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Brain lateralization of holistic versus analytic processing of emotional facial expressions

Manuel G. Calvo *, David Beltrán

University of La Laguna, Tenerife, Spain

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ABSTRACT

This study investigated the neurocognitive mechanisms underlying the role of the eye and the mouth regions in the recognition of facial happiness, anger, and surprise. To this end, face stimuli were shown in three formats (whole face, upper half visible, and lower half visible) and behavioral categorization, computational modeling, and ERP (event-related potentials) measures were combined. N170 (150–180 ms post-stimulus; *right* hemisphere) and EPN (early posterior negativity; 200–300 ms; mainly, *right* hemisphere) were modulated by expression of *whole* faces, but not by separate halves. This suggests that expression encoding (N170) and emotional assessment (EPN) require *holistic* processing, mainly in the right hemisphere. In contrast, the mouth region of happy faces enhanced *left* temporo-occipital activity (150–180 ms), and also the LPC (late positive complex; centro-parietal) activity (350–450 ms) earlier than the angry eyes (450–600 ms) or other face regions. Relatedly, computational modeling revealed that the mouth region of happy faces was also visually salient by 150 ms following stimulus onset. This suggests that analytical or *part-based* processing of the salient smile occurs early (150–180 ms) and lateralized (*left*), and is subsequently used as a shortcut to identify the expression of happiness (350–450 ms). This would account for the happy face advantage in behavioral recognition tasks when the smile is visible.

Introduction

Facial expressions reflect emotions and intentions, motives and needs. Adaptive social behavior thus depends on expressers and observers conveying and interpreting such non-verbal information quickly and accurately. The human face contains two primary sources of expressive information, i.e., the eye and the mouth regions. Prior studies using behavioral and modeling measures have shown the relative weight of the eyes and the mouth in expression recognition for the different basic categories of facial affect (see Blais et al., 2012). While there is some agreement that angry and fearful expressions are mainly dependent on changes in the eye region, that disgust relies more on the mouth region, and that sadness and surprise may be similarly recognizable from both regions, different paradigms have shown the critical contribution of the smiling mouth to the recognition of facial happiness (Calder et al., 2000; Calvo et al., 2014; Nusseck et al., 2008; Smith et al., 2005; Wang et al., 2011).

The special informative or diagnostic value of the smile can be attributed to its uniqueness as a distinctive facial feature. That is, the smiling mouth is systematically associated with facial happiness, whereas features in the other expressions overlap to some extent across categories (Calvo and Marrero, 2009; Kohler et al., 2004). Being a single diagnostic feature, the smile has been proposed to be used by observers as a shortcut for a quick and accurate categorization of a face as happy (Adolphs, 2002; Leppänen and Hietanen, 2007). The distinctiveness of the smile would thus account for the typical recognition advantage of happy expressions (e.g., Calvo and Lundqvist, 2008; Palermo and Coltheart, 2004; Tottenham et al., 2009; see Nelson and Russell, 2013). In the current study, we investigated the neurocognitive basis of the special diagnostic role of the smile relative to other expressive sources, and how this is relevant to examine the mechanisms of holistic versus analytic encoding and brain lateralization in facial expression processing.

ERP research on the role of expressive sources in a face

Numerous studies using EEG measures have investigated the processes and time course of facial expression processing. Emotional expression modulates a wide range of ERP (event-related potentials) components, from earlier to later stages: (a) P1 (100 to 130-ms peak latency from stimulus onset; occipital brain scalp sites) or N1 (100–150 ms; widely distributed over the entire scalp; e.g., Luo et al., 2010; Pourtois et al., 2005); (b) N170 (150–200 ms; lateral occipital and infero-temporal; e.g., Batty and Taylor, 2003; Williams et al., 2006) and VPP or vertex positive potential (150–200 ms; central midline sites; e.g., Smith et al., 2013; Willis et al., 2010); (c) P2 (150–275 ms; frontal and central sites; e.g., Calvo et al., 2013b; Paulmann and Pell, 2009), N2 (200–350 ms; central; e.g., Ashley et al., 2004; Williams et al., 2006), and EPN or early posterior negativity (200–350 ms;

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* Corresponding author at: Department of Cognitive Psychology, University of La Laguna, 38205 Tenerife, Spain. Fax: +34 922 317 461.
E-mail addresses: mgcalvo@ull.es (M.G. Calvo), dbeltran@ull.es (D. Beltrán).

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temporo-occipital; e.g., Rellecke et al., 2011; Schupp et al., 2004); and (d) P3 and LPP or late positive potential (350–700 ms; widespread over fronto-central-parietal areas; e.g., Frühholz et al., 2009; Leppänen et al., 2007).

Nevertheless, prior ERP research on emotional facial expressions has typically used only whole-face stimuli, rather than presenting the eye or the mouth regions separately.[1] Therefore, the relative diagnostic value of these expressive sources could not be established. Leppänen et al. (2008) used an approach aimed to determine the role of specific expressive sources in a face (see also Meletti et al., 2012; Weymar et al., 2011).[2] Leppänen et al. (2008) compared fearful and neutral expressions under different display conditions: whole faces (with the eyes visible), faces with eyes covered, faces with eyes and eyebrows covered, isolated eyes and eyebrows, and isolated eyes. Results showed a negative shift in ERPs for fearful relative to neutral expressions over occipital–temporal scalp sites starting at the latency of the N170 (160–210 ms post-stimulus), and also later over lateral–temporal electrode sites (210–260 ms; EPN). Such effects were observed not only for whole faces but also when both the eyes and eyebrows were shown in isolation; in contrast, the effects were abolished when isolated eyes were presented or when the eyes and eyebrows were covered. This reveals that the eye region (with the eyebrows) is critical for the rapid ERP differentiation between fearful and neutral faces.

We aim to extend this approach to other expressions and also to the mouth region. To this end, we used happy, angry, and surprised faces, in addition to neutral faces, each with three formats (whole face, eye region visible, or mouth region visible). Regarding the expressions, our selection was based on the results of prior behavioral research in which the eye and mouth regions were manipulated to examine their informative value (see above): For happy faces, the mouth is highly diagnostic; for angry faces, the eyes are more diagnostic than the mouth; and for surprised faces, both the eyes and the mouth are similarly (but not highly) diagnostic. Regarding the stimulus format, and given that the isolated eyes or mouth (with no surrounding facial context) loose informative weight (see Leppänen et al., 2008), we presented them within the face top or bottom halves, respectively (see Calder et al., 2000). The other half of the face (bottom or top) was scrambled, rather than simply being removed, to keep the perceptual shape of a face and equivalent low-level properties. In an expression categorization task, participants had to identify the emotional expression conveyed by each face stimulus.

This paradigm allowed us to determine the role of the eye and the mouth region in expression recognition, as well as the underlying neurophysiological processes and their time course. Following the rationale of the behavioral studies, we hypothesize that, if the mouth region of happy faces (or the eye region of angry faces) is diagnostic, it can be used as a cue to access the holistic template and build a cognitive representation of the whole facial expression (see Rossion, 2013). This implies that happy and angry faces will be explicitly categorized more accurately and faster when the mouth or the eye region, respectively, are visible—even in the absence of the whole face—relative to the other combinations of regions and expressions. To assess the processes involved, we recorded EEG activity for 800 ms following the face stimulus onset, and ERP components were examined from the early P1 to the late LPP. This provided us with information about when and how brain processes are sensitive to each major expressive source in a face. The N170 and the EPN components are particularly related to the processing of facial expression (N170; for a review, see Rellecke et al., 2013) and emotional content (EPN; for a review, see Hajcak et al., 2012). Accordingly, if diagnostic sources (e.g., the happy smile or the angry eyes) are used to encode the expression or to extract emotional significance, they will enhance N170 or EPN activity.

