Neurophysiological correlates of face gender processing in humans

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Abstract

Event-related potentials (ERPs) were recorded while subjects were involved in three gender-processing tasks based on human faces and on human hands. In one condition all stimuli were only of one gender, preventing any gender discrimination. In a second condition, faces (or hands) of men and women were intermixed but the gender was irrelevant for the subject’s task; hence gender discrimination was assumed to be incidental. In the third condition, the task required explicit gender discrimination; gender processing was therefore assumed to be intentional. Gender processing had no effect on the occipito-temporal negative potential at ~170 ms after stimulation (N170 component of the ERP), suggesting that the neural mechanisms involved in the structural encoding of faces are different from those involved in the extraction of gender-related facial features. In contrast, incidental and intentional processing of face (but not hand) gender affected the ERPs between 145 and 185 ms from stimulus onset at more anterior scalp locations. This effect was interpreted as evidence for the direct visual processing of faces as described in Bruce and Young’s model [Bruce, V. & Young, A. (1986) Br. J. Psychol., 77, 305–327]. Additional gender discrimination effects were observed for both faces and hands at mid-parietal sites around 45–85 ms latency, in the incidental task only. This difference was tentatively assumed to reflect an early mechanism of coarse visual categorization. Finally, intentional (but not incidental) gender processing affected the ERPs during a later epoch starting from ~200 ms and ending at ~250 ms for faces, and ~350 ms for hands. This later effect might be related to attention-based gender categorization or to a more general categorization activity.

Introduction

Human face recognition is probably one of the best examples for the capacity of the visual system to rapidly and efficiently discriminate among thousands of exemplars of the same category. Perceiving a face, people are able, without explicit training, to decide accurately and effortlessly whether the face is familiar or unfamiliar, one of a male or female, and to correctly appreciate its emotional expression, age, race, etc.

The complexity and variety of the cognitive processes involved in face recognition have been well represented in the theoretical model suggested by Bruce & Young (1986). This model assumes the existence of separate face processing pathways: one is designed to identify the person, while others, acting in parallel, are supposed to process the age, race or gender, or assess the emotion expressed in the face. The common starting point of these different pathways is the elaboration of a configurational representation of faces through the ‘structural encoding’ module. According to the model, the mechanisms subtending age, race or gender judgements are activated following the structural encoding of facial features and form the ‘directed-visual encoding’ module.

Various aspects of this model have been supported, to differing extents, by empirical and neuropsychological evidence. The finding that prosopagnosic patients never fail to realize that they are looking at a face, and many of them are capable of matching different photographs of the same individual without showing any recognition of familiar faces, supports a distinction between a fairly normally functioning structural encoding module and a deficient face identification system (Benton & Van Allen, 1972; Malone et al., 1982; De Renzi et al., 1991). Obviously, given that face identification is dependent on efficient structural encoding (Bentin et al., 1999; see also Eimer & McCarthy, 1999), a neuropsychological double dissociation between the face identification and structural encoding mechanisms is impossible. However, the independence of these two mechanisms has been recently shown in normal subjects using event-related potentials (ERP) (Bentin & Deouell, 1999). The distinction between the face identification system and a system devoted to the appreciation of facial emotional expression has also been demonstrated by neuropsychological dissociation. The identification of emotional expressions is preserved in the great majority of prosopagnosics, while it may be impaired in patients who do not have problems in recognizing familiar faces (Kurukz & Feldmar, 1979). Relative to face identification and appreciation of emotional expression, the function of the direct encoding module has been less investigated. With a few exceptions (Newcombe & Russel, 1969; De Renzi et al., 1989; Carlessimo & Caltagirone, 1995), prosopagnosic patients can discriminate a person’s gender and race and can estimate his/her age by looking at his/her face. This finding supports Bruce and Young’s (1986) suggested dissociation between these processes and those required for face recognition. However, the finding that the
The experiment was divided into two sessions, one including face stimuli (Face session) and the other including hand stimuli (Control session). Each session included five experimental conditions using three gender discrimination tasks. In all conditions, the subject’s task was to mentally count the number of targets delivered randomly among non-targets.

### Materials and methods

#### Subjects

Sixteen right-handed subjects (eight males and eight females, 18–32 years old) with normal vision or corrected-to-normal vision participated as paid volunteers. All were fully informed of the recording technique, which was noninvasive.

