



HAL
open science

Task-related modulation of facial expression processing: An FPVS-EEG study

Jean-Yves Baudouin, Fanny Poncet, Armand Polinori, Diane Rekow, Fabrice Damon, Arnaud Leleu, Laurence Faivre, Nicolas Baltenneck

► **To cite this version:**

Jean-Yves Baudouin, Fanny Poncet, Armand Polinori, Diane Rekow, Fabrice Damon, et al.. Task-related modulation of facial expression processing: An FPVS-EEG study. *Emotion*, 2023, Advance online publication. 10.1037/emo0001223 . hal-04094472

HAL Id: hal-04094472

<https://hal.inrae.fr/hal-04094472>

Submitted on 28 Mar 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Task-related modulation of facial expression processing: an FPVS-EEG study

Jean-Yves Baudouin ¹, Fanny Poncet ², Armand Polinori ¹, Diane Rekow ², Fabrice Damon ²,
Arnaud Leleu ², Laurence Faivre³, and Nicolas Baltenneck ¹

¹ Laboratoire "Développement, Individu, Processus, Handicap, Éducation" (DIPHE), Department Psychologie du Développement, de l'Éducation et des Vulnérabilités (PsyDÉV), Institut de psychologie, Université de Lyon (Lumière Lyon 2), 5, avenue Pierre-Mendès-France, 69676 Bron cedex, France

² Development of Olfactory Communication & Cognition Lab, Centre des Sciences du Goût et de l'Alimentation, Université Bourgogne Franche-Comté, CNRS, Institut Agro Dijon, Inrae, F-21000 Dijon, France

³ Inserm UMR 1231 GAD, Genetics of Developmental disorders, and Centre de Référence Maladies Rares "Anomalies du Développement et syndromes malformatifs", FHU TRANSLAD, CHU Dijon and Université de Bourgogne-Franche Comté, 21000 Dijon, France

Corresponding author: JYB (j.baudouin@univ-lyon2.fr)

Corresponding address: Département de psychologie du Développement, de l'Éducation et des Vulnérabilités (psyDEV), Bureau L 150, 5 Avenue Pierre Mendès-France, 69676 Bron Cedex, France

Abstract

In the current study, we examined the role of task-related top-down mechanisms in the recognition of facial expressions. An expression of increasing intensity was displayed at a frequency of 1.5 Hz among the neutral faces of the same model that displayed at a frequency of 12 Hz (i.e., 12 frames per second, with the expression occurring every 8 frames). Twenty-two participants were asked either to recognize the emotion at the expression-specific frequency (1.5 Hz) or to perform an orthogonal task in separate blocks, while a scalp electroencephalogram (EEG) was recorded. A significant 1.5 Hz response emerged with the increase in expressive intensity over medial occipital, right and left occipito-temporal, and centro-frontal regions. In these three regions, the magnitude of this response was greater when participants were involved in expression recognition, especially when the intensity of expression was low and ambiguous. Time domain analysis revealed that engagement in the explicit recognition of facial expression caused a modulation of the response even before the onset of the expression over centro-frontal regions. The response was then amplified over the medial occipital and right and left occipito-temporal regions. Overall, the procedure developed in the present study allowed us to document different stages of the voluntary recognition of facial expressions, from detection to recognition, through the implementation of task-related top-down mechanisms that modulated the incoming information flow.

Keywords Fast Periodic Visual Stimulation coupled with EEG, facial expression recognition, task-related top-down mechanisms

Introduction

Emotional communication has been a central topic of scientific research since Darwin published his book "The Expression of the Emotions in Man and Animals" in 1872. A hotly debated issue is whether there are discrete facial expressions of emotion that are universally and innately recognized, allowing interpersonal communication of emotional state regardless of cultural background (Darwin, 1872; Ekman & Friesen, 1971; Izard, 1971; Tomkins, 1962), or whether emotions relate to a cognitive and/or social construct, which integrates the experience of the individual within the framework of a specific cultural environment, including native language (Wundt, 1896; Plutchik, 1962, 1980; Russell & Fernandez-Dols, 1997; Barrett, 2012, 2017). Beyond these fundamental implications, difficulties in recognizing emotional facial expressions are present in many diseases where the disorders appear to affect high-level cognitive functions more than the visual perceptual mechanisms themselves (e.g., in schizophrenia: Baudouin, Martin, Tiberghien, Verlut, & Franck, 2002; Berkovitch, Del Cul, Maheu, & Dehaene, 2018). Therefore, understanding how the brain and cognitive systems enable the recognition of emotional facial expressions requires taking into account both the bottom-up and top-down aspects as well as the fundamental and applied perspectives. In other words, it is essential to have a picture of all the mechanisms involved (whether automatic or controlled, task-specific or not) to understand how emotion is read in facial expression in the neurotypical population and why certain neurological and psychiatric disorders prevent or impair this ability.

Scalp electroencephalography (EEG) has been widely used to investigate the temporal course of emotional facial expression processing due to its very good temporal resolution (for reviews, see Calvo & Nummenmaa, 2015; Vuilleumier & Pourtois, 2007). Classical event-related potentials (ERPs) show that the differential processing of emotional vs. neutral faces occurs approximately 150-300 ms poststimulus over occipito-temporal and occipito-parietal sites (e.g., Calvo, Marrero, & Beltrán, 2013; Leleu, Godard, Dollion, Durand, Schaal, & Baudouin, 2015; Williams, Palmer, Liddell, Song, & Gordon, 2006). The categorization of facial expressions in discrete categories is examined further from

approximately 300 ms after stimulus onset at the level of several late components with distinct topographies across studies (P3b: Luo, Feng, He, Wang, & Luo, 2010; late positive potential/LPP: Leppänen, Kauppinen, Peltola, & Hietanen, 2007; slow positive waves/SPWs: Calvo & Beltrán, 2013; posterior negativity: Ashley, Vuilleumier, & Swick, 2004). The coupling of frontal and parietal regions has also been shown to be important in the recognition of facial expressions in magnetoencephalography (Kajal, Fioravanti, Elshahabi, Ruiz, Sitaram, & Braun, 2020). Conclusions regarding brain facial expression categorization remain unclear, however, since no solid and systematic pattern has been reliably found (for discussions, see Calvo & Nummenmaa, 2015; Dzhelyova et al., 2017).

A growing number of studies have investigated the automatic brain response to facial emotions using a new approach coupling fast periodic visual stimulation with electroencephalography recordings (FPVS-EEG approach; for a review, see Norcia, Appelbaum, Ales, Cottareau, & Rossion, 2015). The periodic display of a set of visual stimuli at a defined and rapid frequency (e.g., 6 Hz, corresponding to 6 images per second) triggers a periodic response from the brain at the same frequency (also referred to as “steady-state visually evoked potential”, Regan, 1966, 1989; see also Adrian & Matthews, 1934). This noninvasive approach has several advantages, as it is objective (i.e., the brain response is investigated at a predetermined frequency), provides high signal-to-noise ratio (SNR) data (especially when compared to the traditional ERP approach), and is recorded in a relatively short amount of time (i.e., in a few minutes) (Norcia et al., 2015). Furthermore, by periodically inserting a type of stimuli (e.g., faces) at a frequency of interest (e.g., 1.2 Hz) among a stream of other stimuli (e.g., various objects) displayed at the base frequency (e.g., 6 Hz, with 6 pictures per second, and 1 face every 5 stimulations), two brain responses can be dissociated within a single stimulation sequence. The base response recorded at 6 Hz reflects brain synchronization to the visual presentations of multiple object categories, a visual general response. The response measured at the frequency of interest (i.e., 1.2 Hz) is the face-specific response, a direct marker of the brain discrimination between faces and nonface objects without subtracting any

control condition response (i.e., a direct differential response to the perceived change of category). This approach allowed to isolate a neural signature of face categorization in adults (Rossion, Torfs, Jacques, & Liu-Shuang, 2015) and in infants (de Heering & Rossion, 2015; see also Leleu, Rekow, Poncet, Schaal, Durand, Rossion, & Baudouin, 2020) and children (Lochy, de Heering, & Rossion, 2019). Similar signatures were also reported for face identity processing (Xu, Liu-Shuang, Rossion, & Tanaka, 2017; see also Damon, Leleu, Rekow, Poncet, & Baudouin, 2020; for a review: Rossion, Retter, & Liu-Shuang, 2020), gender categorization (Rekow, Baudouin, Rossion, & Leleu, 2020), facial attractiveness discrimination (Luo, Rossion, & Dzhelyova, 2019), or, more central to our purpose, facial expression discrimination (Dzhelyova, Jacques, & Rossion, 2017).

Investigating automatic facial expression processing with this approach, Dzhelyova et al. (2017) displayed expressive faces at a specific frequency among neutral faces of the same model displayed at the base frequency. They recorded a response to the brief facial expression changes over occipito-temporal scalp regions that tended to be larger over the right hemisphere, with slight topographical differences between expressions and a strong reduction following picture-plane inversion. In the time domain, the differential response between expressive and neutral faces took the form of three components: an early positivity at approximately 100–130 ms over posterior dorsal regions, followed by a negativity at approximately 150–210 ms, and a later positivity at approximately 210–310 ms, both over occipito-temporal regions. Dzhelyova et al. (2017) proposed that the two first components reflected the early activation within the ventral and lateral occipito-temporal cortex corresponding to expression-change detection, while the third component supported more elaborate processing. Replicating the occipito-temporal response to facial emotion discrimination with the same or other expressions, Leleu et al. (2018) also reported that the response increases with expression intensity, especially for intensities close to the perception threshold, indicating a categorical perception (see also Gray, Flack, Yu, Lygo, & Baker, 2020). In time domain analysis, this categorical perception operates from 300 ms onward, affecting only the third component. Expanding these findings, Poncet, Baudouin, Dzhelyova, Rossion and Leleu (2019)

further reported a specific neural signature for each emotion category by periodically displaying an expression at the expression-specific frequency with the other expressions randomly displayed at the base frequency (see also Schettino, Porcu, Gundlach, Keitel, & Müller, 2020; Coll, Murphy, Catmur, Bird, & Brewer, 2019).