Holistic vs. analytic processing and lateralization

The current approach is also relevant to the issues of holistic (or configural or relational) versus part-based (or analytic or featural) processing and hemispheric lateralization, as applied to facial expression and emotional content. Holistic versus part-based perception refer to the integration versus isolated encoding of facial features or regions (e.g., the eyes and the mouth) in a face (e.g., Calder et al., 2000; Richler et al., 2012; Rossion, 2013). Holistic processing is thought to be preferentially executed by the right hemisphere, whereas the left hemisphere is regarded as more involved in part-based processing (see Ramon and Rossion, 2012). With fMRI measures, Maurer et al. (2007) observed that the areas that showed greater activity for featural changes in the face (shape or size of the eyes or mouth) were mostly located in the left prefrontal areas, whereas areas of the right fusiform gyrus and the right frontal cortex showed more activity for configural changes (relative location or distance of the eyes and mouth) (see also Lobmaier et al., 2008). Consistently, with EEG measures, Scott and Nelson (2006) found that the right-hemisphere N170 was greater for configural relative to featural changes, whereas the left-hemisphere N170 exhibited the opposite pattern. In the same vein, TMS (transcraneal magnetic stimulation) research has shown that the right inferior frontal cortex is causally involved in configural processing, whereas the left middle frontal gyrus is involved in featural analysis (Renzi et al., 2013).

The prior studies on holistic versus analytic processing and lateralization have used face stimuli devoid of emotional expression (i.e., neutral faces), and have measured recognition or matching of face identity. In the current study, we extend this work to the recognition of *emotional expressions*. We hypothesize that, if the mouth or the eye regions *alone* can drive analytic encoding of the facial expression or its emotional content, ERP modulations of the corresponding processes (e.g., N170 and EPN, respectively) will occur when the mouth region of happy faces, or the eye region of angry faces, are presented separately. Such face part-based ERP modulations will, nevertheless, occur earlier for the happy mouth than for the angry eyes. This would be due to the greater saliency and distinctiveness of the former than the latter region (e.g., Calvo et al., 2014). In contrast, if expression or emotional processing requires holistic encoding, ERP modulations will occur only when the *whole* face is shown. Furthermore, to the extent that the part-based analysis and the holistic encoding of the diagnostic regions are lateralized, this will be reflected in an enhanced neural activity in the left or the right hemisphere, respectively.

In sum, we used a part-whole paradigm to determine the role of configural processing of emotional facial expressions. The part- (or isolated region) versus whole-face comparisons will provide the relevant evidence. The whole-face condition allows for perceptual integration of all regions at the same time, and thus holistic processing is possible. In contrast, in the part-face conditions, only single expressive sources are available, thus allowing for analytical but preventing on-line holistic processing. For behavioral measures, higher expression categorization accuracy and faster correct responses for the whole than for the part condition would reveal holistic encoding, whereas equivalent (or higher) performance for the part conditions would be indicative of dependence on analytical encoding. For ERP measures, expression modulation of a

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[1] In numerous ERP studies using neutral faces, whole face stimuli have been compared with half-face (e.g., Jacques and Rossion, 2009, 2010) or isolated facial regions (e.g., Bentin et al., 1996). Nevertheless, emotional expression was not manipulated and expression recognition was not assessed, but rather face identification or identity matching, or detection of task-irrelevant stimulus aspects. In the current study, we aimed to extend the whole vs. part or region comparison approach to faces with emotional expressions and to expression recognition processes.

[2] Weymar et al. (2011) used schematic instead of real faces, and a visual search instead of an expression recognition task. Generalizations across the two types of stimuli and tasks may, however, not be warranted (see Becker et al., 2011; Horstmann et al., 2012). Meletti et al.(2012) used an expression recognition task and compared whole faces with isolated eye or mouth regions of happy, fearful, and neutral real faces. Intracranial ERPs recorded from depth electrodes in the amygdala (of four epileptic patients) showed increased amplitudes in response to the eye regions of both happy and, especially, fearful, compared to whole faces and to the mouth region. This suggests a special role of the amygdala in the processing of emotional signals conveyed by expressive eyes.

given electrophysiological component only by whole-face stimuli would reveal holistic encoding, whereas modulation by part-face stimuli would reflect analytical encoding. Specifically, the N170 activity (at right temporo-occipital sites) is a neural signature of the structural processing of "faceness" (i.e., the configuration of a face as a face; Bentin et al., 1996; Rossion and Jacques, 2012). The modulation of this component in the right hemisphere by whole-face expressions would thus indicate holistic encoding, whereas modulation in the left hemisphere by face regions would indicate analytical encoding.

Method

Participants

Twenty-two psychology undergraduates (15 females; all between 18 and 25 years of age) gave informed consent, and received either course credit or were paid (7 Euro per hour) for their participation. All were right-handed and reported normal or corrected-to-normal vision and no neurological or neuropsychological disorder. Four additional subjects were excluded because of excessive eye-movements.

Stimuli

We selected 80 digitized color photographs from the KDEF (Lundqvist et al., 1998) stimulus set. The experimental face stimuli portrayed 20 individuals (10 females: KDEF no. 01, 07, 09, 11, 14, 19, 20, 26, 29, and 31; and 10 males: KDEF no. 05, 10, 11, 12, 13, 22, 23, 25, 29, and 31), each posing four expressions (neutral, happiness, anger, and surprise). Nonfacial areas (e.g., hair, etc.) were removed by applying an ellipsoidal mask. The faces were presented against a black background. Each face stimulus was 11.5 cm high by 8.5 cm wide, equalling a visual angle of 9.40° (vertical) × 6.95° (horizontal) at 70-cm viewing distance. In addition to a condition in which the original KDEF face was presented as a whole, we generated two more stimulus format conditions in which only the upper half or only the lower half of each face was visible, while the other (bottom or top, respectively) half was scrambled pixel-by-pixel, and therefore masked (for an illustration, see Fig. 1). These two conditions were included to determine the contribution of the eye region or the mouth region, relative to the whole face. An average scrambled mask was used, so that all the faces were comparable in the covered half while their visible half remained different.

Assessment of low-level image statistics

The face image physical attributes such as luminance, RMS or root mean square contrast, skewness, SNR or signal-to-noise ratio, and energy were assessed with Matlab 7.0 (The Mathworks, Natick, MA). Each of these measures was analyzed by means of a 4 (facial Expression: angry, surprised, happy, and neutral) × 3 (face Format: whole face vs. upper vs. lower half) ANOVA. A main effect of format emerged for all the dependent variables (all $Fs \geq 14$, $ps \leq .0001$), with significant differences for all the comparisons across format conditions. However, importantly for the aims of this study, no significant differences appeared between expression categories (all $Fs \leq 1.91$, $ps \geq .13$), and there was no expression by format interaction (all $Fs < 1.76$, $ps \geq .11$).

Apparatus and procedure

The stimuli were presented on a 24″ monitor. Stimulus presentation and response collection were controlled by means of Presentation software (version 15.1, Neurobehavioral Systems, Inc.). On each trial, after a 500-ms central fixation cross, a face was displayed for 150 ms in the centre of the screen, followed by a black screen for 650 ms, and then a probe word. In an expression categorization task, participants responded whether or not the word represented the expression conveyed by the face, by pressing one of two keys (labeled as "Yes" or "No"). Response latencies were time-locked to the presentation of the probe word. There was a 2-s intertrial interval. Participants were told to look at the centre of the screen and to blink only during the interval. A short, 150-ms stimulus display was used to avoid eye movements. A 150-ms display has otherwise proved to allow for an average 87% recognition accuracy of similar face stimuli in expression categorization tasks (Calvo et al., 2014).

Following 24 practice trials, each participant was presented with 40 experimental trials of each of the four expressions and each of the three stimulus formats (i.e., whole face, upper half visible, and lower half visible), in six blocks. Each stimulus was presented twice to each participant. Each block consisted of a total of 80 trials, with 20 different faces of each expression in one or another of the three formats. The probe words (*happy*, *angry*, *surprised*, and *neutral*) represented the actually displayed facial expression on 50% of trials (once for each different stimulus), and a different expression on the other 50%. Within each block, trial order was randomly established for each participant. Recognition performance measures of accuracy and correct response reaction times were collected.