#### Stimuli

Twelve hundred grey-scale photographs were digitally scanned. They included four stimulus types: human faces with no eyeglasses, human faces with eyeglasses, human hands and human torsos. The faces and torsos were presented in a roughly front view, whereas the backs of the hands, half of them being left and the other half right, were viewed from above. Half of the faces, half of the hands and half of the torsos were of men and the other half of women. Across categories, the stimuli were matched for luminance and were of equal size (100 × 120 mm). The stimuli were presented foveally, subtending a visual angle of 6.9°, for 300 ms at a rate of one every 1.4 s. A fixation point was present at the centre of the screen between each presentation. No stimulus was repeated.

#### Procedure

The experiment consisted of two consecutive sessions, each including five experimental conditions. The stimuli in each condition were presented in blocks of 50. Face stimuli were presented during the first session (Face session), whereas during the second, we presented hand and torso stimuli (Control session). In all the conditions, subjects performed an oddball detection task reporting verbally, at the end of each block, the number of target items detected; target items (20% of total) were delivered randomly among non-target items (see Table 1 for details). In conditions 1 and 2, referred to as No-gender discrimination task, target as well as non-target stimuli were of only one gender. In the Face session, the targets were either male (condition 1) or female (condition 2) faces with glasses delivered among faces without glasses, while in the Control session the targets were male (condition 1) or female (condition 2) torsos delivered among hands. The order of presentation of conditions 1 and 2 was counterbalanced across subjects. Condition 3 (Incidental-gender discrimination task) was similar to conditions 1 and 2, except that the stimuli included male and female equally mixed. The subjects were assumed here to analyse the stimuli at the same level as in the two previous conditions, but they could also incidentally process the gender of the stimulus. Conditions 4 and 5 (Intentional-gender discrimination task) followed condition 3 with a counterbalanced order between subjects. In these two conditions, subjects had to process explicitly the stimuli according to their gender.
gender: the targets were either male (condition 4) or female (condition 5) faces among female or male faces, respectively, in the Face session, and male or female hands among female or male hands, respectively, in the Control session.

**EEG recording**

EEG was continuously recorded at a sampling rate of 1kHz (0.03–320Hz analogue bandwidth) from 32 Ag-AgCl scalp electrodes referred to the nose, of which 20 were placed according to the international 10–20 system (Fz, Cz, Pz, Iz, Fp1, F7, F3, C3, P3, T3, T5, O1 and their counterparts on the right hemiscalp), and two at the left and right mastoids (M1 and M2). The remaining positions were midway between two positions of the 10–20 system: CP5 (between T3 and P3), CP1 (between C3 and Pz), PO3 (between O1 and P3), POz (between Pz and Oz), and IM1 (between Iz and M1), and their counterparts on the right hemiscalp. The EOG was monitored from the outer canthus of the right eye (YH) and the channels Fp1 and Fp2. Electrode impedances were <3kΩ. The ERPs were averaged off-line over a 1000-ms period including a 100-ms prestimulus baseline, and digitally filtered (0.03–20Hz). Trials in which the potential exceeded 150μV at any electrode were automatically rejected.

**Data analysis**

Only the responses to non-target stimuli were analysed. The ERPs elicited by male and female faces or male and female hands (conditions 1 and 2, and conditions 4 and 5) were collapsed yielding three levels of gender processing (No-gender, Incidental-gender and Intentional-gender discrimination), with an equal number of stimuli presented at each level. Analysis of ERP involved two steps.

(i) The effects of gender processing on the latency and amplitude of the N170 component (negativity at ~170ms) were tested using three-way within-subjects analyses of variance (ANOVA) with factors: Type of task (No-, Incidental-, Intentional-gender discrimination), Stimulus type (Faces, Hands), and Hemisphere (left, right). Latency of N170 was measured at T5/T6 sites where the potential value was maximum in the grand average over all subjects. The N170 amplitude was quantified for each subject as the mean potential value in time over a ±25 ms-window around the peak latency of the grand average. Reflecting the slightly more anterior scalp distribution of the N170 elicited by hands relative to faces, different subsets of electrodes were included in spatial averaging. For faces, the sites included were IM1, M1, T5 and their homologous sites on the right hemiscape, and for hands, T5, P3 and CP5 and their homologous locations on the right hemisphere. Significance levels for the F-values were adjusted with Greenhouse–Geisser correction whenever necessary.