However, it is worth noting that in the aforementioned studies, facial expression processing was implicit and automatic, as participants were engaged in an orthogonal task driving attention away from the face (e.g., to detect a change in color or shape in the fixation shape displayed at the center of the face). Critically, the explicit recognition of the emotional content of facial expressions was not needed. Although such studies inform our understanding of the implicit and automatic recognition processes of emotional facial expressions, they fall short of explaining how the brain integrates this information. Indeed, explicit emotional information processing mobilizes or reinforces task-related top-down processes aimed at interpreting the content of facial expression. Numerous studies have pointed out that facial expressions are inherently ambiguous and that contextual factors influence their perception through feedback or top-down processes associated with the processing of contextual information or high-level cognitive functions, such as language (Barrett, Adolphs, Marsella, Martinez, & Pollak, 2019; Gendron, Lindquist, Barsalou, & Barrett, 2012; for reviews, see Barrett, Mesquita, & Gendron, 2011; Hassin, Aviezer, & Bentin, 2013; Wieser, & Brosch, 2012). In other words, discriminating emotional facial expressions is not a mere decoding of discrete facial actions through upward visual processing. The very meaning of these facial actions is built based on the context of their occurrences associated with the personal experience and the emotional concepts possessed by the individual (Hoemann, Xu, & Barrett, 2019). Within this framework, facial expression recognition relies on the processing of bottom-up visual information as much as on the feedback and top-down processes from high-level cognitive functions structuring perception. The latter could arise especially when the individual engages in an active recognition process.

Several studies have shown that involving participants in a specific task may shape the way the brain responds to their visual environment through task-related top-down influences over earlier

processing stages (for reviews and discussions, see de Lange, Heilbron, & Kok, 2018; Gilbert & Li, 2013). Such task-related modulation of neural responses was reported in high-level visual regions of the ventral temporal cortex that specifically respond to categories such as words, houses, or faces (Furey et al., 2006; Kay & Yeatman, 2017; see also Baldauf & Desimone, 2014; Kanwisher & Wojciulik, 2000; Peelen, Fei-Fei, & Kastner, 2009; Summerfield, Eger, Mangels, & Hirsch, 2006). Specifically, with regard to the recognition of emotional facial expressions, asking participants to explicitly recognize the expression increases the brain response in regions that are part of the facial emotion recognition system compared to implicit tasks or tasks that require processing other facial dimensions (e.g., Critchley et al., 2000; Fusar-Poli et al., 2009; Gorno-Tempini et al., 2001; Habel et al., 2007; Scheuerecker et al., 2007; Winston, O'doherty, & Dolan, 2003). It has also been found that attending to facial emotion also enhances effective connectivity between these regions (e.g., Cohen Kadosh, Cohen Kadosh, Dick, & Johnson, 2011) and cortical sensitivity (or representation) of facial expression in related areas (Dobs, Schultz, Bülhoff, & Gardner, 2018; see also Wang, Song, Zhen, & Liu, 2016). Regarding the temporal course of the modulation related to engagement in explicit facial emotion recognition, EEG and MEG studies showed that they started early, from approximately 150 ms after stimulus onset, at the level of N170 (see Eimer & Holmes, 2007; Hinojosa, Mercado, & Carretié, 2015; Streit et al., 1999; Monroe et al., 2013; Wronka & Walentowska, 2011), or perhaps from 100 ms (e.g., Wronka & Walentowska, 2014). These modulating effects frequently correspond either to an increase in the cerebral response or to the emergence of a differentiated response to the various expressions.

To our knowledge, three studies have already used the FPVS-EEG approach with tasks that explicitly asked to process the faces at the specific frequency (Quek, Liu-Shuang, Goffaux, & Rossion, 2018a; Quek, Nemrodov, Rossion, Liu-Shuang, 2018b) or at both the specific and base frequencies (Yan, Liu-Shuang, & Rossion, 2019), in order to compare the brain response obtained with that which occurs during an implicit task (Quek et al., 2018b; Yan et al., 2019). Neither investigated emotional facial expression processing, and in the two studies that compared explicit and implicit tasks, the

explicit task (detecting a female/male face) was designed to focus attention on the faces but did not directly address the information displayed at the specific frequency, i.e., they did not tag task-related top-down effects (face categorization in Queck et al., 2018b; individual face discrimination in Yan et al., 2019). However, they did show that attention to faces increases the occipito-temporal face categorization response, particularly in the nonpreferred hemisphere (i.e., typically the left hemisphere), with an increase in the amplitude and/or duration of the first two components in the time domain (Queck et al., 2018b; only the second component was amplified in the study by Yan et al., 2019). It also causes the appearance of central parietal and prefrontal responses associated with attentional processes (Yan et al., 2019).

Given these considerations, the present study investigated the brain's response to facial expressions when the participant is voluntarily engaged in emotion recognition using the FPVS-EEG approach. We displayed expressive faces at the expression-specific frequency (i.e., 1.5 Hz) with an expressive intensity that steadily increased during the stimulation sequence, while the neutral face of the same model was displayed at the base frequency (12 Hz). Participants were asked to perform two different tasks in separate stimulation sequences: either to detect the random change in color of the fixation cross (i.e., an implicit face processing task) or to recognize the expression that appears at the expression-specific frequency (i.e., an explicit facial expression processing task). Explicitly asking participants to recognize the expression at the specific frequency allowed us to tag the response from all the regions involved in facial expression recognition. The response of these regions, whether they are involved in the visual detection and discrimination of expressions or correspond to the implementation of higher-level cognitive mechanisms (e.g., cognitive monitoring of attention, verbal labeling), was locked in the expression-specific frequency (i.e., at 1.5 Hz). In contrast, in the implicit face-processing task, only the regions involved in the implicit and automatic discrimination of expressions were locked in on the expression-specific frequency. Hence, it was possible to demonstrate the implementation of task-related mechanisms (whether or not they are specific to

the processing of facial expressions) and their role in modulating visual discrimination responses by top-down influences.

Methods

We report how we determined our sample size, all data exclusions (if any), all manipulations, and all measures in the study.

Participants

Twenty-two participants (12 females, mean age=23.7 ± 4.5 (SD), range 20.2–34.9, 2 left-handed (1 female)) were included in the experiment. All of them reported normal or corrected-to-normal vision, and none reported a history of psychiatric or neurological disorders. Two additional participants were tested but not included in the analyses due to too there being many artifacts associated with their motor and/or oral responses. The sample size was estimated from previous studies that reported an occipito-temporal response to facial expressions (from 15 to 18 participants; Dzhelyova et al., 2017; Leleu et al., 2018; Poncet et al., 2019). Participants provided written informed consent prior to the experiment and received financial compensation. Testing was conducted in accordance with the Declaration of Helsinki and approved by the French ethics committee (CPP Sud-Est III-2016-A02056-45).

Visual stimuli

We used photographs of 6 models (3 females) from the KDEF database (Lundqvist, Flykt, & Öhman, 1998). The female models were F05, F09, and F21. The male models were M14, M32, and M34. For each model, we selected 6 front view pictures, one neutral and one for each emotion category (anger, disgust, fear, happiness, sadness). These expressions were well recognized in a previous study involving 40 adult participants (20 females; see Poncet et al., 2021) (anger: mean=96.3%, range=95-97.5; disgust: mean=90.8%, range=80-97.5; happiness: mean=100%, range=100-100; fear: mean=90.4%, range=77.5-97.5; sadness: mean=91.7%, range=85-97.5). Each of the 5 emotional expressions was morphed with the neutral expression with Morpheus software to obtain the progressive transition from the neutral to the emotional expression. Eleven levels of

morphing were extracted, starting from 0% emotional expression (i.e., neutral face) to 100% (i.e., fully expressive face), in steps of 10%. The pictures with the emotional expressions were adjusted to superimpose the main expressive features with the corresponding features in the neutral face, with the purpose of approximating a visual impression of a dynamic expression when an expressive face replaced the neutral face. The pictures were resized to 200x155 pixels from the top of the skull to the middle of the neck, with the face size adjusted to approximately 6×4.8 cm ($6 \times 4.8^\circ$ of visual angle at a viewing distance of 57 cm), and displayed in an oval-shaped medallion (see Figure 1).