Assessment of visual saliency

According to computational models, visual saliency determines shifts of attention, especially at early stages (see Borji and Itti, 2013). As we investigated the role of the eye and the mouth regions in the early neurocognitive processes of expression recognition, it was

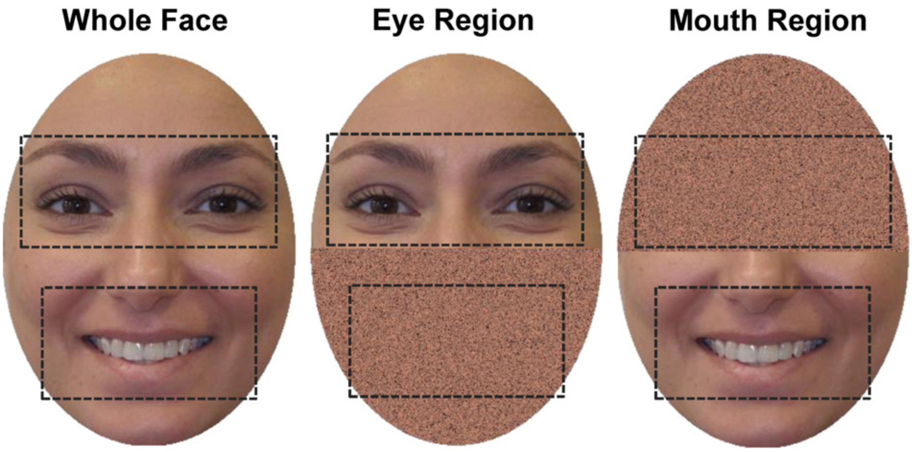

Fig. 1. *Stimulus format example*. Sample of face stimuli of each stimulus format condition. *Note*. The dotted-line boxes (they were not visible in the stimuli) represent the eye and the mouth areas of which visual saliency was computed relative to the whole image. For copyright reasons, a different face stimulus is shown in the figure, instead of the original KDEF pictures.

important to examine the visual saliency of the respective image areas. To address this issue, we modeled the saliency of the face region surrounding the eyes (subtending an area of 241 pixels wide by 112 pixels high; see Fig. 1) and the region surrounding the mouth (subtending 209 pixels wide by 112 pixels high; see Fig. 1), by means of the iLab Neuromorphic Vision C++ Toolkit (iNVT; http://ilab.usc.edu/toolkit/) algorithm (e.g., Itti and Koch, 2000). The resulting saliency maps represent the visual conspicuity of an image as a function of a combination of contrast, color, and spatial orientation.

We first computed the *mean saliency* values for the eye and the mouth regions relative to the whole face image.[3] Second, we computed the *saliency dynamics* of each region over time, given that the saliency weights for each image region are updated after each attentional shift.[4] To this end, the following saliency time course indices were calculated for the eyes and the mouth: (a) the probability that the eyes or the mouth were the very *first salient region* of the whole image, (b) the probability that the first saliency outburst of a region occurred during the *first 150 ms* (as this was the face stimulus display duration), (c) the saliency *onset* (i.e., the time at which a region became salient first over the rest of the image), and (d) the *sequence* in which the first saliency outburst occurred for each region. The saliency data that were computationally modelled represent the available information for an ideal observer of the face stimuli, rather than actual data obtained from the participants in the current study.

EEG recording

EEG and EOG signals were recorded using Ag/AgCl electrodes mounted in elastic Quick-caps (Neuromedical Supplies, Compumedics Inc., Charlotte). EOG signal was measured from two bipolar channels: One was formed by two electrodes placed at the outer canthus of each eye; another, by two electrodes below and above the left eye. EEG signal was recorded from 60 electrodes arranged according to the standard 10–20 system. All EEG electrodes were referenced on-line to an electrode at vertex, and recomputed off-line against the average reference. EEG and EOG signals were amplified at 500 Hz sampling rate using Synamp2 amplifier (Neuroscan, Compumedics Inc., Charlotte), with high- and low-pass filter set at 0.05 and 100 Hz, respectively. EEG electrode impedance was kept below 5 kΩ.

EEG data pre-processing was conducted using Edit 4.5 (Neuroscan, Compumedics Inc., Charlotte). The following transforms were applied to each participant's dataset. Data were initially down-sampled to 250 Hz and low-pass filtered at 30 Hz. EEG segments were then extracted with an interval of 200 ms preceding and 800 ms following the face onset. On these segments, artifact rejection was performed in two steps. First, trials containing activity exceeding a threshold of ± 70 μV at vertical and horizontal EOG and EEG channels were automatically detected and rejected. Second, non-automatically rejected artifacts were manually removed, including trials with saccades identified over the horizontal EOG channel. For the computation of ERPs, artifact-free segments were averaged separately for each of the 12 experimental conditions. A total of 10.7% of trials were excluded because of artifacts (mainly, eye blinks, drifts, and saccades). Baseline correction of averaged data was carried out using the 200-ms period preceding face onset.

ERP components

We identified several well-known components in the processing of facial expressions and other emotional pictures (see Hajcak et al., 2012). Within the first 300 ms, the anterior N1 (peaking at approximately 110 ms following the face stimulus onset), the VPP (peaking at ≈160 ms), and the N2 (peaking at ≈230 ms) were located at frontal and central sites of the scalp; and the P1 (peaking at ≈115 ms), the N170 (peaking at ≈160 ms), and the posterior P2 (peaking at ≈230 ms), at temporal and occipital sites. Later on, the LPC complex was identified at central and parietal sites, with one positive peak at ≈370 ms and another at ≈540 ms reflecting the activity of the P3b and the LPP components, respectively. In addition, and following the literature on ERPs in emotional picture and face processing, we analyzed EPN modulations (e.g., Schupp et al., 2004; see Hajcak et al., 2012). The EPN is a negative difference in processing emotional relative to neutral stimuli at temporo-occipital sites, which tends to overlap with the posterior P2. We therefore examined the differences occurring around the P2 peak as representative of an EPN modulation. Three of these components (N170, EPN, and LPC) are central for the aims of the current study. We used faces, which could convey emotional meaning or not, and they had to be explicitly judged as a function of expression. The N170, EPN, and LPC were thus aimed at assessing sensitivity to faceness, emotionality, and categorization, respectively.

The ERP values used for data analysis were computed as follows. Initially, three different clusters of scalp sites were formed: fronto-central (electrodes: F1, Fz, F2, FC1, FCz, FC2), centro-parietal (C1, Cz, C2, CP1, CPz, CP2), and occipito-temporal (left: TP7, P7, PO7; and right: TP8, P8, PO8). The lateralization of the occipito-temporal cluster allows us to examine hemispheric differences in relation to configural versus featural processing. Next, the mean amplitude value of each ERP component was calculated for each participant, expression, and format as the average of the selected time window. The mean activity in the fronto-central cluster was calculated for the interval between 100 and 140 ms post stimulus to evaluate the N1, between 150 and 180 ms for the VPP, and between 200 and 320 ms for the N2. The activity in the occipito-temporal cluster was calculated between 100 and 140 ms for the P1, between 150 and 180 for the N170, and between 200 and 320 for the EPN. The activity at centro-parietal sites of the LPC was decomposed into two stages: Between 350 and 450 ms for P3b, and between 450 and 600 ms for LPP. In support of this two-stage segmentation, there is evidence that the long-lasting LPC in response to emotional stimuli involves at least two sub-components (Foti et al., 2009). This allowed us to estimate time course differences as a function of expression (for a similar approach, see Holmes et al., 2009).

Results

Analysis of visual saliency

The *mean* visual saliency of the eyes and the mouth, the probability that each region was the *first salient* region, and the probability that the first saliency outburst occurred during *the first 150 ms* post stimulus onset, were analyzed by means of 4 (Expression: happy, angry, surprised, neutral) × 2 (Region: eye vs. mouth) ANOVAs, separately for each type of face format (whole face, upper face visible with lower half masked, and upper face masked with lower half visible). To decompose the interactions, separate one-way (Expression) ANOVAs were conducted for each region, followed by Bonferroni-corrected (alpha level, $p < .05$) multiple post hoc comparisons (see the mean scores and contrasts in Table 1). The statistical analyses were performed on the output of the saliency model (see above; unlike the analyses of the behavioral and the electrophysiological data, which were conducted on the actual categorization and ERP participants' responses).