(ii) Other possible effects of gender processing were assessed in the following way. Firstly, they were quantified in the difference waves obtained by subtracting the responses to the no-gender task from the responses to incidental (Incidental–No) and intentional (Intentional–No) gender tasks, respectively. Student’s t-tests comparing the amplitude of the difference waves with zero were computed for each sample at each electrode. Student’s t-maps could then be obtained at each latency. Spatio-temporal patterns having a stable topography with a significant amplitude (P<0.01) at least two adjacent electrodes for 20 consecutive 20-ms samples were considered as significant gender task effects (Rugg et al., 1995; see also Thorpe et al., 1996).

Scalp potential maps were generated using a two-dimensional spherical spline interpolation (Perrin et al., 1989) with colour scale normalized to the peak voltage value at the considered latencies.

**Results**

For all stimulus types and gender tasks, the ERPs were characterized by a series of positive and negative deflections peaking successively around 100 ms at O1–O2 (a positive peak P100), around 165 ms at T5–T6 (a negative peak N170), and around 220 ms at PO3–PO4 (a positive peak) (Fig. 1). This latter peak was followed by a sustained positivity, lasting up to ~350–400 ms, the morphology of which could differ according to the gender task and the stimulus type.

**Effects of gender processing on the N170 component**

Figure 2a shows the scalp potential distribution, at 165 ms latency, of the N170 component elicited by face and hand stimuli in the no-gender task. Both stimulus types activated occipito-temporal regions with, however, a distribution slightly more anterior for hands than for faces. Influence of the gender discrimination tasks on the mean amplitude and peak latency of N170 was tested through three-way ANOVA with the Type of task, Stimulus type and Hemisphere as factors (see Materials and Methods). No main effect of the Type of task, nor interaction between this factor and any other factors, were found on the mean amplitude or peak latency of N170. The only significant effect was a shorter peak latency for faces (157 ms) than for hands (170 ms; F1,15 = 60.39, P<0.0001).

**Other ERP effects of gender discrimination tasks**

Both for face and for hand stimuli, the effects of incidental- and intentional-gender discrimination tasks were quantified in the difference between the ERPs elicited in each of these tasks and the ERPs elicited in the no-gender task (Incidental–No waves and Intentional–No waves, respectively). Student’s t-maps computed on these difference waves revealed three spatiotemporal patterns of significant task effects (see Materials and Methods), that could vary with the nature of the gender discrimination task (incidental or intentional) and the stimulus type (face or hand). The earliest component of the difference pattern spread over the mid-parietal areas from ~40 to 90 ms, the second was observed over the central areas from ~140 to 190 ms, and the latest extended over the occipito-parietal regions from ~200 ms to 350 ms. Figures 3 and 4 detail the statistical significance of the difference waves over the electrodes and periods characterizing these spatiotemporal patterns of interest. Figure 2B and C displays the topography of the difference waves and the corresponding t-map at an illustrative latency for each pattern. Table 2 gives the mean amplitude and significance of the difference waves over the whole patterns. These different patterns are analysed in detail below.

**Event-related potential at 40–90 ms**

Between 40 and 90 ms (Fig. 2B and C, line a), significant effects of the incidental-gender task (compared with the no-gender task) were found for both face and hand stimuli: the ERP amplitudes of the Incidental–No difference waves reached statistical significance (P<0.01) from ~45 to 70 ms latency at the left mid-parietal electrodes for faces (Fig. 3A left part; mean amplitude over 40–90 ms, ~0.74 μV), and over 40–90 ms at the centro-parietal sites for hands (Fig. 3A right part; mean amplitude ~0.79 μV; see Table 2). Figure 2B, line a, illustrates the topography of these effects at 65 ms latency. No corresponding patterns were observed for the intentional-gender task, for either faces or hands (Fig. 2C, line a; Fig. 4A; Table 2).
**Event-related potential at 140–190 ms**