Procedure

Stimuli were displayed on a computer screen (60 Hz refresh rate) with a mid-level gray background (i.e., 128/255 in grayscale) at a rapid rate of 12 Hz using custom software written in Java. At this rate, each stimulus lasted ≈ 83 ms. Neutral faces were displayed at the 12 Hz base rate, and an emotional expression was introduced every 8th stimuli, resulting in the brief occurrence of an expression at a rate of $12/8=1.5$ Hz (i.e., ≈ 677 ms between two expressive faces). To reduce expression change detection based on low-level visual cues, stimulus size was randomly varied between 90% and 110% at every stimulus onset (initial size was set to $6 \times 4.8^\circ$ of visual angle when displayed on the screen). A stimulation sequence started with a prestimulation interval of 0.5 s, followed by a 1.25 s fade-in of increasing contrast modulation depth. The stimulation at full contrast started immediately after the fade-in with the neutral face at both expression-specific and base frequencies for 4 seconds (i.e., displayed 6 times at expression-specific frequency). Then, the expression increased in intensity by 10% every 6 expression-specific stimulation cycles (i.e., every 4 sec). Ultimately, 100% expression was displayed 6 times at full contrast during an additional sequence of 3.417 s being replaced by another expression in half trials (randomly selected among the 4 other expressions) to introduce a new expression (see below). The full-contrast stimulation lasted 47.417 s ($(11 \text{ intensities} \times 4 \text{ s}) + 3.417 \text{ s}$). It was followed by a 0.583-sec fade-out of decreasing contrast modulation depth and a poststimulation interval of 0.25 s. The five expression conditions (anger, disgust, fear, happiness, and sadness) were repeated 12 times (6 individual faces \times 2 tasks),

resulting in 60 sequences of 50 s. Thus, each participant was stimulated with 2 Tasks x 5 Expressions x 6 Models = 60 sequences.

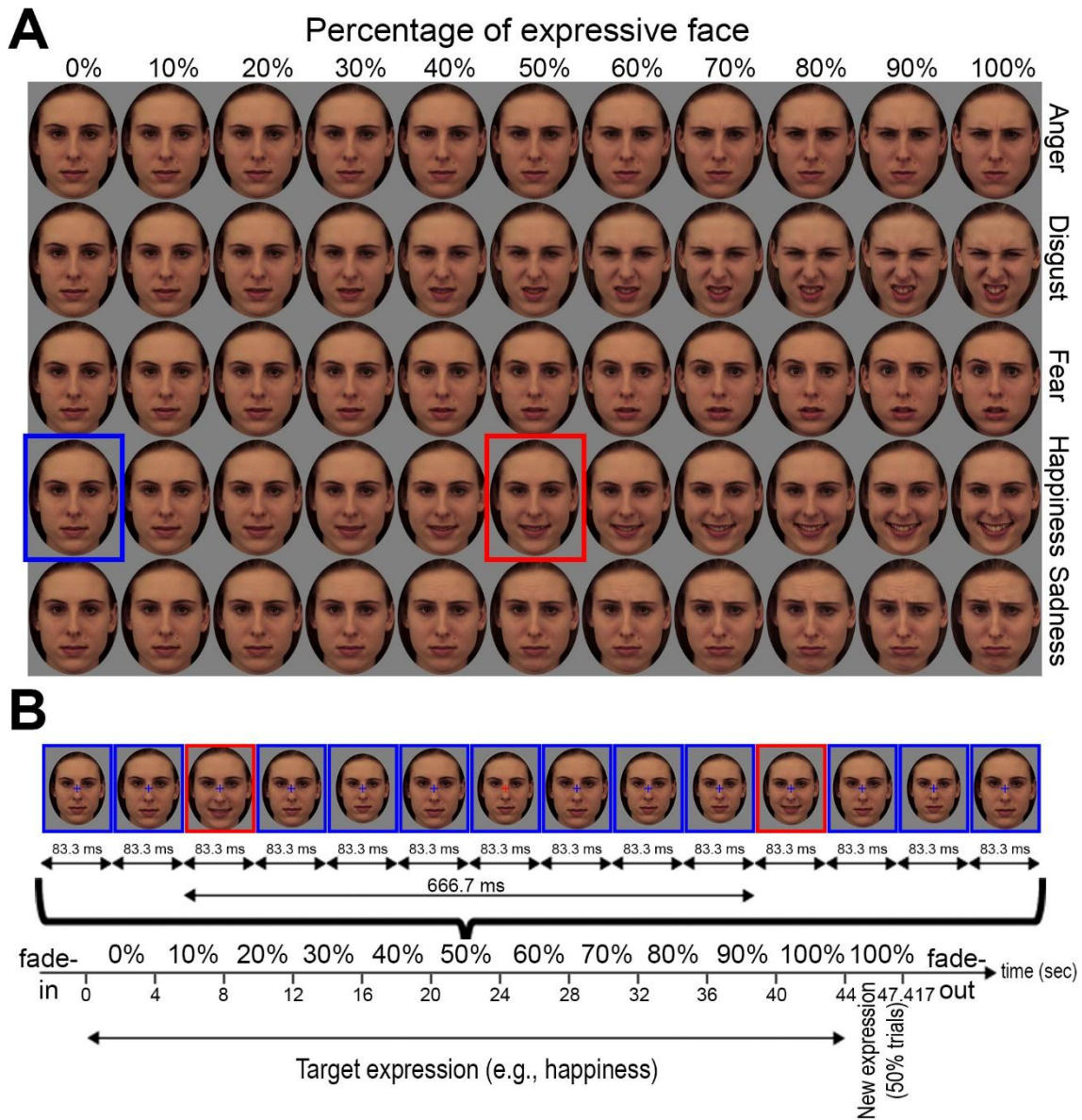


Figure 1. Illustration of the materials and procedure. **A:** The different intensities of expression for Model F09. Each expression was morphed with the neutral face of the same model. Eleven morph/intensity levels were created, ranging from neutral face (0% expressive face) to full expression (100% expressive face), with 10% steps. **B:** Illustration of the procedure for the presentation of the different items. After the fade-in, the neutral face was displayed at the base frequency (12 Hz, i.e., 12 times per second, with each image displayed for 83.3 ms). The expressive faces were inserted every 8 images at the expression-specific frequency (i.e., 1.5 Hz, with an interval of 667 ms between each expressive face). The face at the expression-specific frequency was neutral for the first 4 seconds, and then the intensity of the expression increased in steps of 10% every 4 seconds (i.e., after 6 stimulations) until it reached 100% (full expression) for 4 seconds. Thus, the entire stimulation of interest lasted 11 intensities x 4 seconds = 44 seconds. Before the fade-out, the full expression was displayed again at the expression-specific frequency (1.5 Hz) for 6 stimulations

(lasting 3.417 seconds) in half of the trials or was replaced by another randomly selected full expression in the other half.

Each participant completed 4 blocks of 15 sequences. In two blocks (emotion task), they had to recognize the emotional facial expression appearing at 1.5 Hz by pressing the space bar with both index fingers as soon as they recognized it and then verbally naming the emotion. Expression conditions were displayed in a random order within each block. To keep their attention on the faces even after they made their choice, they were informed that the expression might change after their response (i.e., corresponding to the second 3.417-sec of the 100% expression, with a 50% chance of new expression) and that they had to press the space bar a second time each time this happened. In the other two blocks (cross task), they had to press the space bar as quickly as possible again with both index fingers each time the blue cross at the center of the faces turned red. The cross randomly turned red 5 times during the sequence. Note that both motor and verbal responses occurred only one to five times during a sequence and were not periodic or synchronized with the frequencies of interest (1.5 and 6 Hz). The participants alternated between a block on the cross task and a block on the expression task, with the order of the blocks alternating between them.

EEG recording

EEG was continuously recorded from a 64-channel BioSemi Active-Two amplifier system (BioSemi, The Netherlands) with Ag/AgCl electrodes located according to the 10–10 classification system. During recording, the common mode sense (CMS) active electrode was used as a reference, and the driven right leg (DRL) passive electrode was used as the ground. Electrode offset was reduced between $\pm 25 \mu\text{V}$ for each electrode. EEG was digitalized at a sampling rate of 1024 Hz.

EEG preprocessing

EEG data were bandpass filtered at 0.1–100 Hz using a 4th order Butterworth filter and resampled to 512 Hz. Then, data were cropped in segments lasting 51.25 sec starting 1 s before the fade-in and ending 0.5 s after the fade-out, with a total of 60 sequences per participant (2 tasks x 5 expressions x 6 models), with the exception of two participants who were missing one sequence due

to technical problems during recording. To remove eye blinks and artifacts recorded over frontal electrodes (Fp1, Fpz, Fp2), we applied an independent component analysis (ICA) using the runica algorithm (Bell & Sejnowski, 1995). Muscular or other artifacts related to participants' activity (e.g., response-related movements) were corrected by rebuilding channels using linear interpolation from the four nearest electrodes. Our tasks required both a manual motor response and an oral response (in the emotion condition), with long sequences (51.25 sec) relative to other studies. The occurrence of at least one artifact during a sequence was frequent, and the application of strict criteria for interpolating the electrodes (e.g., channels containing activities exceeding 100 μV in at least two trials for the same emotion; Leleu et al., 2018) would result in a high proportion of interpolation (> 5%). However, these artifacts were not phase-locked with a specific frequency across sequences and occurred at a low frequency, different from the frequencies of interest in the FFT (i.e., 1.5 and 12 Hz and their harmonics). Thus, only those with strong consequences on low frequencies in FFT analyses (i.e., with activities exceeding $\pm 1000 \mu\text{V}$ in the time domain) were corrected (0.79% of channels). EEG segments were then rereferenced to a common average reference before further analyses.

Frequency-domain analysis

To avoid spectral leakage, the preprocessed EEG data were resegmented into epochs starting from the first full-contrast stimulation at expression-specific frequency minus 217 ms (i.e., after 2 stimulations at the base frequency before the first onset of an expression) and lasting 44 s or 22 528 bins (i.e., until the last stimulation at the expression-specific frequency + 5 stimulations at base frequency), with an integer number of cycles of expression change frequency (i.e., 1.5 Hz = 0.667 s or 341.33 bins per cycle). The 6 epochs for each emotion (i.e., from the 6 different models) were then averaged to reduce EEG activity nonphase-locked to the stimuli. Segments were transformed with the fast Fourier transform algorithm (FFT), and amplitude spectra were extracted for all channels with a frequency resolution of $1/44 = 0.0227$ Hz.