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[3] To compute the *mean saliency values* of each predefined face region (eyes, mouth), we followed two steps. First, the iNVT command "ezvision --just-initial-saliency-map --in = frame000000.png" was used to generate and save the image saliency map before any shift of attention. This was supplemented with the command "--retina-mask = <filename>" to remove the outer, non-face area beyond the face contour. Second, the function "pfmreadmatlab.m" was used to load the iNVT generated PFM saliency map into Matlab and do the region analysis.

[4] To compute the *saliency time course indices* for each region, we used the iNVT command "ezvision --top5 --in = frame000000.png", which estimated the most salient spatial points in the image at each of five subsequent time points. In addition, the command "--retina-mask = <filename>" served to remove the non-face area beyond the face contour.

Table 1
Mean visual saliency values of the eye and the mouth regions, and saliency time course, for each facial expression and face format.

Face format and saliency indices for each region	Type of expression			
	Happy	Angry	Surprised	Neutral
Whole face: saliency of eye region				
Mean saliency	3.81b	**7.25a**	**6.18a**	**7.45a**
Saliency within ≤150 ms (%)	0	25	25	10
Saliency onset (in ms)	463	360	324	424
Whole face: saliency of mouth region				
Mean saliency	**13.42a**	5.88b	4.37b	3.77b
Saliency within ≤150 ms (%)	**100a**	25b	20b	5b
Saliency onset (in ms)	**91a**	318b	359b	385b
Eyes masked: saliency of mouth region				
Mean saliency	**13.62a**	6.93b	8.40b	7.25b
Saliency within ≤150 ms (%)	**100a**	20b	40b	20b
Saliency onset (in ms)	**84a**	216b	253b	296b
Mouth masked: saliency of eye region				
Mean saliency	5.78	7.55	5.07	6.21
Saliency within ≤150 ms (%)	10	30	35	15
Saliency onset (in ms)	528	337	336	393

Note. Mean scores with a different letter (horizontally, for type of expression) are significantly different; means sharing a letter, or no letter, are equivalent.

Whole-face format: (1) Mean saliency

The ANOVA yielded an expression by region interaction, $F(3, 76) = 23.56$, $p < .0001$, $\eta_p^2 = .482$. For the *eye* region, $F(3, 76) = 3.79$, $p = .014$, $\eta_p^2 = .130$, the eyes of happy faces were *less* salient than those of all the other faces, which did not differ from each other (unless otherwise indicated). For the *mouth* region, $F(3, 76) = 31.64$, $p < .0001$, $\eta_p^2 = .555$, the mouth of happy faces was *more* salient than that of all the other faces.

Whole-face: (2) Saliency time course

An expression by region interaction emerged for the probability of the first saliency outburst, $F(3, 76) = 20.87$, $p < .0001$, $\eta_p^2 = .452$, and the probability that it occurred during the first 150 ms, $F(3, 76) = 22.72$, $p < .0001$, $\eta_p^2 = .473$. The *mouth region* of happy faces was more likely to be salient first, relative to the mouth of the other expressions, $F(3, 76) = 37.25$, $p < .0001$, $\eta_p^2 = .595$, and during the first 150 ms, $F(3, 76) = 34.79$, $p < .0001$, $\eta_p^2 = .579$. Also, the average saliency onset, $F(3, 72) = 10.39$, $p < .0001$, $\eta_p^2 = .302$, and the order of the first saliency outburst, $F(3, 72) = 14.65$, $p < .0001$, $\eta_p^2 = .379$, occurred earlier for the happy mouth. For the *eye region*, there was a nonsignificant opposite trend.

Eye region masked with lower face half visible: (1) Mean visual saliency

The ANOVA yielded an expression by region interaction, $F(3, 76) = 19.03$, $p < .0001$, $\eta_p^2 = .429$. The separate ANOVA for the *mouth* region, $F(3, 76) = 10.44$, $p < .0001$, $\eta_p^2 = .292$, revealed that it was *more* salient for happy faces than for all the other expressions.

Eye region masked with lower face half visible: (2) Saliency time course

An expression by region interaction emerged for the probability of the first saliency outburst, $F(3, 76) = 41.57$, $p < .0001$, $\eta_p^2 = .621$, and the probability that it occurred during the first 150 ms, $F(3, 76) = 19.45$, $p < .0001$, $\eta_p^2 = .434$. The *mouth region* of happy faces was more likely to be salient first, relative to all the other expressions, $F(3, 76) = 41.57$, $p < .0001$, $\eta_p^2 = .621$, and during the first 150 ms, $F(3, 76) = 19.45$, $p < .0001$, $\eta_p^2 = .434$. Also, the average saliency onset, $F(3, 69) = 7.31$, $p < .0001$, $\eta_p^2 = .241$, and the order of the first saliency outburst, $F(3, 69) = 6.79$, $p < .0001$, $\eta_p^2 = .228$, occurred earlier for the happy mouth. The location of the *eye region* was never salient first or during the first 150 ms.

Mouth region masked with upper face half visible: (1) Mean visual saliency and (2) Saliency time course

The ANOVAs yielded no significant effects on visual saliency in this face format condition.

In sum, whenever the lower half of the face—including the whole face condition—was visible, the mouth of happy expressions was more salient than any other region of all the expressions, it became salient before the other regions, and this saliency advantage generally occurred within the first 150 ms following stimulus onset.

Behavioral data: categorization performance

Response accuracy and reaction times of correct responses were analyzed by means of 4 (Expression: happy vs. angry vs. surprised vs. neutral) × 3 (Format: whole face vs. upper half vs. lower half) repeated-measures ANOVAs. Greenhouse–Geisser corrections were applied, and Bonferroni adjustments ($p < .05$) were performed for post hoc multiple comparisons (see the mean scores and contrasts in Table 2).

For *response accuracy*, effects of expression, $F(3, 63) = 6.62$, $p < .001$, $\eta_p^2 = .240$, and format, $F(2, 42) = 18.81$, $p < .0001$, $\eta_p^2 = .472$, emerged. Happy expressions were correctly recognized more likely ($M = 97.4\%$) than the other expressions (angry: 92.4; surprised: 94.5; neutral: 94.3). Accuracy was higher in the whole face ($M = 97.4\%$) than in the upper (93.7) and the lower (94.2) face half conditions. These effects were qualified by an interaction, $F(6, 126) = 13.67$, $p < .0001$, $\eta_p^2 = .394$. In the whole face, $F(3, 63) = 5.82$, $p < .01$, $\eta_p^2 = .217$, and the lower face half, $F(3, 63) = 20.00$, $p < .0001$, $\eta_p^2 = .488$, conditions, accuracy was higher for happy faces than for the other expressions. In the upper face half condition, $F(3, 63) = 4.08$, $p = .019$, $\eta_p^2 = .163$, the angry faces were recognized more accurately than the others.

For *reaction times*, effects of expression, $F(3, 63) = 13.03$, $p < .0001$, $\eta_p^2 = .383$, and format, $F(2, 42) = 13.50$, $p < .0001$, $\eta_p^2 = .391$, revealed that happy faces were correctly recognized faster ($M = 784$ ms) than the others (angry: 854; surprised: 827; neutral: 867), and responses were faster in the whole face ($M = 802$ ms) than in the upper (861) and the lower (836) face half conditions. These effects were qualified by an interaction, $F(6, 126) = 8.14$, $p < .0001$, $\eta_p^2 = .279$. In the whole face, $F(3, 63) = 7.92$, $p < .001$, $\eta_p^2 = .274$, and the lower face half, $F(3, 63) = 15.74$, $p < .0001$, $\eta_p^2 = .428$, conditions, responses were faster for happy faces than for the others. In the upper half condition, $F(3, 63) = 8.63$, $p < .01$, $\eta_p^2 = .291$, all three emotional expressions were recognized faster than the neutral faces.

Complementary analyses explored the diagnostic value of the eyes and the mouth for each expression, by means of one-way ANOVAs (Format: whole face vs. upper vs. lower face halves; see Table 2). For *happy* faces, accuracy was higher, $F(2, 42) = 14.18$, $p < .0001$, $\eta_p^2 = .403$, and reaction times were shorter, $F(2, 42) = 23.21$, $p < .0001$, $\eta_p^2 = .525$, in the whole face and the lower face half

Table 2
Mean probability of response accuracy (%) and reaction times (ms) of correct responses for each facial expression and face format, in the expression categorization task.

