Research Article

The Speed of Individual Face Categorization

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ABSTRACT—How fast does the human visual system discriminate individual faces? To address this question, we used a continuous-stimulation paradigm in which eventrelated potentials (ERPs) to a face stimulus are recorded with respect to another face stimulus, rather than to a preceding blank-screen baseline epoch. Following the shift between two face stimuli, posterior sites showed an early negative ERP deflection that started at 130 ms and peaked at 160 ms, the latency of the N170, an ERP component associated with discriminating faces from objects. The ERP we recorded was larger in amplitude when the preceding stimulus was perceived as a different individual face rather than the same individual face, although face pairs were of equal physical distance in the two conditions. These findings provide direct evidence that individual face discrimination in humans can take place as early as 130 ms following stimulus onset, during the same time window as face detection.

The human visual system is exceedingly efficient and fast both in detecting isolated faces among objects from other categories or embedded in a visual scene (Lewis & Edmonds, 2003; Rousselet, Macé, & Fabre-Thorpe, 2004) and in discriminating individual faces from each other (Tanaka, 2001). However, the relative speed at which face detection and individual face discrimination take place is still a matter of debate. In humans, this question has been addressed mainly by recording event-related potentials (ERPs) on the scalp, a method that allows one to track the time course of perceptual, cognitive, and motor processes with an excellent temporal resolution (see Handy, 2004). ERP studies have disclosed that following the presentation of a face stimulus, an early face-sensitive component starts at about 130 ms over occipito-temporal scalp regions and peaks at around 170 ms (the N170; e.g., Bentin, McCarthy, Perez, Puce, & Allison, 1996; Itier & Taylor, 2004; Rossion et al., 2000; Rousselet et al., 2004). The N170 is systematically larger in amplitude than the negative component elicited at the same latency in response to other object categories (e.g., Bentin et al., 1996; Itier & Taylor, 2004; Rossion et al., 2000; Rousselet et al., 2004). Several ERP studies have failed to identify any differential activity between distinct faces at the level of the N170 (e.g., Bentin & Deouell, 2000; Ito, Thompson, & Cacioppo, 2004; Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002). This absence of sensitivity to individual faces has been taken as evidence that the N170 indexes a face-detection stage that acts on basic physiognomic features to discriminate faces from other kinds of objects, and thus precedes individual face discrimination, which takes place much later (about 250 ms following stimulus onset; see Bentin & Deouell, 2000; Eimer, 2000; Schweinberger et al., 2002).

However, this proposal is at odds with recent behavioral evidence showing that, at least for foveal presentation, individual face discrimination can be as fast as face detection (Tanaka, 2001). Most important, single-cell recording studies in the monkey brain suggest that individual faces can be discriminated during the first 150 ms following stimulus onset. In the monkey inferior temporal cortex (IT), neurons responding preferentially to faces (e.g., Perrett, Rolls, & Caan, 1982; Rolls, 1992) discharge with different spike rates to distinct faces, allowing encoding of information useful for identifying individual faces in a sparsely distributed network (Baylis, Rolls, & Leonard, 1985; Rolls & Tovee, 1995; Young & Yamane, 1992). These neurons start responding at a latency of about 80 to 130 ms after stimulus onset (Bullier, 2001), and individual face selectivity arises early in their response (Rolls, Tovee, & Panzeri, 1999; Tovee & Rolls, 1995). Even taking into account the differential speed of visual processing in the visual systems of humans and monkeys, these latencies suggest that individual face discrimination is achieved in humans at around 150 ms.