In this latency range (Fig. 2B and C, line b), both the Incidental–No (Fig. 2B, line b) and the Intentional–No (Fig. 2C, line b) difference waves showed significant positive amplitudes over a wide central region (eight electrodes) for face but not for hand stimuli (Figs 3B and 4B). For faces, the amplitude of the Incidental–No wave reached statistical significance ($P < 0.01$) at F3–C3 from 145 ms latency, and at all the selected electrodes ($P < 0.01$ or $P < 0.001$) from 155 to 185 ms (Fig. 3B left part; mean amplitude over 140–190 ms, $-1.06 \mu V$). In the Intentional–No difference wave, the amplitude reached statistical significance ($P < 0.01$) at most electrodes from 145 ms, and at all the selected electrodes ($P < 0.01$ or $P < 0.001$) from 150 to 185 ms (Fig. 4B left part; mean amplitude $-1.26 \mu V$). No or only marginally significant effects were found for hands during this epoch (see Figs 3B and 4B right side, and Table 2).

**Fig. 1.** Grand average ERPs at posterior and central electrodes for non-target faces and hands in the three gender discrimination tasks (No-, Incidental-, and Intentional-gender). The shaded rectangles indicate the time periods when the responses differ according to the gender tasks. The N170 component (and P100) are indicated at the electrodes where they are maximum.

**Fig. 2.** (A) Scalp potential distributions of the N170 component (A) around its peak latency (165 ms) elicited by non-target faces and hands during the no-gender discrimination task. (B and C) Scalp potential distribution of the incidental–Incidental–No and the intentional–Intentional–No gender discrimination effects at the peak latencies where the differences were maximum (lines a–d), for face and hand stimuli. The range of the coloured calibration scale is different for each component and is given (in $\mu V$) below each map. Right column: Student’s $t$-maps estimated from potential values: the grey colour indicates the scalp areas where Incidental–No or Intentional–No amplitude differs significantly ($P < 0.01$) from zero. The potential maps of the difference patterns between the responses to the incidental- and intentional-gender tasks and the responses to the no-gender task showed: (a) a pattern of activation at 65 ms, over the mid-parietal sites for faces and the central sites for hands, in the incidental-gender task but not in the intentional-gender task; (b) a pattern of activation at 165 ms, over the central areas in the incidental- and the intentional-gender discrimination tasks for face but not for hand stimuli, suggesting a gender processing effect specific for human faces; (c) a pattern of activation at 225 ms, over the occipito-parietal regions for face and hand stimuli, in the intentional-gender task but not in the incidental-gender task; and (d) a sustained positive pattern of activation to $\approx 350$ ms over the posterior regions for hands but not for faces, suggesting that the neural activity related to the intentional-gender task was prolonged up to $\approx 350$ ms for hand but not for face stimuli.

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Figure 2

A

<table>
<thead>
<tr>
<th>No-gender</th>
<th>FACES</th>
<th>HANDS</th>
</tr>
</thead>
<tbody>
<tr>
<td>N170 (165 ms)</td>
<td><img src="image1" alt="Brain map" /></td>
<td><img src="image2" alt="Brain map" /></td>
</tr>
</tbody>
</table>

B

| a) 40-90 ms (65 ms) | ![Brain map](image3) | ![Brain map](image4) |
| b) 140-190 ms (165 ms) | ![Brain map](image5) | ![Brain map](image6) |
| c) 200-250 ms (225 ms) | ![Brain map](image7) | ![Brain map](image8) |
| d) 250-350 ms (350 ms) | ![Brain map](image9) | ![Brain map](image10) |

C

| a) 40-90 ms (65 ms) | ![Brain map](image11) | ![Brain map](image12) |
| b) 140-190 ms (165 ms) | ![Brain map](image13) | ![Brain map](image14) |
| c) 200-250 ms (225 ms) | ![Brain map](image15) | ![Brain map](image16) |
| d) 250-350 ms (350 ms) | ![Brain map](image17) | ![Brain map](image18) |
Event-related potential at 200–250 ms

Significant intentional gender task effects were found between 200 and 250 ms latency (Fig. 2B and C, line c) at occipito-parietal electrodes for both face and hand stimuli. The ERP amplitude of the Intentional-No difference waves reached statistical significance ($P < 0.01$) from $\approx 200$–250 ms for faces (Fig. 4C left part; mean amplitude over 200–250 ms, 1.28 $\mu$V; see Table 2), and for hands (Fig. 4C right part; mean amplitude, 2.15 $\mu$V; see Table 2). This difference lasted longer ($\approx 250$ ms) for hands than for faces (see below). No or only marginally significant effects of the incidental-gender task were found over this period for face or hand stimuli (Fig. 3C).