Face format	Type of expression			
	Happy	Angry	Surprised	Neutral
Response accuracy				
Whole face	**99.6 a/x**	97.4 b/x	97.2 b/x	95.5 b/y
Mouth region	**99.4 a/x**	87.9 c/y	91.8 bc/y	95.6 b/y
Eye region	93.3 b/y	**97.2 a/x**	94.4 b/y	92.0 b/y
Reaction times				
Whole face	**739 a/x**	831 b/x	806 b/x	831 b/x
Mouth region	**764 a/x**	909 c/y	837 b/x	833 b/x
Eye region	849 a/y	821 a/x	837 a/x	930 b/y

Note. Mean scores with a different letter are significantly different; means sharing a letter are equivalent. Letters a, b, c are used for *horizontal* comparison, across type of *expression*; letters x, y, z are used for *vertical* comparisons, across type of *format*.

conditions than in the upper half condition. For *angry* faces, accuracy was higher, $F(2, 42) = 34.85$, $p < .0001$, $\eta_p^2 = .624$, and reaction times were shorter, $F(2, 42) = 6.51$, $p < .01$, $\eta_p^2 = .237$, in the whole face and the upper face half conditions than in the lower half condition. For *surprised* faces, the effect on accuracy, $F(2, 42) = 12.01$, $p < .0001$, $\eta_p^2 = .364$, but not on response times ($F = 1.73$, $p = .20$), showed higher accuracy in the whole face condition. For *neutral* faces, the effect on reaction times, $F(2, 42) = 18.01$, $p < .0001$, $\eta_p^2 = .462$, showed slower responses in the upper face half condition.

In sum, whenever the mouth was visible, happy expressions were more likely to be recognized accurately, and they were recognized faster, than the other expressions, with equivalent recognition performance in the lower face half and the whole face conditions. When only the eye region was visible, angry expressions were recognized more accurately than the other expressions.

Neurophysiological data

Occipito-temporal ERP components (P1, N170, and EPN)

The mean amplitude values in the occipito-temporal cluster (see above, *2.7. ERP components*) were analyzed by means of Expression (4: happy, angry, surprised, and neutral) × face Format (3: whole face, upper half, lower half) × Hemisphere (2: right vs. left) repeated-measures ANOVAs. Greenhouse–Geisser correction was always added for all the analyses, and the main effects were followed by multiple post hoc comparisons.

For P1, effects of expression, $F(3, 63) = 7.85$, $p < .001$, $\eta_p^2 = .272$, and format, $F(2, 42) = 8.63$, $p < .001$, $\eta_p^2 = .291$, with no significant hemisphere effect ($F = 1.39$, $p = .25$) or the interactions (all Fs < 1), revealed a reduced positivity for happy faces ($M = 0.89$ µV) relative to angry ($M = 1.31$) and surprised ($M = 1.29$) faces, but not to neutral faces ($M = 1.10$), and for the whole face ($M = 0.81$) relative to the upper ($M = 1.24$) and the lower ($M = 1.39$) face halves, which did not differ from each other.

For N170, the analyses yielded effects of expression, $F(3, 63) = 5.17$, $p < .01$, $\eta_p^2 = .193$, and format, $F(2, 42) = 3.20$, $p = .050$, $\eta_p^2 = .132$, along with interactions between expression and hemisphere, $F(3, 63) = 3.11$, $p = .044$, $\eta_p^2 = .129$, format and hemisphere, $F(2, 42) = 4.30$, $p = .024$, $\eta_p^2 = .170$, and a three-way interaction, $F(6, 126) = 2.86$, $p = .023$, $\eta_p^2 = .120$. To decompose the interactions, one-way (Expression) ANOVAs were performed for each format and hemisphere. In the *left* hemisphere, no significant differences across expressions appeared for the whole face or the upper half condition (both Fs < 1), but there was an effect in the *lower* face half condition, $F(3, 63) = 4.48$, $p = .010$, $\eta_p^2 = .176$, with an enhanced N170 for happy faces relative to the other expressions, which did not differ from each other. In contrast, in the *right* hemisphere, the expression effect occurred only for the *whole* face condition, $F(3, 63) = 10.72$, $p < .0001$, $\eta_p^2 = .338$: All the emotional faces enhanced the N170 negativity to a greater extent than the neutral faces, and the angry faces enlarged negativity more than the surprised faces, which did not differ from the happy faces. These effects are shown in Figs. 2 (whole face) and 3 (eye and mouth regions).

For EPN, the effects of expression, $F(3, 63) = 5.52$, $p < .01$, $\eta_p^2 = .208$, and format, $F(2, 42) = 14.51$, $p < .0001$, $\eta_p^2 = .455$, but not of hemisphere ($F < 1$), were qualified by an expression by format interaction, $F(6, 126) = 3.88$, $p < .01$, $\eta_p^2 = .156$, and an expression by hemisphere interaction, $F(3, 63) = 3.30$, $p = .033$, $\eta_p^2 = .136$. One-way (Expression) ANOVAs for each format and hemisphere revealed significant differences only in the whole face condition, with a larger EPN for angry faces than for all the other expressions in the right hemisphere, $F(3, 63) = 5.48$, $p < .01$, $\eta_p^2 = .207$, and for angry faces relative to neutral faces also in the left hemisphere, $F(3, 63) = 3.80$, $p = .018$, $\eta_p^2 = .153$. These effects are shown in Figs. 2 and 3.

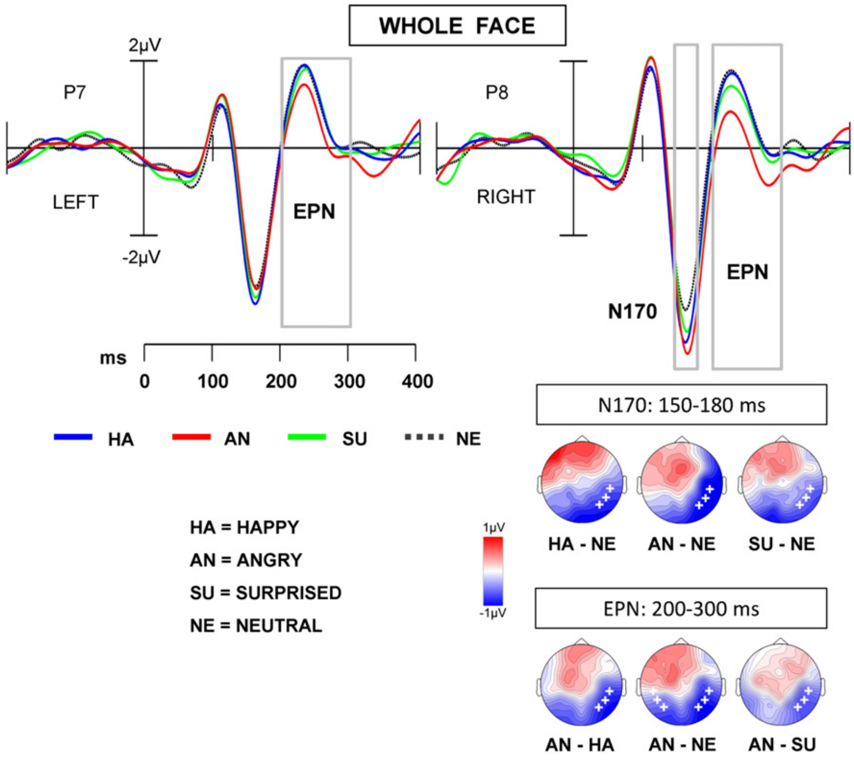


Fig. 2. *Expression and emotional encoding components for whole-face stimuli*. ERPs elicited at left and right temporo-occipital electrodes as a function of facial expression and face format. *Note*. Waves indicate the time course of ERP components (N170 and EPN) as indexed by two representative electrodes (P7/P8). Boxes on waveforms frame the components that were significantly modulated by expression. Maps show the scalp topography distribution of the ERP differences between expressions. Crosses in maps indicate the selected sites that composed the cluster showing significant differences.