In the first step, analyses were run on the entire sequence (i.e., without taking into account the increasing expression intensities during the sequence) to investigate the main effect of the face-related task on the brain response with a good frequency resolution (i.e., 0.0227 Hz, see above). Individual FFT data were grand-averaged across participants for group analysis investigating the responses to the 5 expressions (anger vs. disgust vs. fear vs. happiness vs. sadness) in the two tasks (cross vs. emotion). Significant harmonics were identified for both the general visual (i.e., 12 Hz base stimulation frequency) and the expression-specific (i.e., 1.5 Hz periodic presentation of facial expressions) responses. FFT grand-averaged data were pooled across all electrodes and conditions, and Z scores were calculated at each frequency bin by subtracting the mean surrounding noise amplitude (i.e., estimated from the 20 surrounding frequency bins, 10 on each side, excluding the 2 immediately neighboring and the 2 most extreme values, Dzhelyova et al., 2017) and dividing it by its standard deviation. Harmonics were considered significant until Z scores were no longer above 1.64 ($p < .05$, one-tailed, signal > noise) for two consecutive harmonics. For the general visual response, significant harmonics were found until the 4th harmonic (i.e., 48 Hz, harmonics were not considered after the 50 Hz response elicited by AC power) ($91.81 < Z < 131.65$, $p < .0001$, one-tailed). For the expression-specific response, significant harmonics were found until the 11th harmonic (i.e., 16.5 Hz) ($3.25 < Z < 38.52$, $p < .0006$, one-tailed, after removing the 8th harmonic, i.e., 12 Hz).

To quantify the overall magnitude of each response in microvolts (μV), nonnormalized amplitudes were baseline-corrected (resulting in baseline-corrected amplitudes: bca) by subtracting the mean amplitude of the surrounding noise (i.e., 20 surrounding frequency bins excluding the 2 immediately neighboring and the 2 most extreme values). Summed harmonics were used to quantify the overall responses in single values expressed in microvolts (Retter and Rossion, 2016).

Topographical differences were also normalized according to scalp-wide global power (McCarthy and Wood, 1985), resulting in brain responses expressed in *arbitrary units* (au) (Leleu et al., 2018; Poncet et al., 2019). The resulting summed bca and normalized summed bca were calculated for every condition and participant and grand-averaged across participants for illustration purposes.

For complementary analyses investigating the response to the different expression intensities (from 0% to 100%, by steps of 10%), the previous 44 s time segments were further cropped into 11 segments of 4 s (i.e., 2048 bins). Then, the same procedure described above was used; the 6 epochs for a specific emotion (i.e., 6 models mimicking the same emotion) were averaged, and segments were transformed with the FFT to extract amplitude spectra for all channels with a frequency resolution of $1/4 = 0.25$ Hz (for an illustration, see Supplementary Figure S2A). To quantify the overall brain response, the same number of harmonics was summed as for the whole sequence (i.e., harmonics 1-4 for the general visual response and harmonics 1-7 and 9-11 for the expression-specific response). Note that applying the same procedure as above to select the harmonics gave rise to the same significant harmonics for 12 Hz frequency (harmonics 1-4: $6.91 < Z < 16.51$, $p < .0001$, one-tailed). For 1.5 Hz frequency, significant harmonics were harmonics 4, 5, 7 and 11 ($1.73 < Z < 3.54$, $p < .05$, one-tailed). Nonnormalized amplitudes were baseline-corrected by subtracting the mean amplitude of the surrounding noise (i.e., 8 surrounding frequency bins excluding the 2 most extreme values; the number of bins was reduced to adapt to the lower frequency resolution, see also Quek et al., 2018a). Topographical differences were also normalized according to scalp-wide global power (McCarthy and Wood, 1985). The resulting nonnormalized and normalized summed bca were calculated for every condition and participant and grand-averaged across participants for illustration purposes.

To define regions of interest (ROIs), we computed both average nonnormalized and average normalized summed bca for each participant at each electrode separately for the cross and emotion tasks. The electrodes were then ranked from the most responsive to the least responsive (see Supplementary table S1A for nonnormalized bca and Supplementary table S1B for normalized bca). In addition, Student's *t* tests were performed to assess the main effect of task demands for each electrode, and electrodes were ranked from the strongest to the weakest effect. From these data and previous studies investigating brain response to facial expressions with a similar FPVS-EEG approach (see Dzhelyova et al., 2017; Leleu et al., 2018; Poncet et al., 2019), four ROIs were defined.

The first three ROIs were the medial occipital cortex (mO: Iz, O1, Oz, O2, and POz), the right occipito-temporal cortex (rOT: PO4, PO8, P6, P8, and P10), and the left occipito-temporal cortex (lOT: PO3, PO7, P5, P7, and P9). They included electrodes that displayed both high nonnormalized or normalized amplitudes (see supplementary Tables S1A and S1B, respectively) and were among the electrodes used in previous studies to define ROIs. A fourth centro-frontal ROI (CF: Cz, FC1, FCz, FC2, and Fz) was also defined by identifying the electrodes most sensitive to the task effect using a data-driven procedure (comparing the response in the two tasks over the entire scalp; see Supplementary Tables S1). The electrodes in this ROI were among those with the strongest and most significant task demand effect after Student's *t* tests and Bonferroni correction for multiple comparisons (i.e., $p < .0008$). Note that four electrodes could have been included in the latter ROI (F1/2 and C1/2), but they were dropped to balance the number of electrodes per ROI. This ROI is also close to a region over which Yan et al. (2019) observed a task effect. The same ROIs were used to analyze both the expression-specific and general visual neural responses.

Repeated-measures ANOVAs were run on individual nonnormalized and normalized summed bca for both general and expression-specific responses with *Task* (cross vs. emotion), *Expression* (anger vs. disgust vs. fear vs. happiness vs. sadness), and *ROI* (mO vs. rOT vs. lOT vs. CF) as within-subject factors. For complementary analyses investigating the evolution of brain response with expression intensity, similar repeated-measures ANOVAs were run with an additional factor: *Intensity* (from 0% to 100% expression, by steps of 10%; i.e., 11 levels; within-subjects), and the factor *Expression* was not considered to reduce the number of factors (i.e., data for the different expressions were averaged). Mauchly's test for sphericity violation was performed, and Greenhouse–Geisser correction was applied whenever the sphericity assumption was violated. Linear contrasts were used to test for the effects of *task* and *expression* for the different modalities of *ROI*. Post hoc comparisons (Tukey's HSD tests) were conducted for significant effects in other cases. Effect sizes are reported as partial eta squared (η_p^2).

One of the advantages of the FPVS-EEG approach is that the quality of the SNR makes it possible to analyze the responses of each participant individually (Dzhelyova et al., 2017). We will not present these analyses in the manuscript. However, they are available in Supplement: Individual Analysis.

Time-domain analysis

The time course of the brain response in the different ROI's was assessed to determine the timing of the responses observed in the frequency domain. We first applied a 30 Hz low-pass FFT filter with a 1 Hz cutoff to the 512 Hz resampled data (i.e., after applying a 4th order Butterworth filter, with a bandpass of 0.1–100 Hz; see preprocessing for frequency analysis). Then, an FFT multinotch narrowband filter with a 0.5 Hz width and a slope cutoff width of 2 Hz was applied to the 12 Hz base rate and its significant harmonics (until 48 Hz) to remove the periodic brain response time-locked to the general stimulation at this frequency. Then, each sequence (N = 60) was cropped into segments lasting 51.25 sec (i.e., from 1 s before the fade-in to 0.5 s after the fade-out). EEG sequences were rereferenced to a common average reference and segmented from 167 ms before to 667 ms after the onset of expression-specific stimulation (i.e., until the next expression-specific stimulus displayed at 1.5 Hz) and were baseline-corrected by subtracting the signal within the 167 ms time-window before stimulus onset, corresponding to 2 cycles of the base rate. Further analyses were performed on epochs for expression intensities from 30% to 100%, i.e., 1440 epochs for each task (8 intensities x 6 repetitions by intensity x 5 expressions x 6 models). Each epoch was baseline corrected by subtracting the signal within the 167 ms stimulus onset, corresponding roughly to 2 cycles of the base rate. Epochs containing amplitudes greater than +/- 100 μ V over at least one channel (corresponding to eye blinks, artifacts, and so forth) were discarded (mean remaining epochs per participant: 1248 in the cross task, 1199 in the emotion task). To illustrate the time course of the processing over the scalp, average waveforms for all expressions with an intensity of 30% to 100% were computed for all electrodes (excluding prefrontal and temporal electrodes), separately for the

two tasks (see Figure 6A). 3D scalp topographies were computed to illustrate the topographies of responses at peak latencies (see Figure 6B). These figures are for illustrative purposes only.

Statistical analyses were performed on the electrodes included in the ROIs defined previously in the frequency-domain analysis. The epochs for the 6 models for the different expressions and for intensities from 30% to 100% were averaged (intensities from 0% to 20% were excluded to restrict the analysis to those intensities for which a clear response to expression-specific frequency was observed in the frequency domain at the group level) separately for the cross and the emotion tasks. We further averaged the 5 electrodes within the same ROI and determined the bins when the waveform for the cross and emotion tasks consistently differed by computing paired *t* tests at each time bin between -167 and +667 ms in regard to the expression-change onset. Our objective was to identify which periods in the processing of the effects reported in the frequency domain were significant, and the same threshold was used for each bin in the frequency analyses (i.e., $p < .05$, two-tailed). However, to reduce the risk of false-positives, a criterion of 16 consecutive significant bins (31.25 ms) was used to determine the time-course of significant differences (Dzhelyova et al., 2017; Leleu et al., 2018). This procedure allowed us to identify the periods in the time domain that supported the effect in the frequency domain in a sustained manner (i.e., excluding short periods of a few milliseconds or periods that alternate between significant and nonsignificant differences from one bin to another, which may result in false-positives).