As this intentional gender task effect was maximal at posterior sites (Fig. 2C, line c), its topography was compared with that of the N170 component (recorded in the no-gender condition) in order to explore whether the two activities were generated within the same brain structures. Two-way ANOVA on normalized data (mean amplitude over $\pm 25$ ms around the peak latency for N170, and over 200–250 ms latency for the intentional-gender effect) with the factors Condition (No-gender, Intentional-No) and Electrode (IM1, IM2, M1, M2, O1, O2, T5, T6) showed a significant interaction between the two factors ($F_{4,55} = 4.44$, $P < 0.004$, $GG = 0.52$), indicating different topographies for the two waves.

Event-related potential at 250–350 ms

The intentional gender task effect observed between 200 and 250 ms (Fig. 2B and C, line d) lasted longer for hands than for faces (Fig. 2C, lines c and d). Highly significant amplitude differences ($P < 0.001$) with a stable topography were observed up to $\approx 350$–400 ms (Fig. 4C right part; mean amplitude over 250–350 ms, 4.56 $\mu$V; see Table 2).

There was no corresponding pattern within the same period for faces (Fig. 4C left part; mean amplitude, 0.31 $\mu$V).

Discussion

The results can be summarised in the following way: (i) There was no effect of gender processing on either the amplitude or latency of the N170 component. (ii) Incidental-gender processing elicited electrical activities that were significantly different from those elicited when all stimuli were of one gender. These differences were observed around 45–85 ms from stimulus onset over mid-parietal sites for both face and hand stimuli, and around 145–185 ms over central sites for faces only. (iii) Intentional-gender processing elicited electrical activity that was significantly different from that elicited when stimuli of only one gender were presented. Similar to the activity generated by incidental-gender processing, this difference was significant only for faces over central sites between 145 and 185 ms from stimulus onset. In contrast to the activity specific to incidental processing, however, intentional processing did not show the early effect. Instead, there were longer-latency effects, between 200 and 250 ms, for both face and hand stimuli over posterior sites, and this effect lasted longer for hands than for faces (up to $\approx 350$ ms).

Separate processes for structural encoding and gender processing of faces

The occipito-temporal N170 component responding to face stimuli has been associated with the neurophysiological mechanisms underlying structural encoding of facial features (Bentin et al., 1996; George et al., 1996; see also Allison et al., 1994 for intracranial ERP
FIG. 4. Statistical significance of the intentional-gender task (compared with the no- gender task) at selective electrodes in the same three latency ranges as in Fig. 3 for face and hand stimuli. The distribution of the significant effects suggests an effect for faces but not for hands between 140 and 190 ms, and a later effect from ≈200 to ≈250 ms for the two stimulus types, this last effect lasting longer (up to ≈350–400 ms) for hands than for faces.

Table 2. Differences between the responses in the Incidental- and Intentional-gender tasks and the responses in the No-gender tasks.

<table>
<thead>
<tr>
<th>Electrode sites</th>
<th>Face session: ERP time periods analysed</th>
<th>Hand session: ERP time periods analysed</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>40–90 ms</td>
<td>140–190 ms</td>
</tr>
<tr>
<td>O1-PO3-T5-P3-CP1-POz</td>
<td>F3-C3-CP1-Fz-Cz-Pz</td>
<td>T5-PO3-O1-IM1-Iz-IM2-02-PO4-T6</td>
</tr>
<tr>
<td>Difference in response (µV)</td>
<td>Incidental-No gender</td>
<td>-0.74 ± 0.24**</td>
</tr>
<tr>
<td>Intentional-No gender</td>
<td>-0.20 ± 0.31</td>
<td>-1.26 ± 0.28**</td>
</tr>
</tbody>
</table>

Mean amplitude ± SEM of the differences between responses in the Incidental- and Intentional-gender tasks and the responses in the No-gender tasks, averaged in time and in space as indicated. **P<0.01 and *P<0.05, Student’s t-test.

