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Brain potential correlates of the ''internal features advantage'' in face recognition

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ABSTRACT

Whereas some behavioral studies have shown that internal features are crucial for efficient face recognition in healthy adults, compared to external features, the brain mechanisms underlying this ''internal features advantage'' are still unknown. In the present study, the differential relevance of both subsets of facial features is addressed analyzing N400-like potentials elicited in a face-feature matching task, where external or internal features and complete face targets were displayed consecutively in each trial. Experiment 1 revealed a larger and longer-lasting N400-like effect with the prior presentation of internal features, which suggests more efficient processing of long-term face-related information. An analysis of neural sources in Experiment 2 revealed greater activation of frontal and left temporal brain areas in the processing of mismatching targets when preceded by internal features. Thus, brain electrical correlates of the ''internal features advantage'' could be verified around 300-400 ms post-stimulus and supported by a face-identity related neural network.

1. Introduction

Recognizing faces becomes more efficient under certain circumstances. Priming studies have demonstrated that the recognition of an individual face can be largely facilitated (shorter reaction times, higher accuracy) by prior exposure to the same face even from a different view or when only some partial structural information (e.g. certain facial features) is provided to the perceiver (Bruce et al., 1998; Ellis et al., 1987; Ellis et al., 1997; Goshen-Gottstein and Ganel, 2000; Lander and Bruce, 2004; Pourtois et al., 2005). Over the last few decades behavioral studies have proposed that internal facial features (eyes, eyebrows, nose, cheeks and mouth), compared to external features (hairstyle and facial contour line), are especially relevant for the recognition of highly familiar faces (Brunas et al., 1990; Ellis et al., 1979; Young et al., 1985). This ''internal features advantage'' may be due to the inner facial components generally containing a larger and more consistent amount of information concerning the identity of a person and, importantly, visual signals involved in emotional expression and communication behaviors (Ellis et al., 1979; Shepherd et al., 1981). On the other hand, several cognitive developmental studies have found that the facial contour is relevant for face recognition in both infants and children (Campbell et al., 1995; Mondloch et al., 2002; Simion et al., 2001). Furthermore, recent clinical neuropsychological research has indicated that prosopagnosic patients are impaired in the perception and recognition of both internal and external facial regions (Caldara et al., 2005; Le Grand et al., 2006). These data suggest that both facial regions provide special sensorial inputs for the efficient processing of faces, however, to our knowledge, there is still no neurofunctional evidence regarding the specific function that such face parts might play in face recognition in adults.

From a broader theoretical framework, an electrophysiological approximation to the distinction between contour and internal parts processing in objects was recently carried out by Schendan and Kutas (2007a, b). In their studies, the role of contour *vs*. global shapes in object representation was assessed by comparing ERPs elicited by object images. Different memory conditions were analyzed in which contours between study and test differed (where one picture had lines its ''complementary'' picture at test had gaps) but the higher-order structure of the whole object did not. These authors reported a reduction on the early occipito–temporal P200 only when both study and test items were fragmented, which was considered a correlate of perceptual (grouping) processing (Schendan and Kutas, 2007b). In turn, a fronto-central N350 (similar repetition effects in all experimental conditions) was related to object model selection and implicit memory system engagement (Schendan and Kutas, 2007a). The ERP data from the latter study indicated that the all-inclusive global shapes were reactivated and influenced processing during the N350. It was considered a locus for higher-order neural computations involving recurrent and feedback interactions within several brain perceptual areas and with other anterior areas, such as the ventro-lateral prefrontal cortex. To date, there is no comparable ERP evidence specifically concerning face

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processing to understand the spatio-temporal brain dynamic underlying the "internal features advantage" for efficient face recognition.

To advance in this area, in the present study we aimed to characterize the electrophysiological neurocognitive responses accounting for the differential role of external and internal facial features in familiar (famous) face recognition by analyzing long-latency ERPs. Of special interest here are the N400-like components; negative deflections arising between 250 and 500 ms after semantic incongruities in language studies (Kutas and Hillyard, 1980), which have generally been considered markers of the ease or difficulty with which information can be retrieved from long-term memory. Indeed, larger N400 amplitudes have been observed with unexpected items which are preceded by stronger contextual constraints (Kutas and Hillyard, 1980; Kutas and Federmeier, 2000; Van Petten and Luka, 2006). Moreover, the "knowledge inhibition hypothesis" (Debruille, 2007) suggests that N400 amplitude is proportional to the amount of information that is inhibited and to the strength of its previous activation: the stronger the previous activation, the greater the required inhibition and the greater the N400 amplitude elicited by unexpected or inappropriate targets.

With regard to face recognition, in previous studies the greatest N400-like amplitude, elicited by mismatching face targets in identity and face-feature matching tasks (see for example Barrett et al., 1988; Barrett and Rugg, 1989; Debruille et al., 1996; Jemel et al., 1999; Mnatsakanian and Tarkka, 2003; Olivares et al., 1999; Olivares et al., 2003) has been interpreted as reflecting a lack of association between the eliciting item and the preceding context, in relation to the processing and the retrieval of stored information of familiar or previously learned faces. In the same way that classic N400 has been considered a measure of verbal stimuli's unexpectedness (Kutas and Hillyard, 1980), face-elicited N400s are thought to reflect expectancy violations in a non-linguistic domain (Bobes et al., 1994; Olivares et al., 1994). Thus, in the case of facial stimuli "contextual" faces or face parts presented at the beginning of the trial as perceptual cues are thought to create expectancies about the remainder of trial stimuli, leading to the activation of structural (perceptual) and semantic memory representations concerning knowledge about individuals. The subsequent arrival of an unexpected/incongruent target is argued to generate a representation different from the pre-activated ones, eliciting the N400-like negativities found. These negativities might be functionally analogous to the N350 cited above, indicative of higher-order neural subroutines regarding the activation of structural descriptions for objects (Schendan and Kutas, 2007a, b).

