to 10 trials that each presented a different flower and 64 trials in each of which a different exemplar from one of the other stimulus categories was presented. The participants were instructed to silently count target trials in which schematically drawn flowers were presented, while ignoring the other stimuli. The ERPs of interest, however, were those elicited by stimuli presented in nontarget trials.

The first and the third blocks were identical, each presenting the various pairs of schematic eyes. The two shapes in a pair were horizontally separated from one another by about 1.7° (3 cm). The second block was designed to prime the perception of the stimuli in Block 3 either as eyes in a schematic face (in the experimental group) or as objects (in the control group). The face context was induced by intercalating each pair of line shapes inside an oval contour and adding more lines to represent a schematic nose and mouth. The nonface context was induced by presenting the 64 inanimate object drawings. In a

Fig. 1. Examples of stimuli used in this study: isolated schematic eyes used in Blocks 1 and 3 (a), a smiley face presented in Block 2 to the experimental group (b), an object presented in Block 2 to the control group (c), and flowers (d), the targets monitored by the participants in both groups.

fourth block presented to both groups, the 64 schematic eyes and 64 schematic faces were mixed. One purpose of this block was to examine whether with schematic illustrations the N170 elicited by eyes would be larger than the N170 elicited by full faces, as had been previously found mixing photographs of natural eyes and faces (Bentin et al., 1996). In addition, this block provided ERPs in response to schematic faces in the control group.

Procedure

The experiment was run in a Faradically isolated and sound-attenuated chamber. After the ElectroCap was mounted (see the next paragraph), the four blocks were presented in a fixed sequence with about a 2-min interval between blocks. Within a block the stimuli were randomized. They were presented at gaze fixation with an interstimulus interval that varied randomly between 650 and 750 ms. The stimulus exposure time was 350 ms.

Recording Procedures

Electroencephalogram (EEG) was recorded continuously via 48 electrodes mounted on a custom-made cap (ElectroCap International, Eaton, Ohio; see Fig. 2c), sampled at a rate of 250 Hz, amplified by a factor of 20,000 with an analog band-pass filter of 0.01 Hz to 30 Hz, and stored for off-line analysis. Electro-oculogram (EOG) was recorded with two electrodes, one located at the outer canthus of the right eye and the other at the infraorbital region of the same eye. An electrode on the tip of the nose was used as common reference for both EEG and EOG recordings.

ERPs resulted from averaging epochs starting 100 ms before and ending 900 ms after stimulus onset. Epochs with EEG or EOG exceeding ±100 μV were excluded from the averaging. The remaining epochs were averaged separately for each stimulus type. The baseline was adjusted by subtracting the mean amplitude of the prestimulus period of each ERP from all the data points in the epoch.

RESULTS

ERPs elicited by nontarget stimuli in each block were assessed by averaging the EEG recorded in all of the nontarget trials uncontaminated by eye movements or blinks (never fewer than 45 trials per condition). In all subjects, schematic faces elicited a pronounced N170 clearly distinguishable from the ERP elicited by objects in the same latency range. In contrast, the ERPs elicited by the schematic eyes in the first block were similar to those elicited by objects. In the third block, however, following priming, the ERPs elicited by the schematic eyes were different in the experimental and the control groups. In the experimental group, after participants had seen full schematic faces (in Block 2), the ERPs elicited by isolated schematic eyes (in Block 3) included an N170 that was very similar to that elicited by full faces (Fig. 2a). In contrast, in the control group, after participants had seen objects (in Block 2), the ERPs elicited by isolated schematic eyes (in Block 3) were very similar to those elicited by the same stimuli before priming (in Block 1) and different from the ERPs elicited by schematic faces (in Block 4; Fig. 2b).