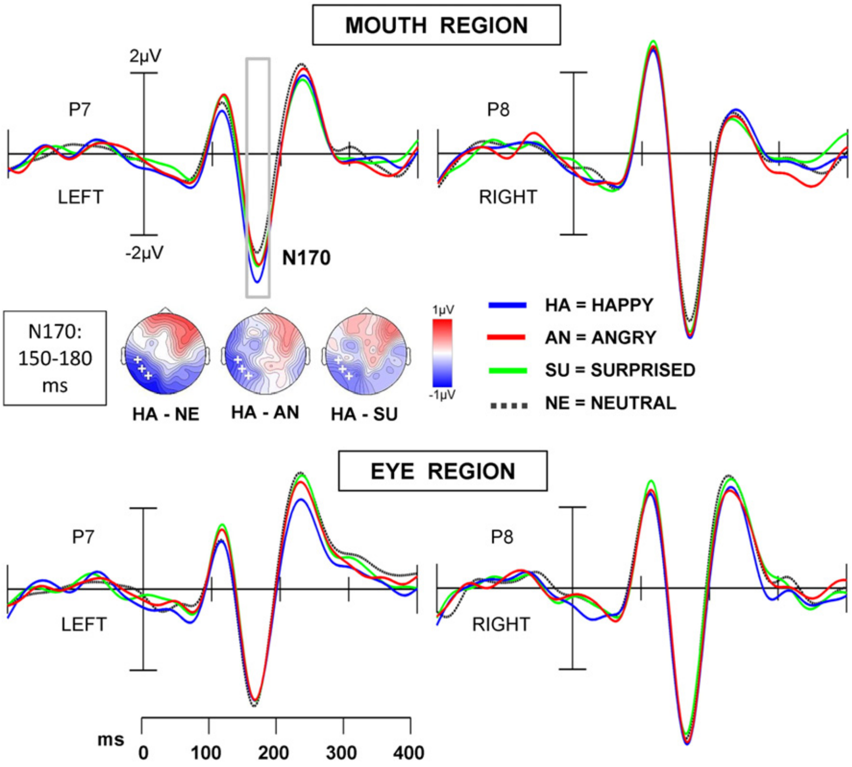


Fig. 3. *Expression encoding and emotional components for mouth and eye region stmuli*. ERPs elicited at left and right temporo-occipital electrodes as a function of facial expression and face format. *Note*. Waves indicate the time course of ERP components (N170 and EPN) as indexed by two representative electrodes (P7/P8). Boxes on waveforms frame the components that were significantly modulated by expression. Maps show the scalp topography distribution of the ERP differences between expressions. Crosses in maps indicate the selected sites that composed the cluster showing significant differences.

Fronto-central (N1, VPP, and N2) and centro-parietal (LPC) ERP components

To assess effects in the fronto-central cluster, we conducted Expression (4: happy, angry, surprised, and neutral) × face Format (3: whole face, upper half, lower half) repeated-measures ANOVAs. To analyze the LPC in the centro-parietal cluster, we included time segment as an additional factor in an Expression (4) × Format (3) × Time (2: 300–450 ms—or P3b—vs. 450–600 ms—or LPP) ANOVA.

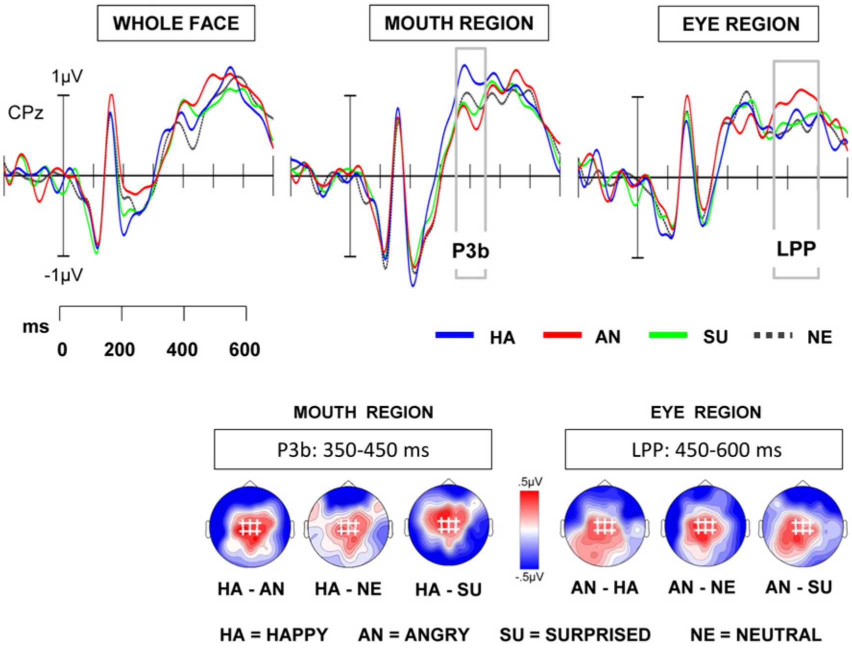


Fig. 4. *Expression categorization components*. ERPs elicited at centro-parietal electrodes as a function of facial expression and face format. *Note*. Waves indicate the time course of ERP components (P3b and LPP) as indexed by one representative electrode (CPz). Boxes on waveforms frame the components that were significantly modulated by expression. Maps show the scalp topography distribution of the ERP differences between expressions. Crosses in maps indicate the selected sites that composed the cluster showing significant differences.

For N1, effects of expression, $F(3, 63) = 5.11$, $p < .01$, $\eta_p^2 = .196$, and format, $F(2, 42) = 9.25$, $p < .001$, $\eta_p^2 = .306$, with no significant interaction ($F < 1$), revealed a reduced negativity for happy faces ($M = -0.66\ \mu V$) relative to angry ($M = -0.98$) and surprised faces ($M = -0.99$), but not to neutral faces ($M = -0.81$), and for the whole face ($M = -0.56$) relative to the upper ($M = -1.00$) and the lower ($M = -1.02$) face halves. For VPP, only the format effect was significant, $F(2, 42) = 6.21$, $p < .01$, $\eta_p^2 = .228$, with an enhanced positivity for the whole face ($M = 2.57\ \mu V$) and the lower face half ($M = 2.54$) relative to the upper half ($M = 2.08$). Consistently, for N2, only the format effect, $F(2, 42) = 56.41$, $p < .01$, $\eta_p^2 = .228$, showed a reduced negativity for the whole face ($M = -1.06\ \mu V$) and the lower face half ($M = -0.93$) relative to the upper half ($M = -2.22$).

For the LPC, effects of format, $F(2, 42) = 4.64$, $p = .021$, $\eta_p^2 = .181$, and time segment, $F(1, 21) = 5.92$, $p = .024$, $\eta_p^2 = .220$, emerged, along with an expression by time segment, $F(3, 63) = 4.78$, $p < .01$, $\eta_p^2 = .185$, and a three-way, $F(6, 126) = 5.04$, $p < .001$, $\eta_p^2 = .194$, interactions. Subsequently, one-way (Expression) ANOVAs were performed for each face format and time segment. No significant differences appeared in the whole face condition ($Fs \leq 1$). However, in the *lower* face half condition, there was an effect of expression on the *first* segment, $F(3, 63) = 4.36$, $p < .01$, $\eta_p^2 = .172$, with an enhanced P3b for *happy* faces relative to the other expressions, which did not differ from each other. In contrast, in the *upper* face half condition, there was an effect of expression on the *second* segment, $F(3, 63) = 4.25$, $p = .016$, $\eta_p^2 = .168$, with an enhanced LPP for *angry* faces relative to the other expressions, which did not differ from each other. These effects are shown in Fig. 4.

In sum, when *whole* faces were presented, all the emotional expressions elicited a greater *right* hemisphere N170 (150–180 ms) and EPN (200–300 ms) activity than neutral expressions. When only the lower face half (*mouth* region) was displayed, *left* temporo-occipital activity (150–180 ms) was more negative for happy faces than for the others. In addition, the LPC (*centro*-parietal) activity was enhanced by the happy mouth earlier (350–450 ms) than by the angry eyes (450–600 ms).