An important result of the present study is that gender processing influenced neither the latency nor the amplitude of N170. Although exclusive effects of face gender discrimination were observed during similar time ranges, the sites at which these effects were observed were different from those of the N170 component. This pattern indicates that face gender processing is performed (at least partly) in parallel with its structural encoding by different brain mechanisms; i.e. the gender processing stage can begin before the structural encoding stage is completed. This conclusion is also consistent with PET findings that have shown that face gender processing activates neuroanatomical regions different from those involved in the perceptual analysis of the facial features (Sergent et al., 1992; Kapur et al., 1995; Andreasen et al., 1996). Therefore, our results bring additional (electrophysiological) support to Bruce and Young’s (1986) model of face processing, according to which perceptual analysis and gender extraction are subserved by two functionally distinct modules, the structural and the directed-visual encoding modules, respectively. In contrast to what was suggested in this model, however, the time-course of the face-specific gender processing effect (145–185 ms) suggests that direct perception is not subsequent to structural encoding.

Early (45–85 ms) incidental discrimination effects

An unpredicted result of our study was the very early epoch (45–85 ms) of the differences observed between the ERP s elicited by both faces and hands during the incidental-gender discrimination task as compared with the no-gender task. Apparently, this result indicates that the visual information available at this time is already used for automatic distinction between genders. Although early signs of face processing have been reported in monkeys (Tovee et al., 1993: 20–
50 ms) and in humans (Seck et al., 1997: 50–90 ms), it is difficult, however, to assume that the effects observed at this latency (45–85 ms) over parietal regions are specifically related to the processing of gender information. Indeed, such latencies correspond to the first cortical potentials elicited by visual stimulation in the striate cortex (Clark et al., 1995). An alternative explanation of the early difference between the incidental- and no-gender processing conditions may refer to the fact that the incidental-gender task was the only one among the five experimental conditions in which the two gender categories were intermixed in the non-targets. It is therefore possible that this effect reflects an early, automatic process of rapid but coarse categorization between two stimulus classes on the basis of visual characteristics. To this end, it would be interesting to know whether this early categorization process may occur only for biological stimuli with strong psychosocial significance for humans, or whether it indicates a more general ability of the visual system to cursorily categorize wide classes of stimuli at an early stage of sensory processing.

**Specificity of face gender processing**

The pattern of gender processing effects for faces and for hands showed both similarities and differences. As discussed above, the very early effect of incidental-gender processing was similar for both types of stimuli. This similarity suggests that the perceptual mechanisms associated with this activity, whatever their nature, are not face-specific. Between 145 and 185 ms from stimulus onset, however, gender processing (intentional- as well as incidental-) affected the ERP's elicited by faces but not those elicited by hands. These results have two implications. Firstly, the similarity of the incidental- and intentional-gender discrimination ERP effects imply that gender information is extracted from faces automatically and that, at this stage, this process is not influenced by top-down strategic factors. Secondly, because these ERP effects were not found for hands, they might index the specificity of the physiological operations underlying face gender processing: gender judgements from other body parts such as hands would be mediated through other (later) brain mechanisms.

**Additional gender discrimination effects**

Regardless of whether the stimuli were faces or hands, the ERPs elicited from ≈200 ms poststimulation in the intentional-gender discrimination task were significantly different from those elicited when explicit discrimination between the genders was not required. The effect was significant up to ≈250 ms for faces, and up to ≈350 ms for hands. This pattern, partly common for faces and hands, is not compatible with the activity of the directed-visual processing pathway stipulated by Bruce and Young (1986). Rather, it suggests that the type of gender processing reflected at this level is associated with the explicit process of discrimination between the two gender categories. The fact that this effect lasted longer for hands than for faces may be explained by the higher difficulty of discriminating gender from hands than from faces. This could be because faces carry more gender-specific information than hands, because humans may be better trained to distinguish gender on the basis of the face than on the basis of the hands, because the gender of the face has already been determined by direct visual perception mechanisms, or all of these reasons. In the absence of a nongender discrimination task for similar stimuli however, we cannot unequivocally determine whether the activity observed during the latter time epochs for intentional- but not incidental-gender discrimination is associated specifically with gender processing or with a more general categorical discrimination activity. In any case, these discrimination effects could express the expertise that humans have developed in processing faces compared with other body parts such as hands.

**Abbreviations**

ERP, event-related potential; N170, negative potential at ≈170 ms after stimulation.

**References**