Results

Behavioral data

Behavioral data for the cross task showed that the mean accuracy for detecting blue-to-red changes was 99.3% ($SD = 1.4$, range: 94-100%), with a mean correct response time of 398 ms ($SD = 42$ ms, range: 341-494 ms). This indicated that the participants were attentive to the cross during this task. There were no differences between facial expressions for either accuracy or response times (both $F_s < 1$). For the emotion task, participants pressed the key to indicate that they

recognized the expression in 95.5% of the sequences ($SD = 5.1$, range: 80-100%). Their accuracy was 70.9% ($SD = 10.3$, range: 46.7-86.7%), with a significant effect of *Expression* ($F(4,84) = 14.08$, $\eta^2_p = 0.40$, $p < .0001$). The accuracy was significantly better for happiness (94.7% +/- 11.9 SD) than for anger (71.2% +/- 18.7 SD), disgust (65.2% +/- 25.1 SD), sadness (63.6% +/- 17.5 SD), and fear (59.8% +/- 17.6 SD) (all $ps < .0004$ after Tukey's tests), without any other significant differences. The intensity at which participants indicated that they recognized the expression was, on average, 54.4% ($SD = 7.5$). It was 54.5% ($SD = 7$) when they recognized it correctly, with a significant difference between expressions in the latter case ($F(4,84) = 28.26$, $\eta^2_p = 0.57$, $p < .0001$): disgust and happiness (42.4% +/- 13.6 SD and 43.4% +/- 10 SD , respectively) were correctly recognized from a significantly lower intensity than sadness, anger, and fear (57.4% +/- 11.2 SD , 61.7% +/- 10.4 SD , and 67.7% +/- 11.2 SD , respectively) (all $ps < .0003$ after Tukey's tests). Sadness was also correctly recognized at a lower intensity than fear ($p = .0085$ after Tukey's test). The distribution of correct responses by expression intensities indicated that they were more frequent for intensities ranging from 30% to 60% (70.9% of responses), with a median response intensity of 50% (quartile 1 = 40%, quartile 3 = 70%).

Frequency-domain analyses

Expression-change response according to Task

For both tasks, facial expressions of increasing intensity resulted in an identifiable brain response with a high SNR, specifically for the emotion task (from 1.65 in the cross task to 2.22 in the emotion task, i.e., 65% to 122% of the signal increase compared with the surrounding noise level) (Figure 2A and 2B). The topographical maps of summed bca indicated that the response was more pronounced over the right occipito-temporal sites in the cross task, but a brain response also emerged over the left occipito-temporal and the centro-frontal regions in the emotion task (Figure 2C).

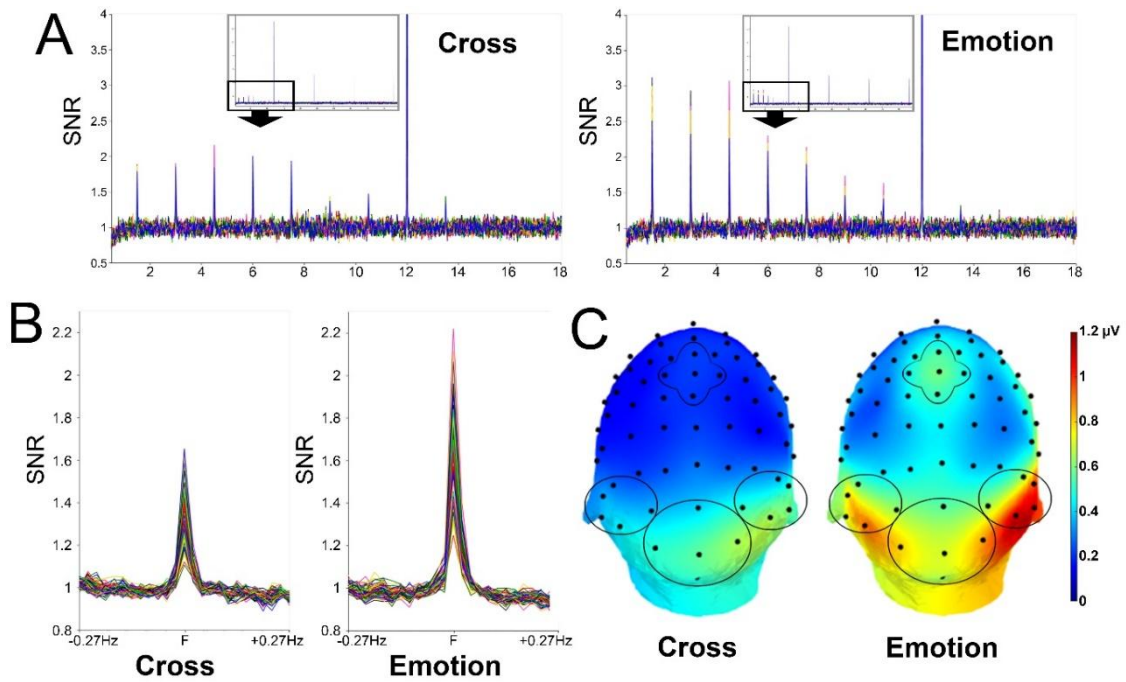


Figure 2. Expression-specific response according to task demands. A: FFT signal-to-noise ratio (SNR) spectra for all channels according to task demands. The SNR for the expression-specific response is visible at the 1.5 Hz frequency and its harmonics (i.e., integer multiples, e.g., 3 Hz, 4.5 Hz) in the large graphics, with a larger amplitude in the emotion task than in the cross task. The SNR for the general response is visible at the 12 Hz frequency and its harmonics (i.e., 24 Hz, 36 Hz, and 48 Hz; small graphics). **B:** FFT signal-to-noise ratio (SNR) spectra calculated on the sum of significant harmonics of the 1.5 Hz expression-specific frequency (until the 11th harmonic, i.e., Hz, excluding the 12 Hz base frequency) for all channels and the two tasks. The SNR was larger in the emotion task (SNR \approx 2.22, 122% of signal increase) than in the cross task (SNR \approx 1.65, 65% of signal increase). **C:** 3D-topographical maps (superior posterior view) of summed baseline-corrected amplitudes (bca) for the expression-specific response (in μV). The shapes indicate the ROIs that were identified and used in subsequent analyses. While the cross task resulted in a response primarily over the right occipito-temporal region, the emotion task led to a larger response over bilateral occipito-temporal regions. A response also emerged over the centro-frontal region for the latter task.

Preliminary analyses of nonnormalized summed bca revealed large amplitude differences between expressions and ROIs (see Supplementary Figure S1). Thus, we normalized the response amplitude across the whole scalp (McCarthy and Wood, 1985; see Dzhelyova et al., 2017) and ran a repeated-measures ANOVA with *task* (cross vs. emotion), *expression* (anger vs. disgust vs. fear vs. happiness vs. sadness), and *ROI* (mO vs. rOT vs. IOT vs. CF) on normalized summed bca. The main results are illustrated in Figure 3. The ANOVA revealed a significant main effect of *Task* ($F(1,21) = 24.38, \eta_p^2 = 0.54, p < .0001$), with a larger response in the emotion (0.15 au \pm 0.02 SD) than in the cross (0.13 au \pm 0.02 SD) task. In addition, we found a significant effect of *ROI* ($F(3,63) = 14.33, \eta_p^2 = 0.41, p < .0001$), with a larger response over the rOT (0.17 au \pm 0.04 SD) than

the IOT (0.14 au +/- 0.05 SD, $p = .0306$ after Tukey's test). The response over the mO (0.15 au +/- 0.04 SD) did not differ from the two lateral OT ROIs, whereas the response over the CF (0.09 au +/- 0.03 SD) was significantly lower than that over the three other ROIs (all $ps < .0035$ after Tukey's test). More importantly, a significant interaction between *Task* and *ROI* ($F(3,63) = 7.51, \eta^2_p = 0.26, p = .0002$) indicated that *Task* had a strong effect on the response recorded over CF ($F(1,21) = 39.43, p < .0001$) but also on the response over the rOT ($F(1,21) = 6.74, p = .0168$) and IOT ($F(1,21) = 8.54, p = .0081$). *Task* had no effect on the mO response ($F(1,21) = 2.5, p = .129$).

The main effect of *Expression* was also significant ($F(2.66,55.92) = 14.54, \epsilon = 0.67, \eta^2_p = 0.41, p < .0001$), with a larger response for disgust and happiness than for anger, fear, and sadness (all $ps < .004$). However, it was qualified by the interaction between *Expression* and *ROI* ($F(6.28,131.95) = 2.77, \epsilon = 0.52, \eta^2_p = 0.12, p = .0131$) and between *Expression* and *Task* ($F(2.44,51.18) = 5.13, \epsilon = 0.61, \eta^2_p = 0.20, p = .006$). The *Expression* x *ROI* interaction indicated a significant effect of *Expression* over the mO ($F(4,84) = 16.79, p < .0001$), the rOT ($F(4,84) = 4.04, p = .0048$), and the CF ($F(4,84) = 2.84, p = .029$) but not over the IOT ($F(4,84) = 1.02, p = .4013$). In the mO, the response was larger for disgust and happiness than for the other expressions (all $ps < .0116$ after Tukey's tests; see Figure 3A). In the rOT, the response was larger for disgust than for sadness ($p = .0082$) and marginally larger than for anger and fear ($p < .0797$). No significant difference occurred in the CF after post hoc Tukey's test. The *expression* x *task* interaction was also significant (see Figure 3A). It indicated a main effect of *Expression* in both the cross ($F(4,84) = 10.92, p < .0001$) and the emotion ($F(4,84) = 5.00, p = .0011$) tasks. In the cross task, the response was larger for disgust and happiness than for anger, fear and sadness (all $ps < .0304$ after Tukey's test). The pattern was almost the same in the emotion task, but the differences between expressions were strongly reduced, none reaching the significance level after Tukey's test (all $ps > .4409$).