The reliability of this pattern was assessed by analyses of variance run separately in each group, with stimulus condition (experimental group: schematic eyes in Block 1, faces in Block 2, schematic eyes in Block 3; control group: schematic eyes in Block 1, objects in Block 2,

Priming Visual Face-Processing Mechanisms
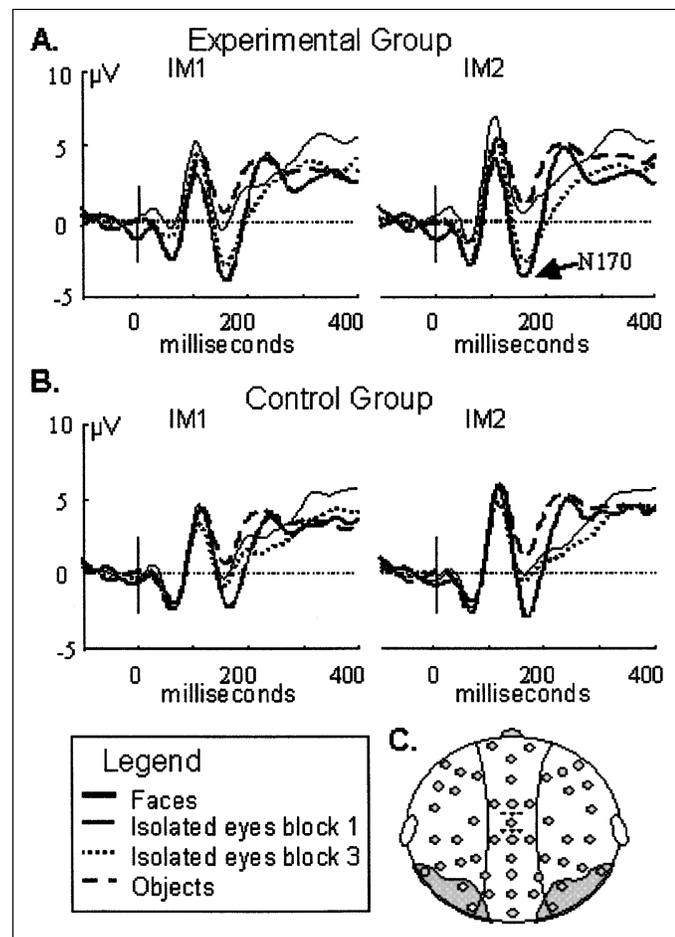
Fig. 2. Event-related potentials (ERPs) elicited at the posterior inferior temporal scalp locations IM1 and IM2 (see recording sites in c) by schematic eyes before and after priming, compared with the ERPs elicited by schematic faces and by objects, in the experimental (a) and control (b) groups.

schematic eyes in Block 3, faces in Block 4), hemisphere, and site as independent variables. The dependent variable was the amplitude of the N170 recorded at three posterior temporal sites (right and left mastoid, PO8 and PO7, and IM2 and IM1; see shaded area in Fig. 2c). These sites were selected a priori and, indeed, in the present study as well as in previous studies, these were the sites at which the face-specificity of the N170 was most conspicuous.

In both the experimental and the control groups, the stimulus condition had a significant effect, $F(2, 34) = 13.8$, $p < .0001$, and $F(3, 51) = 6.7$, $p < .001$, for the experimental and control groups, respectively. Post hoc univariate exploration of this effect, however, revealed important differences between the two groups. In the experimental group, the amplitude of the N170 elicited by schematic eyes before priming (-1.43 μV) was significantly smaller than the amplitude of the N170 elicited by the same stimuli after priming (-4.3 μV), $F(1, 17) = 17.6$, $p < .001$. The latter amplitude did not differ from that of the N170 elicited by full schematic faces in Block 2 (-5.0 μV), $F(1, 17) = 1.4$, n.s. In contrast, in the control group, the negative deflections elicited by schematic eyes in Blocks 1 and 3 were similar (-3.2

μV and -3.0 μV, respectively), $F(1, 17) < 1.0$. These negative deflections were not significantly different from those elicited by objects (-1.3 μV), $F(1, 17) = 3.1$, n.s., but they were significantly smaller than the N170 elicited by schematic faces in Block 4 (-5.2 μV), $F(1, 17) = 15.7$, $p < .001$.