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How can these observations at the single-cell level be reconciled with the absence of sensitivity to individual faces in the time window of the N170? This discrepancy can be better understood if one considers that the amplitude of the N170 recorded on the scalp reflects the global (postsynaptic) activity of synchronized populations of neurons. However, in high-level visual areas of the temporal lobe, different face stimuli may be coded by differential distributions of activity in neural populations (i.e., population coding; Rolls, 1992; Rolls & Tovee, 1995), rather than by different levels of activity at the population level. Accordingly, the increase of activity in response to one face stimuli in a population of cells will be reflected on the scalp, or on the cortical surface (Allison, Puce, Spencer, & McCarthy, 1999), by the same voltage amplitude as the increase for another face stimulus. To put it differently, even though different faces may be associated with qualitatively different patterns of activity in a local distributed network at this latency, they will most likely give rise to equally large field potentials on the scalp, with a similar topography.

To investigate this issue, we used an ERP paradigm in which different individual face stimuli were alternated continuously, that is, without the presentation of a baseline epoch between events. When a face stimulus is presented following such a baseline epoch (e.g., a blank screen), the visual potentials elicited reflect the onset of the synchronized neural activity in the whole visual system. In contrast, we hypothesized that following an immediate shift from face A to face B, visual potentials recorded on the scalp will reflect only the difference in the distribution of activity in the network of neurons coding for the two facial identities. The onset latency of the earliest potential elicited will thus provide information about the time course of individual face discrimination, and this latency should be compatible with the timing of single-cell discharges in IT (100–150 ms).

To control for minor low-level visual changes between alternating face stimuli, we used the phenomenon of categorical perception (Harnad, 1987), which has been observed for multidimensional stimuli such as familiar (e.g., Beale & Keil, 1995) and unfamiliar (Levin & Beale, 2000) faces. Pairs of faces were morphed, and synthetic faces that were equally spaced apart were extracted from each morphed continuum. To ensure that the morphed continua were perceived categorically, we conducted a behavioral experiment. In the ERP experiment, we compared ERPs evoked by a face stimulus when it was preceded by a different face stimulus that was perceived as having the same identity and when it was preceded by a different face stimulus that was perceived as having a different identity. The physical distance between the successive faces was equal in the two cases. We hypothesized that the earliest ERP response would be larger when the preceding face stimulus was perceived as having a different identity than when it was perceived as having the same identity.

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METHOD

Subjects

Sixteen subjects (12 females, 1 left-handed, mean age = 22.5 ± 4.29 years) volunteered to participate in the ERP experiment and received cash as compensation. An additional set of 14 subjects (10 females, 2 left-handed, mean age = 20.5 ± 1.95 years) participated in the behavioral experiment for course credit. All subjects had normal or corrected-to-normal vision.

Stimuli

Digital photographs of 10 faces without glasses, facial hair, or makeup were taken as base images. The faces were full-front views of 6 Caucasian males and 4 Caucasian females with neutral expressions. They were cropped using Adobe[®] Photoshop[®] 4.0 to remove hair, backgrounds, and everything below the chin. Faces were paired in order to generate five continua (three male and two female) using morphing software (Morph[™]) that, given any two images as endpoints, can produce a linear continuum of images between the two end images (see, e.g., Beale & Keil, 1995). For each face pair, around 100 to 130 control points were used. The points were placed on all salient features of the face: contour (\sim 45 points), mouth (\sim 15 points), eyes (~11 points each), eyebrows (5 points each), and nose (~ 20 points). Faces within each pair were equated in mean luminance before they were morphed. For the ERP experiment, we extracted from each continuum 3 images: 95% of face A (5% of face B), 65%A (35%B), and 35%A (65%B); thus, there were 15 different stimuli in total. For the behavioral experiment, we extracted from each continuum 11 images, ranging from 100%A (0%B) to 0%A (100%B) in 10% steps (Fig. 1). Stimuli were shown in full color and subtended an approximate size of $150 \times$ 200 pixels at a resolution of 72 dpi.