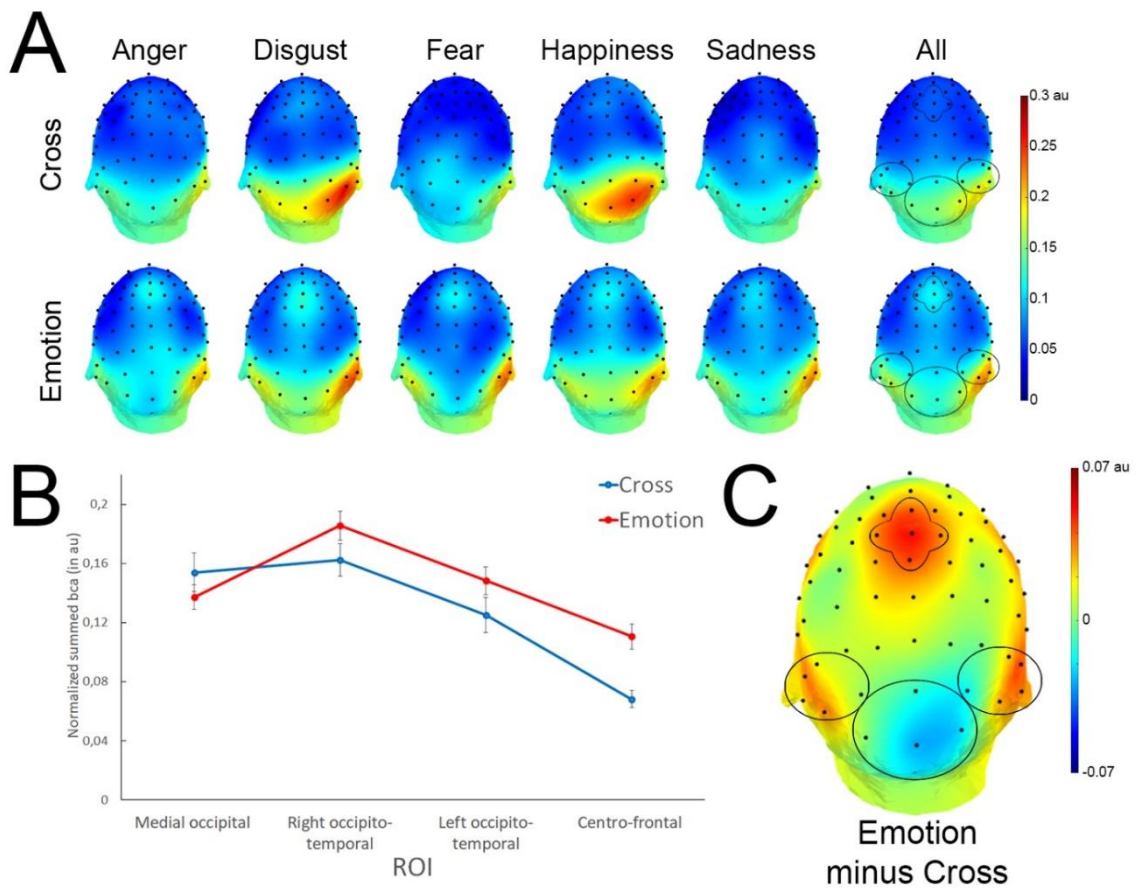


Figure 3. Expression-specific response according to *task* and *expression* (normalized summed baseline-corrected amplitude). **A:** 3D-topographical maps of normalized summed baseline-corrected amplitudes (bca, in arbitrary units) for the expression-specific response, according to *Expression* and *Task*. **B:** Mean normalized bca (in arbitrary units) for the expression-specific response, according to regions of interest (ROIs) and *tasks*. Error bars are SEM. **C:** 3D-topographical map of the difference between the emotion and the cross tasks (in normalized summed bca) for the expression-specific response. Explicitly asking participants to recognize emotion at the expression-specific frequency resulted in an increased response over the right and left occipito-temporal regions, as well as over the centro-frontal region.

As in previous studies using the FPVS-EEG approach opposing expressions to neutral faces (Dzhelyova et al., 2017; Leleu et al., 2018; Matt et al., 2021), response topographies to the different expressions were slightly different in the cross task (see Figure 3A, first line). On the other hand, they were more similar in the emotion task (see Figure 3A, second line). This visual impression is partly supported by the ANOVA indicating that the overall amplitude of responses was more similar in the emotion than in the control task (see *Expression* x *Task* interaction). However, the nonsignificant overall interaction also suggests that task demands modulated the overall (normalized) amplitude for

the different expressions, without supporting the conclusion of more similar topographies for the different expressions in the emotion than in the cross task.

To further assess whether the topographies of responses to the different expressions were more similar when participants were explicitly asked to recognize facial emotions, we computed the average normalized summed bca for each expression and task separately for all 64 electrodes (i.e., not only for the 20 electrodes included in ROIs). Then, we computed Cronbach's α to estimate the consistency of the normalized summed bca response over the whole scalp across the 5 expressions in the two tasks separately. It indicated a high reliability that was significantly stronger in the emotion ($\alpha = .983$, 95% CI: .975-.989) than in the cross task ($\alpha = .954$, 95% CI: .934-.97) ($t(62) = 10.18$; $p < .0001$). Note that we observed similar results after analyzing nonnormalized summed bca (emotion task: $\alpha = .958$, 95% CI: .939-.972; cross task: $\alpha = .911$, 95% CI: .872-.941; $t(62) = 7.20$; $p < .0001$). We also considered whether the higher reliability in the emotion task compared to the cross task was consistent between participants. Cronbach coefficients were computed for each participant in the two tasks separately. Student's t test confirmed that the reliability among expressions was higher in the emotion ($M = 0.86 \pm 0.07$ SD, range: .68-.97) than in the cross task ($M = 0.69 \pm 0.21$ SD, range: .29-.93) ($t(21) = 3.84$, Cohen's $d' = .82$, $p = .0009$). Thus, telling participants to categorize facial emotions led to a normalization and calibration of the way the brain responded to the different facial expressions.

Correlational analyses

Previous analyses indicated that involving participants in recognizing the expressions led to an increase in response (i.e., an effect of Task) in three ROIs: the rOT, the IOT, and the CF. To study the interrelation or, on the contrary, the independence of these responses, we subtracted the normalized summed bca in the cross task from the normalized summed bca in the emotion task over each ROI and for each participant to compute the size of the *task* effect. Then, we computed the Bravais-Pearson correlation coefficients between the sizes of task effects reported in the different

ROIs. This analysis revealed a positive correlation between the CF and the rOT ($r(20) = .69, p = .0003$) and between the CF and the IOT ($r(20) = .57, p = .006$), which were significant after Bonferroni's correction for multiple comparisons ($p < .0083$ for $\alpha = .05$). There was no correlation between the rOT and the IOT ($r(20) = .16$). Note that the correlations between the CF and the mO and between the mO and the rOT were also high ($r(20) = .50, p = .0174$ and $r(20) = .50, p = .0187$, respectively), but they were no longer significant after Bonferroni's correction. Thus, the CF appears to have played a central role in the task effect reported in this study; the task effects observed over the other regions are all associated with the effect observed over the CF, without any link between them.

Evolution of brain response with expression intensity

We investigated the evolution of the response according to expression intensity to determine how the previous effect emerged with intensity. Sequences in the time domain were cut according to each intensity, from 0% to 100% of the expression, before FFT (see Method). Normalized summed bca (McCarthy & Wood, 1985) were computed, and data for the different expressions were averaged to reduce the number of factors (for illustrations of results with nonnormalized summed bca, see Supplementary figure S2B). Then, we applied a repeated-measures ANOVA with *task* (cross vs. emotion), *intensity* (11 levels from 0% to 100%, by steps of 10%), and *ROI* (mO vs. rOT vs. IOT vs. CF) on normalized summed bca. The main results are illustrated in Figure 4. As previously reported, the main effects of *Task* ($F(1,21) = 16.95, \eta^2_p = 0.45, p = .0005$) and *ROI* ($F(3,63) = 11.42, \eta^2_p = 0.35, p < .0001$) were significant, as was the *Task* x *ROI* interaction ($F(3,63) = 4.09, \eta^2_p = 0.16, p = .0102$). Further analyses revealed the same pattern of differences as in the analyses described above for the whole sequence. Therefore, we will not elaborate further on these results and focus on the effect of *Intensity* and its possible interactions with other factors.