DISCUSSION

The enhancement of N170 amplitude elicited by isolated schematic eyes after they were seen as part of a face, in contrast to the absence of any change from Block 1 to Block 3 when nonface objects were presented in Block 2, implies that the enhancement of the N170 in the experimental group was induced by priming perceptual processes rather than by pure stimulus repetition. Furthermore, the similarity between the N170 elicited in the experimental group by isolated eyes (in Block 3) and that elicited by full faces, together with findings demonstrating the specificity of the N170 to the processing of schematic faces (as well as natural faces; see, e.g., Sagiv & Bentin, 2001), suggests that, following priming, these stimuli elicited face-specific neural activity.

A plausible account for this pattern is that the faces presented in Block 2 provided a perceptual context that was sufficient to bias the interpretation of the undefined meaning of these stimuli. In other words, seeing faces in Block 2 might have suggested a physiognomic meaning (eyes) for the visual patterns seen in Block 1, and this interpretation may have been sufficient to trigger face-specific activity when these stimuli were seen again. Indeed, before priming, the ERPs elicited by the undefined visual patterns were indistinguishable from the ERPs elicited by other objects. Overall, this outcome suggests that the activation of the face-specific processes in the extrastriate visual system depends not only on the existence of predetermined visual cues in the display, but also on the interpretation of the stimuli by the perceiver.

Two types of mechanisms can account for this priming effect. The first is top-down conceptual influence on the formation of mental representations based on visual input. According to this account, facing categorically undefined (but structured) stimuli in the first block, the subjects used general perceptual mechanisms to process their shape. However, interpreted as eyes, these stimuli triggered face-specific perceptual processes in Block 3, as indeed naturally looking eyes presented in isolation elicit face-specific activity (Bentin et al., 1996; Tong, Nakayama, Moscovitch, Weinrib, & Kanwisher, 2000). The second mechanism that could account for the priming effect is based on perceptual (rather than conceptual) priming. If the neurons activated by the undefined shapes are linked to various object networks (faces included), before priming any of these networks (or none) could have been activated with equal probability. According to this account, the links between these neurons and those involved in forming face representations were reinforced by repeated co-occurrence during the priming block. Consequently, when the stimuli were presented again, the probability of these neurons activating face-specific networks was higher.[2]

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2. Note that this interpretation is based on the assumption that the schematic eyes were undefined before a meaningful context was induced. A different question concerns perceptual priorities. Would interpretable stimuli (say, small basketballs, or indeed any other objects) presented small enough to occupy the location of the eyes in a schematic face also be able to induce face-specific activity in similar circumstances? Future studies should address this question.

The present data cannot unequivocally determine whether the priming effect observed here had a conceptual or a perceptual origin. A more recent experiment (reported by Bentin, Goland, & Graber, 2000), however, suggests that the conceptual priming alternative is more likely. In that experiment, we found that simply telling subjects that these patterns were schematic eyes was sufficient to elicit an N170 already in Block 1, with no further change after exposure to faces. These results indicate that face-specific visual mechanisms can be activated without any perceptual manipulation, by conceptually biasing the system to categorize indefinite stimuli as eyes. Support for the conceptual origin for this effect is provided also by the demonstration of an inverse effect: Simple face repetition (i.e., perceptual priming) reduces the amplitude of the intracranial N200 (Puce et al., 1997).

The results reported here suggest a parallel between perceptual modules in audition and vision. The fact that speech perception can be induced using sinusoidal replicas of naturally produced utterances (Remez, Rubin, Pisoni, & Carrell, 1981) shows that, if trained, the phonetic module can be activated by stimuli that do not contain traditional speech cues. This plasticity may represent a general characteristic of content-specific perceptual modules.

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