Procedure for the ERP Experiment

After electrode placement, subjects were seated on a comfortable chair facing a computer monitor in a light- and sound-attenuated room. They were told to fixate the center of the monitor, where face stimuli were presented against a neutral gray background. Viewing distance was 100 cm, and stimuli subtended $3.8^{\circ} \times 2.7^{\circ}$ of visual angle. Stimuli were displayed using E-prime 1.1 (Psychology Software Tools, Inc., Pittsburgh, PA). Subjects performed 20 blocks of 33 trials. In each block, two face stimuli (taken from a single face pair) were used: either a between-identity pair of faces (65% A paired with 35% A) or a within-identity pair (65%A paired with 95%A). In this continuous-presentation mode, the two face stimuli were presented alternately, without any blank screen interleaved between the faces, each face replacing the previous one at exactly the same location. Stimulus onset asynchrony thus was equal to the stimulus duration, which was approximately 600 ms (randomized between 500 and 700 ms). An average stimulus duration of



Fig. 1. Examples of the stimuli and behavioral results. The graph shows the percentage of faces that were identified as face B in the behavioral experiment, as a function of position on the morphed continuum (percentage of face A); the small faces at the bottom of the graph are taken from one of the continuu used in that experiment. Error bars represent standard errors of the mean. The larger faces at the bottom of the figure illustrate the pairs used in the within- and between-identity conditions of the event-related potential (ERP) experiment; the perceptual distance between faces within a pair can be determined by comparing their positions on the response function.

600 ms was chosen because it allowed us to record many trials rapidly, whereas a faster presentation rate would likely have caused an overlap of components elicited by consecutive trials. Each continuum was presented twice per condition (withinidentity and between-identity), and block order was randomized across subjects. To ensure that subjects paid attention to the face stimuli, we had them silently count the number of trials during which a grayscale face appeared. The number of gray-scale faces in each block (zero, one, or two), as well as their temporal location within the blocks, was randomized. Every four blocks, subjects had to report the number of gray-scale faces they had detected during the last four blocks. Trials on which gray-scale faces were displayed and trials immediately following a gray-scale face were not included in the ERP analyses. Subjects performed at ceiling on this counting task.

Behavioral Pilot Experiment

This experiment was conducted to confirm that the face continua were perceived in a categorical fashion. Subjects performed 15 blocks of 22 trials, each of the 11 morphed faces of a given continuum being presented twice per block in a random order. Morphed faces were presented one at a time at the center of the computer monitor for 700 ms, while the endpoint faces remained on the right and left sides of the monitor throughout the block. Subjects performed a two-alternative forced-choice categorization task, categorizing each morphed face as being closer to one of the two endpoints of the continuum. Results from this experiment (Fig. 1) showed that the identity boundary was located roughly at the middle point of the continua on average, and that between-identity pairs (65%A paired with 35%A) were perceived as being more distinct than within-identity pairs (95%A paired with 65%A). Moreover, the response profile displayed a steplike function, consistent with categorical perception of identity (Harnad, 1987).

Electroencephalogram (EEG) Recording

Scalp EEG was recorded from 58 tin electrodes, mounted in an electrode cap (QuikCap, Neuroscan Inc., El Paso, TX). Electrode positions included the standard locations in the 10–20 system, as well as additional intermediate positions. Vertical and horizontal eye movements were monitored using 4 additional electrodes, placed above and below the left orbit and on the outer canthus of each eye. During EEG recording, all electrodes were referenced to the left earlobe, and electrode impedances were kept below 10 k Ω . EEG analog signal was digitized at a 1000-Hz sampling rate. Subjects were instructed to refrain from blinking during stimulus presentation.