Taking account of the findings derived from behavioral studies in healthy adults, we hypothesized that prior presentation of internal facial features, compared to external ones, facilitates the access and retrieval of face-related information of known individuals and creates a highly constrained but rich context for individuation that strongly favors the processing of "correct" items in subsequent facial stimuli. In Experiment 1, which was carried out with a large number of participants and 20 recording sites, our main aim was to define the electrophysiological profiles supporting the "internal features advantage". Thus, we expected to find the most pronounced ERP amplitude differences between matching (facilitated) and mismatching (non-facilitated) identity faces when the internal features were those presented initially in the trial. Considering the data related to the ERP studies mentioned above concerning incongruity effects in familiar face processing, this difference may be reflected in the waveforms by an enhanced negativity around 300-500 ms post-stimulus associated with mismatching faces (compared to matching ones) preceded by internal features.

In Experiment 2 the same task was presented to a different group of participants but using high-density recordings to search for the neural generators involved in the processing of both complete face targets and preceding external and internal facial features. Brain sources that support face processing in humans have been more frequently located in occipital-temporal brain areas, encompassing the lateral fusiform and inferior temporal gyri and the region of the superior temporal sulcus, as pointed out, among others, by both intracranial recordings and neuroimaging studies in healthy and brain damaged individuals (Allison et al., 1999; Barbeau et al., 2008; Clark et al., 1996; Clarke et al., 1997; Dubois et al., 1999; Kanwisher et al., 1997; Ishai, 2008; Gobbini and Haxby, 2007). These areas appear to be more implicated in perceptual-structural processing whereas anterior temporal and left inferior parietal (around posterior superior temporal gyrus) regions have been related more to access to verbal-semantic and multi-sensorial contents associated with facial representations, respectively (Gorno-Tempini et al., 1998; Leveroni et al., 2000; Joassin et al., 2004). Moreover, several studies with non-human primates and humans using different methodological approaches have reported certain involvement of bilateral frontal regions in face processing (Barbeau et al., 2008; Campanella et al., 2001; Joassin et al., 2004; Katanoda et al., 2000; Leveroni et al., 2000; Marinkovic et al., 2000; Schalaide et al., 1997), suggesting a likely contribution of higher-order operations linked to complex memory processes and task-decision selection. In the present study, the role of internal features for a more efficient facial recognition could be reflected, in trials in which such features are initially presented, in the recruitment of a large-scale neural network including high-level perceptual processing areas for faces, but also those more anterior areas related to the access and retrieval of more complex information (including verbal-semantic) associated with face representations.

2. Experiment 1: N400-like effects reveal the "internal features advantage" for familiar face processing

2.1. Methods

2.1.1. Participants

Thirty-eight right-handed volunteer healthy university students (mean age: 21.8 years, 29 females) participated in this study. All had normal or corrected-to-normal vision and gave their written informed consent.

2.1.2. Stimuli and procedure

Eighty six grayscale facial images displayed on a monitor subtending visual angles of $3.6 \times 4.6^{\circ}$ of 43 famous people (2 photos per identity) were used as stimuli. Another 43 photographs of different famous people were used as mismatching stimuli. Internal features stimuli were created by deleting the hair, the chin and the ears from the complete original facial images. The deleted area was then filled in with a blurred surround (Gaussian filtering tool in Corel Photo-Paint 10.0 was fitted in 30 points) made up of the deleted features in order to maintain the original physical properties of the stimuli as much as possible and to minimize ERP modulation by physical image attributes. External features stimuli were created using the same procedure but deleting the internal features. Complete face images were slightly blurred in order to equalize as best as possible the resolution in edited pictures.

An ANOVA was performed to compare the physical attributes of the images that might influence the ERPs apart from the experimental conditions under study. Thus, the histogram of each image, displaying the tonal range of the entire stimulus, was calculated (using Adobe Photoshop 7.0). The horizontal axis of the histogram represents the intensity values, or levels, from darkest (0) at the far left to brightest (255) at the far right; the vertical axis represents the total number of pixels with a given value. The average values were 120.2 (S.D. = 30.4), 122.7 (S.D. = 29.3) and 121.7 (S.D. = 26.1) for external features, internal features and complete faces, respectively, and no significant differences were observed among them.

An identity face-feature matching task was presented with facial features (external or internal) and complete (matching or mismatching identity) famous faces, which were displayed consecutively for 500 ms each (first stimulus displayed after pressing the spacebar, ISI = 700 ms). Following the complete face presentation, the screen went black (700 ms) before the word "RESPOND" appeared for 500 ms (+1000 ms post-interval). The participant had to decide whether the complete face matched the identity or not (pressing the mouse keys) of the previously displayed features (Fig. 1).

A total of 172 trials were presented (86 with complete face matching-identity and 86 mismatching). In half of the matching and mismatching trials (43) target