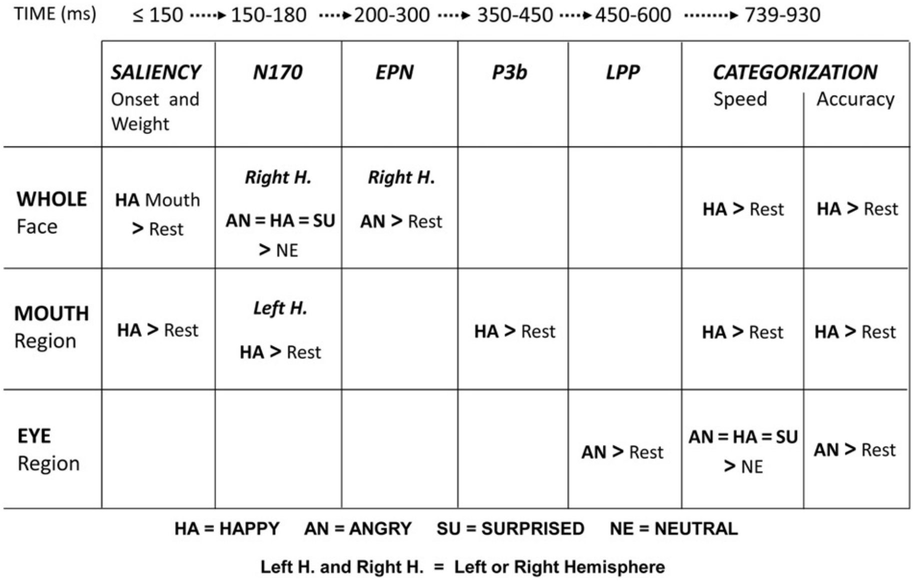
Discussion

Prior ERP research on facial expressions has generally considered the face as a whole. The current study makes a contribution by investigating the ERP modulations produced by informative regions such as the eyes and the mouth separately. By means of behavioral, computational modeling, and EEG measures, we explored the mechanisms underlying the role of the eyes and the mouth in the recognition of facial happiness, anger, and surprise. A major finding that was common to all three measures involved interactions between type of expression and region (or face format). Such interactions are useful to integrate the respective cognitive, perceptual, and neural processes, and examine their interplay in the recognition of emotional expressions.

Major findings and theoretical relevance

First, our ERP data indicated that *right* hemisphere N170 (150–180 ms) and EPN (200–300 ms) were modulated by expression of *whole* faces, but not by separate regions. In contrast, the lower half (mouth region) of happy faces enhanced *left* temporo-occipital activity (150–180 ms), and the LPC (centro-parietal) activity earlier (P3b: 350–450 ms) than the angry eyes (LPP: 450–600 ms) or other regions. Second, behavioral measures showed that, when the *mouth*—but not the eye—region was visible, *happiness* was recognized more accurately *and* faster than the other expressions, and as accurately and fast as when the whole face was displayed, thus demonstrating the highly diagnostic value of the smiling mouth. In contrast, the *eye*—but not the mouth—region facilitated the recognition of *anger*, whereas neither the eyes nor the mouth alone played a significant role in the recognition of surprise. Third, computational modeling of local visual saliencies revealed that the mouth region of happy faces was more salient than any other region of all the expressions. Importantly, this occurred early, within the first 150 ms following stimulus onset, thus allowing for an influence of visual saliency on ERP components such as the N170, which typically unfold in an upcoming time window. These major findings are summarized in Fig. 5.

These results are relevant to link brain lateralization with holistic (i.e., integration of expressive sources in a face) versus analytic (i.e., perception of separate regions) mechanisms, and how visual saliency can selectively drive them. Facial expression recognition is both holistic and analytic (see Tanaka et al., 2012). Our results add to this by showing that the role of each mechanism varies as a function processing stage, hemisphere, and the saliency of expressive face regions. First, ERP measures revealed early holistic encoding at right hemisphere sites, as reflected by modulation of the N170 and EPN amplitude only when whole faces were presented. Nevertheless, there was evidence of early analytic encoding of highly salient regions (i.e., the smiling mouth) at left hemisphere sites (N170 left) when regions were displayed



TIME (ms)	≤ 150	150-180	200-300	350-450	450-600	739-930	
	SALIENCY Onset and Weight	***N170***	***EPN***	***P3b***	***LPP***	***CATEGORIZATION*** Speed	Accuracy
WHOLE Face	**HA** Mouth **>** Rest	***Right H.*** **AN = HA = SU > NE**	***Right H.*** **AN >** Rest			**HA >** Rest	**HA >** Rest
MOUTH Region	**HA >** Rest	***Left H.*** **HA >** Rest		**HA >** Rest		**HA >** Rest	**HA >** Rest
EYE Region					**AN >** Rest	**AN = HA = SU > NE**	**AN >** Rest

HA = HAPPY AN = ANGRY SU = SURPRISED NE = NEUTRAL

Left H. and Right H. = Left or Right Hemisphere

Fig. 5. *Summary of findings*. Comparisons of saliency, ERP, and categorization, as a function of face format and expression.

separately. At later categorization stages, brain activity was also enhanced by encoding of separate regions, but it was no longer lateralized (P3b and LPP, centro-parietal). Second, behavioral measures also revealed holistic encoding, as reflected by the main effect of face format, with the whole face yielding more accurate and faster responses than the part-face conditions. At the same time, however, there was evidence of enhanced recognition of specific regions, such as the smiling mouth and the angry eyes, with equivalent performance when they were presented alone and when the whole face was displayed. Third, visual saliency drives analytic processing specifically at early perceptual stages (N170, left). The enhanced processing of single regions (smiling mouth and angry eyes) at later categorization stages (P3b and LPP, and explicit recognition) is probably due more to their diagnostic value (see Calder et al., 2000; Calvo et al., 2014) than to saliency: Both the smiling mouth and the angry eyes facilitated categorization, and both are highly diagnostic of their respective expressions, yet the angry eyes are not salient.

Altogether, our lateralization effects for N170 and EPN are consistent with those found by fMRI (e.g., Maurer et al., 2007), EEG (Scott and Nelson, 2006), and TMS (Renzi et al., 2013) research on face identity discrimination. Previous studies using these techniques have found an enhanced neural activity at several areas of the right or the left hemisphere during the processing of configural or featural aspects of the faces, respectively (see 1. Introduction). Furthermore, such effects were detected in a temporal window covering the N170 and the EPN components. In the previous studies, face discrimination was investigated (e.g., by means of same/different judgments about pairs of faces) using non-expressive, neutral faces. We have extended this approach to faces with emotional content and to expression recognition tasks. Holistic or configural processing of expressive and emotional information is preferentially performed by the right hemisphere. In contrast, the more analytic or part-based processing occurs in the left hemisphere, but makes little or no contribution to expression or emotional encoding within the first 300 ms following stimulus onset. Analytic processing in central hemisphere locations facilitates the later semantic categorization of expressions.

Specific ERP modulations by facial expression and region (or format)

Early ERP components (N1 and P1)

The N1 and P1 potentials (100–140 ms) were smaller in amplitude for happy relative to angry and surprised, but not neutral, faces. These effects cannot be attributed to attentional capture by emotional content, as the P1/N1 values for neutral faces did not differ from those of the other expressions. In prior research, evidence is not totally consistent in terms of whether emotional faces modulate the P1 and N1 (Calvo and Beltrán, 2013; Frühholz et al., 2009; see Smith et al., 2013). Our findings, nevertheless, converge with those from some studies where N1 and/or P1 were reduced for happy relative to other expressions (generally, fearful and angry; Luo et al., 2010; Rellecke et al., 2012; Santesso et al., 2008; Williams et al., 2006). In any case, the P1/N1 effects are not specifically concerned with the aims and hypotheses of the current study, as we found no interaction between expression and face format. Importantly, the lack of an interaction suggests that the diagnostic value of the eyes and the mouth is not yet encoded at this early stage.