ERP Analyses

EEG data were analyzed using EEprobe 3.1 (ANT, Inc., Enschede, The Netherlands) running on Red Hat Linux 7.0. The EEG was filtered with a digital 30-Hz low-pass filter, with cutoff frequencies of 29 Hz and a stop-band attenuation of -63.5 dB (50 Hz and above). Epochs in which the standard deviation of



Fig. 2. Grand-average event-related potential (ERP) responses to the first and alternated faces. The graphs in (a) present the ERPs recorded at two occipito-temporal electrodes (PO7 and PO8); the waveforms elicited by the onset of the first face of each block and by the onset of alternated faces in the continuous-presentation mode are shown. The scalp topographies (b; back view of the head) depict the distribution of ERP response at 160 ms following the onset of the first face of each block (left) or the alternated 65% A faces (right).

the EEG on any electrode within a sliding 200-ms time window exceeded 35 μ V were removed. The first three trials of each block were not considered in the averages in order to avoid contamination from ERPs related to the onset of the first stimulus of the block. The mean number of trials analyzed was 127 (\pm 10) for each subject in each condition. For each subject, EEG epochs centered around stimulus switch were averaged for each condition separately and baseline corrected using the 200 ms before the stimulus switch. Subject averages were rereferenced to a linked earlobe reference and high-pass filtered at 0.1 Hz.

We analyzed ERP response to the 65%A faces only, the critical distinction between the two conditions being that the 65% A face was preceded by a same-identity face (95% A) in the within-identity condition and by a different-identity face (35%A) in the between-identity condition. Therefore, these analyses compared the ERP response to the very same images in the within- and between-identity conditions, physical distance between alternating faces (30% along the morph continua) being rigorously identical in the two conditions. Analyses included data from 17 electrodes located in the posterior region of the scalp, where the ERP of interest was maximal in amplitude. Peak amplitude and latency were extracted automatically at the minimum value in a 125- to 190-ms time window over each electrode site. Amplitude and latency values were then pooled together according to the location of the electrodes: left (7 electrodes-P7, P07, P5, P05, P3, P03, O1), right (7 electrodes Oz, POz, Pz). Repeated measures analyses of variance (ANOVAs) with factors of condition (within-identity vs. between-identity) and electrode site (left vs. right vs. midline) were then computed on these averaged peak amplitude and latency values.

RESULTS

Following the onset of a face stimulus in the continuous-presentation mode, we observed a negative component that was broadly distributed across posterior electrodes (Fig. 2b; for comparison, the figure also depicts the scalp distribution of the N170 component elicited by the onset of the first face stimulus of each block). The latency of this component was highly similar to that of the N170 elicited by the onset of the first face stimulus of each block (Fig. 2a).

Grand-average ERPs elicited by the 65%A face preceded either by a 95%A face (within-identity condition) or by a 35%A face (between-identity condition) are depicted in Figure 3. Analyses of peak amplitude revealed a main effect of condition, F(1, 15) = 7.38, $p_{\rm rep} = .94$, $\eta^2 = .33$, the between-identity condition eliciting a larger peak amplitude than the within-identity condition. The interaction between condition and electrode site was not significant, F(2, 30) = 1.12, $p_{\rm rep} = .62$, $\eta^2 = .07$.

On average, the latency of this component was approximately 160 ms for the left and right electrode sites and 155 ms for midline electrode sites. Analyses of peak latency did not reveal a significant difference between conditions, F(1, 15) = 1.17, $p_{\rm rep} = .65$, $\eta^2 = .07$, or an interaction between condition and electrode site, F(2, 30) = 1.126, $p_{\rm rep} = .62$, $\eta^2 = .07$.

In addition to the amplitude and latency analyses, we computed point-by-point t tests (df = 15) on the ERP waveforms for the left and right electrode sites between 0 and 800 ms. We considered an effect to be significant if 15 consecutive t values were below the p < .05 level. This analysis (e.g., Thorpe, Fize, & Marlot, 1996) allowed us to determine when change in facial identity was detected—at 120 ms in the left hemisphere and at 130 ms in the right hemisphere. The waveforms remained significantly below zero until around 190 ms in the two hemispheres.