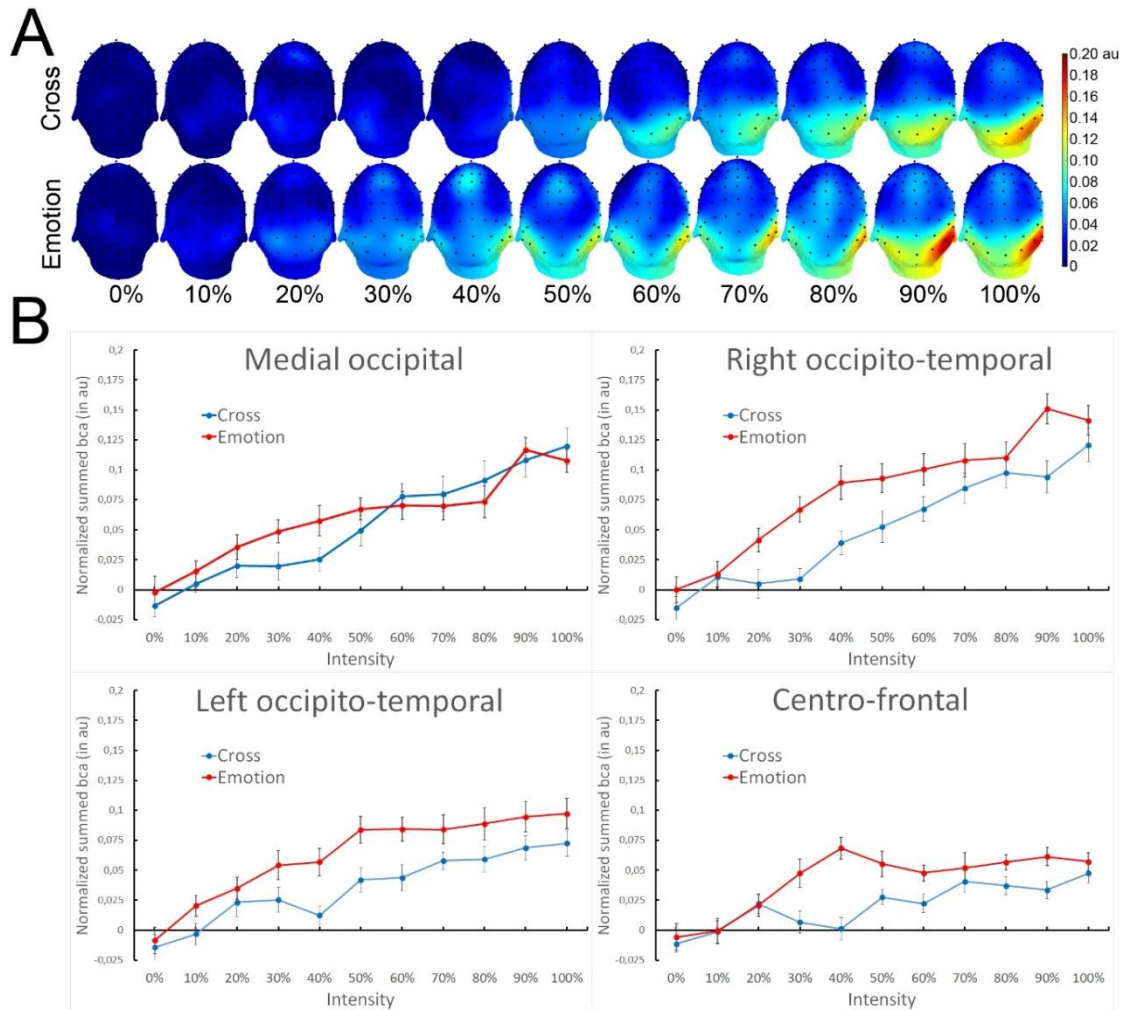


Figure 4. Expression-specific response according to *Intensity*, *Task* and *ROI* (normalized summed baseline-corrected amplitude). **A:** 3D-topographical maps of normalized summed bca (in arbitrary units) for the expression-specific response, according to *Intensity* and *Task*. **B:** Mean normalized bca (in arbitrary units) for the expression-specific response, according to *ROI*, *Intensity*, and *Task*. Error bars are SEM. The response at the expression-specific frequency (i.e., 1.5 Hz) increased regularly with the expression intensity in all regions. However, it no longer increased from expressions of 50% intensity in two regions: the IOT and the CF. A difference emerged between the cross and emotion tasks, especially for intensities ranging from 30 to 50%.

As expected, the main effect of *Intensity* was also significant, with a regular increase in brain response with expression intensity ($F(4.06,85.08) = 46.98$, $\epsilon = 0.41$, $\eta^2_p = 0.69$, $p < .0001$). This effect was modulated by significant interactions between *Intensity* and *Task* ($F(6.12,128.42) = 2.59$, $\epsilon = 0.61$, $\eta^2_p = 0.11$, $p = .0202$) and *Intensity* and *ROI* ($F(8.94,187.77) = 5.04$, $\epsilon = 0.30$, $\eta^2_p = 0.20$, $p < .0001$). Despite a trend, the three-way interaction was not significant ($F(30,630) = 1.39$, $p > .08$). For the first interaction (*Intensity* \times *Task*), post hoc Tukey's tests indicated that the response was larger in the emotion than the cross task at intensities of 30% to 50% (all $ps < .0266$) but not for lower or higher intensity (all $ps > .4738$). The significant *intensity* \times *ROI* interaction indicated that the

response did not increase with intensity the same way in the different ROIs. Figure 4B suggests that whereas it increased linearly for intensity from 0% to 100% over both the mO and the rOT, it slowed or stopped from 50% intensity over both the lOT and the CF. This visual impression was confirmed by a significant linear trend in each ROI (mO: $F(1,21) = 87.37, p < .0001$; rOT: $F(1,21) = 96.14, p < .0001$; lOT: $F(1,21) = 55.31, p < .0001$; CF: $F(1,21) = 47.87, p < .0001$). Nevertheless, whereas this linear trend explained 97.9% and 98.8% of the variance induced by intensity in the mO and the rOT, respectively, it explained only 92.3% in the lOT and 84.4% in the CF, where a plateau was visible from 50%. Furthermore, no trend other than the linear trend was significant in either the mO or the rOT ($F_s < 1$), while the variation with intensity was significantly modulated by trends other than the linear trend in both the lOT ($F(9,189)=2.30, p = .0175$) and the CF ($F(9,189)=2.14, p = .0279$). By further exploring the other possible trends, it appeared that a quadratic trend was significant in these last two ROIs (lOT: $F(1,21)=6.79, p = .0165$; CF: $F(1,21)=11.41, p = .0028$).

The behavioral data indicated that participants recognized facial expressions at 50% intensity on average. The previous analysis therefore suggests that the *task* effect is primarily observed for the intensities at which the expression is recognized and the two immediately preceding intensities. It also suggests that the response increased regularly with expression intensity throughout the sequence in the mO and the rOT (i.e., followed a linear trend) but slowed or stopped from 50% intensity in the lOT and the CF (i.e., displayed a quadratic trend) when the participant recognized expression in the emotion task. To further test this hypothesis, we performed repeated-measures ANOVAs separately for each ROI to contrast the brain response for the 5 intensities that preceded the participants' response (i.e., from 0% to 40%) to those that followed it (i.e., from 60% to 100%). The within-subjects factors were *Intensity* (intensity 1 to 5), participants' *Response* (before vs. after), and *Task* (cross vs. emotion). We only considered whether the effect of *Intensity* was modulated by the participant's *Response*, according to the *Task* or not (i.e., *Intensity* x *Response* and *Intensity* x *Response* x *Task* interactions). In both the mO and the rOT, the main effect of *Intensity* was significant (mO: $F(4,84)=16.87, \eta_p^2 = 0.45, p < .0001$; rOT: $F(4,84)=28.68, \eta_p^2 = 0.58, p < .0001$) and

was not modulated by *Response* (highest F value for the interactions *Intensity* x *Response* or *Intensity* x *Response* x *Task*: $F(4,84)=1.67, p = .1634$). In other words, the brain response increased in a similar way before and after the participants' response. In the IOT, *Intensity* significantly interacted with *Response* ($F(4,84)=2.55, \eta_p^2 = 0.11, p = .0449$), with a significant effect of *Intensity* before ($F(4,84)=8.61, p < .0001$) but not after ($F(4,84)=2.21, p = .0750$) the participants' response. This effect was not modulated by the task (interaction *Intensity* x *Response* x *Task*: $F(4,84)=1.47, p = .2189$). In the CF, the interaction between *Intensity*, *Response* and *Task* was significant ($F(2.70,56.74)=4.79, \epsilon = 0.68, \eta_p^2 = 0.19, p = .0062$). The decomposition of this interaction indicated that in the emotion task, the effect of *Intensity* was significant prior to the participant's response ($F(4,84)=10.90, p < .0001$) but not after ($F < 1$). It was not significant in the cross task, either before ($F(4,84)=2.21$) or after ($F(4,84)=1.60$) the 50% intensity.

General visual response

As illustrated in Figure 5, the stream of faces displayed at the base frequency (12 Hz and its harmonics) gave rise to an identifiable response at posterior scalp regions. This response extended more over the rOT region in the emotion than in the cross task. In that way, the repeated-measures ANOVA with *Task* (cross vs. emotion), *Expression* (anger vs. disgust vs. fear vs. happiness vs. sadness), and *ROI* (mO vs. rOT vs. IOT vs. CF) as within-subject factors was applied to mean normalized summed bca. It revealed a main effect of *ROI* ($F(3,63) = 90.89, \eta_p^2 = 0.81, p < .0001$), with a larger response over the mO (0.27 au +/- 0.04 SD) than over other ROIs (all $ps < .0002$ after Tukey's tests). It was also larger over the rOT (0.16 au +/- 0.04 SD) than both the IOT (0.13 au +/- 0.03 SD, $p = .027$) and the CF (0.08 au +/- 0.2 SD, $p = .0002$), and over the IOT than CF ($p = .0011$). The main effect of *Task* was not significant ($F < 1$). However, the interaction between *Task* and *ROI* was ($F(1.70,35.76) = 8.01, \epsilon = 0.57, \eta_p^2 = 0.28, p = .0022$) and indicated a significant effect of *Task* over both the mO ($F(1,21) = 15, p = .0009$) and the rOT ($F(1,21) = 8.24, p = .0092$) but not over the IOT or the CF ($Fs < 1$). Furthermore, while the effect was a decrease in response in the emotion task over the mO (0.28 au +/- 0.04 SD in the cross task vs. 0.26 au +/- 0.05 SD in the emotion task), it was an

increase over the rOT (0.12 au +/- 0.05 SD in the cross task vs. 0.17 au +/- 0.05 SD in the emotion task) (see Figure 5A and 5B for an illustration). The main effect of *Expression* was not significant and did not interact with other factors (all *ps* < .3694).