Middle-latency range components (VPP and N2; N170 and EPN)

The fronto-central VPP (150–180 ms) and N2 (200–300 ms) components were responsive to stimulus format only, with the upper face half reducing the VPP and enhancing the N2. The lack of expression effects or an interaction downplays the importance of the format effects. Both VPP (Luo et al., 2010; Willis et al., 2010) and N2 (Ashley et al., 2004; Williams et al., 2006) have, nevertheless, proved to be modulated by emotional expression in prior research using intact, whole face stimuli. It is possible that such fronto-central components involve holistic processing—therefore requiring whole face stimuli—and thus the effects disappear when isolated face parts are presented. In fact, when we analyzed the *whole* face condition separately, the effect of expression was significant ($p = .014$), with all the emotional faces enhancing VPP relative to the neutral faces, in concordance with prior research (see Smith et al., 2013).

The temporo-occipital N170 (150–180 ms) and EPN (200–300 ms) potentials were both sensitive to stimulus format and expression; and, most importantly, to specific combinations of format, expression, and hemisphere. The N170 is typically associated with right hemisphere activity and is involved in the configural processing of a face (Rossion and Jacques, 2012). Consistently, in the current study, the N170 was responsive to facial expression in the *right* hemisphere only when the *whole* face was displayed, but not when either the top or the bottom halves were presented. All the emotional faces enhanced the N170 relative to neutral faces. This reveals that emotional expression was discriminated from neutral expression. This adds to a series of studies showing N170 expression modulation (e.g., Frühholz et al., 2009; Luo et al., 2010; Rellecke et al., 2012; Williams et al., 2006), although there are also discrepant findings (for a review, see Rellecke et al., 2013).

In contrast, in the *left* hemisphere, the N170 was modulated by expression when the *bottom* face half was displayed, with an enhanced amplitude for happy faces. As the smiling mouth was visually salient by 150 ms from face onset, and it has been shown to attract overt attention early (see Calvo and Nummenmaa, 2008), the bottom half of happy faces probably augmented the left N170 negativity due to the smile saliency. When holistic encoding is broken down due to the presentation of isolated face regions, discrimination would rely on perceptually salient features. Importantly, however, given that the left-hemisphere effect was equivalent for the angry, surprised, *and neutral* faces, it follows that the effect of happy faces does not reflect emotional processing. The analysis of isolated salient features such as the smile would capture attention, and thus pave the way for the identification of the expressive category later, but would not allow for discrimination of emotional content itself.

Following the N170, an EPN deflection appeared for angry relative to neutral faces and the other expressions. The EPN is linked with the processing of emotional valence and arousal of visual images (see Hajcak et al., 2012; Olofsson et al., 2008) and faces (Calvo and Beltrán, 2013; Frühholz et al., 2011; Rellecke et al., 2012; Wronka and Walentowska, 2011). In our study, the EPN represents an extension of the N170, as both occurred mainly in the right hemisphere and when full faces were displayed. Nevertheless, the enhanced EPN for angry expressions suggests that, beyond the rough discrimination of *affective* versus *neutral* content occurring at the N170 stage, a more refined *negative* versus *non-negative* affect discrimination takes place at the EPN stage. This is consistent with prior research where angry faces normally produce a larger EPN than happy faces (Balconi and Pozzoli, 2003; Rellecke et al., 2011, 2012; Schupp et al., 2004). Importantly, the EPN modulation only by whole face—but not by half face—stimuli further supports the hypothesis that the encoding of emotional significance requires holistic processing.

Late positive complex (P3b and LPP)

Effects at centro-parietal sites were observed for P3b (350–450 ms) and LPP (450–600 ms). An expression by format by time segment interaction revealed an augmented P3b for the bottom half of happy faces, and an enhanced LPP for the top half of angry faces. Prior research has found expression modulation of P3b (Balconi and Mazza, 2009; Luo et al., 2010; Willis et al., 2010) and LPP (Frühholz et al., 2009; Leppänen et al., 2007; Schacht and Sommer, 2009). These components reflect the assignment of processing resources to stimulus evaluation in relation to task performance (Folstein and Van Petten, 2011; Polich, 2012). In the current categorization task, they could thus reveal elaborative processes in discrimination between categories (Schacht and Sommer, 2009). Such a resource allocation took place earlier for the mouth region of happy faces than for the eye region of angry faces.

This suggests that the diagnostic value of an expressive source in a face becomes functional and contributes to expression categorization at this stage. As this effect occurs earlier for happy faces, it is understandable that they finally enjoy a categorization advantage over all the other expressions. Presumably, the representation of the whole happy expression can be easily constructed or inferred from the smiling mouth alone, as a shortcut for expression categorization (see Adolphs, 2002).

Limitations and future directions

To examine the role of holistic processing, we compared whole- versus part-face conditions. Nevertheless, to keep the part-face format as natural as possible, expressive features (e.g., eyes) were presented within a facial context, rather than totally isolated: half of the face was visible and the other half—although masked—kept a normal spatial orientation and contour. The main expressive sources (i.e., eyes and mouth) were thus surrounded by the face areas and structure within which they typically appear in a face. As Rossion (2013) has argued, a whole face representation might be activated automatically even if only part of the face is available to the visual system; and this would be more likely to occur when a facial feature is highly diagnostic and when it is embedded in a relatively large region, as was the case in our study. This implies that, to truly isolate the effect of single expressive features from that of a holistic reconstruction, they should be separated from the typical configural orientation of a face. In addition, as indicated by Richler et al. (2012), different measures of holistic processing map onto different aspects and meanings, and therefore it is important to establish convergent validity by using complementary measures.

Accordingly, to further distinguish between a holistic and an analytic conceptualization, alternative approaches could be adopted, such as the spatial inversion and the composite face paradigms. They have frequently been used to assess processing of face identity (see Richler et al., 2012; Rossion, 2013) and emotional expression (inversion: e.g., Calder et al., 2000, or Calvo et al., 2012; composite: e.g., Calder et al., 2000, or Calvo et al., 2013a). In the inversion task, holistic processing is measured as better recognition when the face is presented upright than when presented upside-down. As inversion disrupts configural rather than featural information, face or expression processing are assumed to be featurally driven to the extent that recognition is not impaired by inversion. In the composite task, participants judge whether one face half (e.g., top) of two faces is the same or different, while ignoring the other face half (e.g., bottom). Holistic processing is measured as interference, i.e., difficulty in the accurate identification of the attended half, when both face parts are aligned (and belong to different identities) relative to when they are misaligned.

These paradigms could be applied to ERP measures and expression recognition. To the extent that the recognition of expressions (particularly, happy) relies on the analysis of a salient and diagnostic feature (e.g., smiling mouth), the enhanced N170 at left hemisphere sites, as well as the enhanced P3b, should remain under stimulus inversion versus upright orientation, and for misaligned relative to aligned composite faces. Also, this would be followed by a preserved (or less impaired) categorization accuracy and response speed for happy faces in the inverted and the misaligned conditions. In contrast, if holistic processing drives the encoding of expressions, the enhanced N170 at right hemisphere sites for all the emotional relative to neutral faces, as well as the enhanced EPN at right sites for angry faces, should disappear (or, at least, be delayed) under inversion (see Rellecke et al., 2013) and misaligned conditions. In general, the presence of a salient and diagnostic feature in a face will resist the disrupting effects of inversion and misalignment on expression recognition.

Conclusions

The present results support the view that holistic and analytic facial expression processing at early stages are lateralized. Early *analytic* encoding of separate facial *regions* occurs mainly in the *left* hemisphere: The mouth region of happy faces enhanced neural activity in the left (temporo-occipital) hemisphere, with this effect (150–180 ms after stimulus onset) being driven by visual saliency, rather than reflecting expression recognition or extraction of affective content. In contrast, *holistic* encoding is performed by the *right* hemisphere, allowing for expression and emotion discrimination: The N170 (150–180 ms) and the EPN (200–300 ms) activity was modulated only (N170) or mainly (EPN) in the right (temporo-occipital) hemisphere when *whole* faces—but not when isolated regions—were presented. The smile itself becomes functional for expression recognition at a later stage where processing resources are allocated before to happy (P3b; 350–450 ms) than to angry (LPP; 450–600 ms) and other expressions, with the effect not being lateralized (centro-parietal sites). This reveals the neurocognitive basis of the smile diagnostic value underlying the typical happy face categorization advantage.

Acknowledgments

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