DISCUSSION

Following the onset of an individual face in a continuous train of alternating presentations, an early negative ERP component peaked around 160 ms over posterior scalp regions. As expected given that low-level stimulation (i.e., luminance, contrast, spatial frequencies) remained roughly constant throughout each



Fig. 3. Grand-average event-related potentials (ERPs) elicited by the within- and between-identity conditions at the left, midline, and right pooled electrode sites.

block of alternating faces, earlier visual potentials (e.g., C1, P1) associated with striate and extrastriate cortical activity (e.g., Clark, Fan, & Hillyard, 1995) were not observed on the scalp. Accordingly, the activity of cells in V1 and early extrastriate visual areas must have been largely sustained during each block of stimulation, and thus not reflected in the cortical ERP recordings, which are thought to be able to "monitor ... abrupt changes in sensory input ... [but not to] record the stable state" (Naatanen & Picton, 1987, p. 387). These abrupt sensory-onset responses may arise either because of the activation of neural systems responding specifically to the onset of stimulation (e.g., face-cell networks in IT) or because only at stimulus onset is the neural response synchronized enough to generate a recordable field potential (Naatanen & Picton, 1987).

The scalp potential related to individual face discrimination is smaller in amplitude than a classical N170, but has a noticeably similar onset and peak latency. Its topographic scalp distribution largely overlaps with that of the N170, although it peaks more dorsally than a classical N170. In humans, multiple nonretinotopic visual areas have been shown to respond more to faces than to other objects (Haxby, Hoffman, & Gobbini, 2000), and these areas may contribute to the generation of the N170. More precisely, evidence from electrophysiological studies and source localization of the scalp N170 (e.g., Itier & Taylor, 2004; Rossion, Joyce, Cottrell, & Tarr, 2003), intracranial recordings of field potentials (e.g., Allison et al., 1999), and combination of EEG and functional magnetic resonance imaging data (Henson et al., 2003) suggest that the N170 originates from a network of occipital and temporal regions including the middle fusiform gyrus, the inferior occipital cortex, the superior temporal sulcus (STS), and the inferior, middle, and superior temporal gyri. These localizations largely overlap with regions where facesensitive activations have been described in neuroimaging studies (see Haxby et al., 2000, for a review). Given its topography, the component recorded in response to individual face discrimination in the present study may arise from a subset of the sources contributing to the N170, perhaps with a larger contribution of sources located in the middle and superior part of the temporal lobe, that is, in the STS (see, e.g., Itier & Taylor, 2004).

The timing of individual face discrimination in humans as evidenced here is in agreement with the speed of processing in the human visual system (Thorpe et al., 1996) and with the temporal dynamics of neuronal responses involved in face identification in the monkey's IT. Single-cell recording studies using information theory (e.g., Rolls et al., 1999; Tovee & Rolls, 1995) have shown that in IT, the initial part of the neurons' response (20 to 50 ms from response onset) conveys a large amount of the information available in longer epochs (e.g., 400-ms epochs). This indicates that the ability of a population of faceselective neurons to discriminate between different individual faces emerges early in their response. Given that face-selective neurons in IT typically start firing from 80 to 130 ms after stimulus onset (Bullier, 2001), one can assume that in the time range of 100 to 200 ms after stimulus onset, sufficient information is available in the neurons' response to perform effective face identification (Sugase, Yamane, Ueno, & Kawano, 1999). This assumption is further supported by studies in which the response duration of face- or shape-selective IT neurons has been reduced (to about 30-70 ms) using backward visual masking with very short stimulus onset asynchrony (Kovacs, Vogels, & Orban, 1995; Rolls et al., 1999) or rapid serial visual presentation (Keysers, Xiao, Foldiak, & Perrett, 2001), thus enforcing very limited processing time. Although the withincategory selectivity of the recorded neurons was reduced during their brief response period, the response still contained significant information about stimulus identity. Under identical stimulation conditions, human and monkey observers were able to perform above-chance face or shape identification, which suggests that the information contained in the initial 30- to 70ms sample of the neurons' response is sufficient for identification.

As predicted by our hypotheses, the ERP response was enhanced when the different alternating faces crossed the perceptual identity boundary (between-identity trials, relative to within-identity trials), although the physical distance between the morphed faces was equal in the two conditions. Together with the fact that the onset time of this component and its topography are compatible with those of high-level visual processes, this observation rules out an interpretation of the amplitude difference in terms of low-level visual differences between alternating faces.

The larger ERP amplitude for between-identity trials relative to within-identity trials can be understood within the theoretical framework of categorical perception (Harnad, 1987). Categorical perception, which is common in the visual modality, refers to how individual observers organize and systematically reduce the visual input into distinct categories that can each be activated by any stimulus falling within the category boundary. In the face perception domain, such categories have been described as individual face representations, each characterized by its attractor field, defined as the range of face inputs that can activate it (Tanaka, Giles, Kremen, & Simon, 1998). As a consequence of categorical perception, a physically linear morphed continuum between two face identities is associated with a nonlinear, steplike continuum in the perceptual space, a continuum that goes from one face's attractor field to the other in a categorical manner. Information coding in the occipito-temporal cortex likely reflects such a nonlinear categorical organization of face representations. More precisely, in our experiment, faces in the within-identity condition fell within a single face's attractor field, whereas faces in the between-identity condition were captured by different attractor fields, which increased the perceptual distance between them. This coupling of a linear physical space with a nonlinear perceptual space was also revealed by the sigmoidal response profile observed in the behavioral experiment. At a physiological level, this categoricalperception effect could be reflected by a smaller overlap of neuronal activation to faces in the between-identity condition relative to faces in the within-identity condition; a smaller overlap of activation, in turn, would lead to a larger modification in the neural response pattern when shifting from one face to the other, and therefore to a larger recorded scalp potential. The present experiment is in line with previous studies indicating that categories in a perceptual space are mapped on the basis of both physical properties of the stimuli (e.g., visual statistics; Tanaka et al., 1998) and perceptual constraints (e.g., relevant diagnostic features distinguishing between categories; e.g., Freedman, Riesenhuber, Poggio, & Miller, 2003; Sigala & Logothetis, 2002).

A number of ERP studies have failed to identify any differential activity between distinct faces at the level of the N170 (e.g., Bentin & Deouell, 2000; Schweinberger et al., 2002). Some researchers (e.g., Bentin & Deouell, 2000) have taken this null effect as evidence that the N170 indexes a face-detection stage that acts on basic physiognomic features to discriminate faces from other object categories and that precedes withincategory discrimination, which occurs around 250 ms following stimulus onset. However, here we have shown that within-category discrimination of faces may occur as early as the onset of the N170, and thus in the same time range as the discrimination of faces from other object categories, at least for foveal presentations of front-view faces. This observation is in line with behavioral evidence (Tanaka, 2001), but also with a functional interpretation of the N170 as corresponding to a structural encoding stage that "capture[s] those aspects of the structure of a face essential to distinguish it from other faces" (Bruce & Young, 1986, p. 307).

Recent behavioral studies using short exposure durations of natural images have shown that perceptual categorization of objects can occur as quickly as object detection (Grill-Spector & Kanwisher, 2005), putting strong constraints on theories of object recognition and offering a tool to address the timing of object-processing stages. Similarly, the paradigm introduced here for human ERP studies may have a wide range of application that goes beyond the question of the timing of individual face discrimination. For instance, previous ERP studies have failed to disclose any modulation of the N170 by different facial expressions (e.g., Eimer & Holmes, 2002), leading researchers to conclude that facial expression is not coded during this time window. However, single-cell recording studies suggest that facial identity and facial expression are coded in partially distinct populations of cells in IT and the STS, discharging at about the same latency (Hasselmo, Rolls, & Baylis, 1989). This suggests that measuring ERPs to facial stimuli that change expression continuously and dynamically, rather than to static pictures that display different expressions and follow blank stimulation, may help clarify the time course of expression decoding in humans.

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