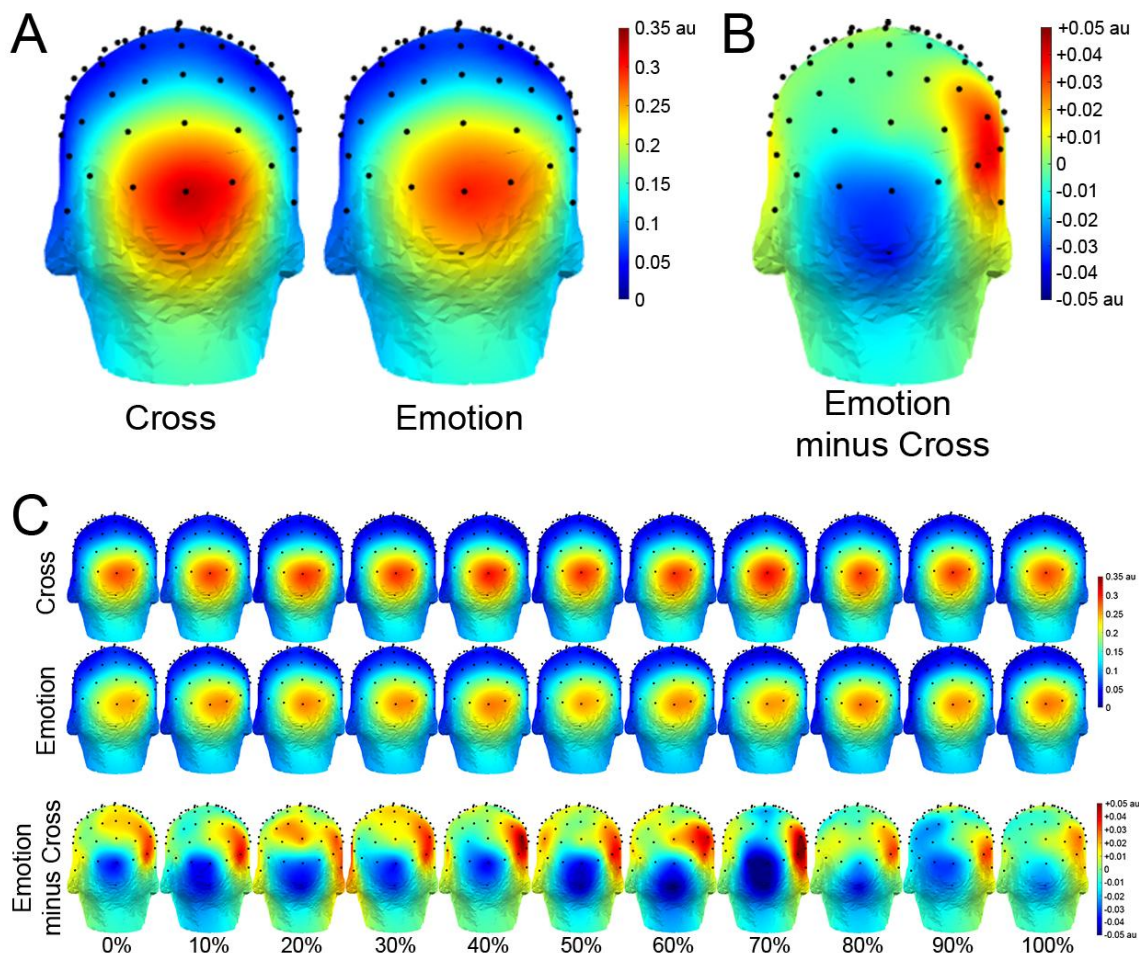


Figure 5. General visual response according to Task and Intensity (normalized summed baseline-corrected amplitude). **A:** 3D-topographical maps (posterior view) of normalized summed baseline-corrected amplitudes (bca, in arbitrary units) at the base frequency (i.e., 12 Hz) for the cross and the expression tasks. **B:** 3D-topographical map (posterior view) of the difference in normalized summed bca (in au) between the two tasks. This map illustrates the *task* effect on the general response to the flow of predominantly neutral faces displayed at the base frequency (i.e., 12 Hz). **C:** The same maps as in A (first two lines) and B (third line) for each expression intensity (from 0% to 100%, by steps of 10%). These maps illustrate a response to the (mainly) neutral faces displayed at base frequency (i.e., 12 Hz), which was larger over the right occipito-temporal region when the subject was voluntarily involved in the recognition of emotional facial expression, even when the expression was not yet perceivable (i.e., for low expression intensity).

Previous analyses indicated that a response similar to that reported over the rOT at the expression-specific frequency also emerged at the base frequency in the emotion task. This suggests that participants preactivated the rOT when they were explicitly told to recognize the expression at

the target frequency, and this region responded to the flow of faces that were displayed at the base frequency, whether they were expressive or not. At the same time, the response over the mO was reduced. To ascertain that this effect was not related to the regular occurrence of an expressive face at the base frequency, the normalized summed bca for the base frequency (i.e., 12 Hz and its harmonics) was considered for each intensity (as was the response to the expression-specific frequency, see above) and submitted to a repeated-measures ANOVA with *Task* (cross vs. emotion), *Intensity* (11 levels from 0% to 100%, by steps of 10%), and *ROI* (mO vs. rOT vs. IOT vs. CF). The hypothesis was that if the expressive face displayed among the neutral ones explained the effect, then (i) the response should increase as the intensity of expression increased (as the response of this region usually does; see previous analyses and Leleu et al. 2018, 2019), and (ii) the response should be weak or absent when the intensity of expression is low. In the latter case, in particular, the 0% intensity consisted of displaying the same neutral face at both the expression-specific and baseline frequencies.

Figure 5C illustrates the *task* effect for the different expression intensities. It shows that this effect was visible and of quite similar amplitude at the different intensities, including the lowest ones. This visual impression was confirmed by the ANOVA that revealed a significant main effect of *ROI* ($F(2.30,48.33) = 74.41$, $\varepsilon = 0.77$, $\eta_p^2 = 0.78$, $p < .0001$), with a larger response over the mO than the other ROIs (all $ps < .0002$ after Tukey's tests) and over the rOT than the CF ($p = .0017$). The main effect of *Task* was not significant ($F < 1$), but the *Task* x *ROI* interaction was ($F(1.95,40.92) = 7.96$, $\varepsilon = 0.65$, $\eta_p^2 = 0.27$, $p = .0013$), with a *Task* effect over the mO ($F(1,21) = 7.18$, $p = .0141$) and the rOT ($F(1,21) = 7.41$, $p = .0128$). More importantly, for our purpose, this effect was not modulated by *Intensity* (interactions *Task* x *Intensity* and *Task* x *Intensity* x *ROI*: $p > .3282$). Moreover, the main effect of *Intensity* was not significant ($F(4.9,102.81) = 1.56$, $\varepsilon = 0.49$, $p = .1802$) and did not interact with *ROI* ($F(9.14,191.96) = 1.06$, $\varepsilon = 0.30$, $p = .3916$). Note that the same analyses applied to nonnormalized summed bca showed the same increase in response over the rOT but did not confirm

the decrease over the mO. It also indicated that the response, far from increasing, tended to decrease with intensities across ROIs (see Supplementary Figure 3).

Time domain: time course of the brain response over the different regions

Figures 6A and 6B illustrate the time course of the differential responses over the scalp in the two tasks after notch filtering out the base-frequency rate response. The waveforms for the four ROIs (averaged across the 5 electrodes of each ROI) are illustrated in Figure 6C. These waveforms reflect the time course of the differential responses between the emotional expression displayed at an expression-specific frequency and the neutral expression displayed at the base frequency. Figure 6C reveals that the emotion task provoked a differential response over the CF that differed from the cross task 31 ms *before* the occurrence of the expression. It amplified and extended until more than 400 ms after the stimulus onset, affecting the response over this region during the entire course of processing. Over the mO, the task effect resulted in a lower positively oriented differential response in the emotion task starting from 41 ms after stimulus onset and extending until the first deflection picking at 115 ms. This effect resumed at the time of the negative component at approximately 190 ms to extend to the component that peaked at 310 ms in the cross task. Overall, these significant differences resulted from a lower 110 ms component in the emotion task, with a larger 195 ms component and a latter third component, which peaked at approximately 390 ms. A late positivity (i.e., after 400 ms) also emerged in the emotion task. Over the rOT, the curves diverged significantly from 109 ms, with a more negatively oriented response in the emotion task. This resulted in smaller positive components than in the cross task (namely, approximately 110 and 270 ms) but a larger negative component at approximately 200 ms. The IOT displayed an effect of task from 161 ms, only, with a larger negativity for the emotion task. This effect is associated with a larger negative component at approximately 200 ms during the emotion task than during the cross task. We must also note the presence of a positive component that peaked at 390 ms (i.e., a third component that peaked later in the emotion task than in the cross task) and lasted several dozen ms over both the IOT and the mO.

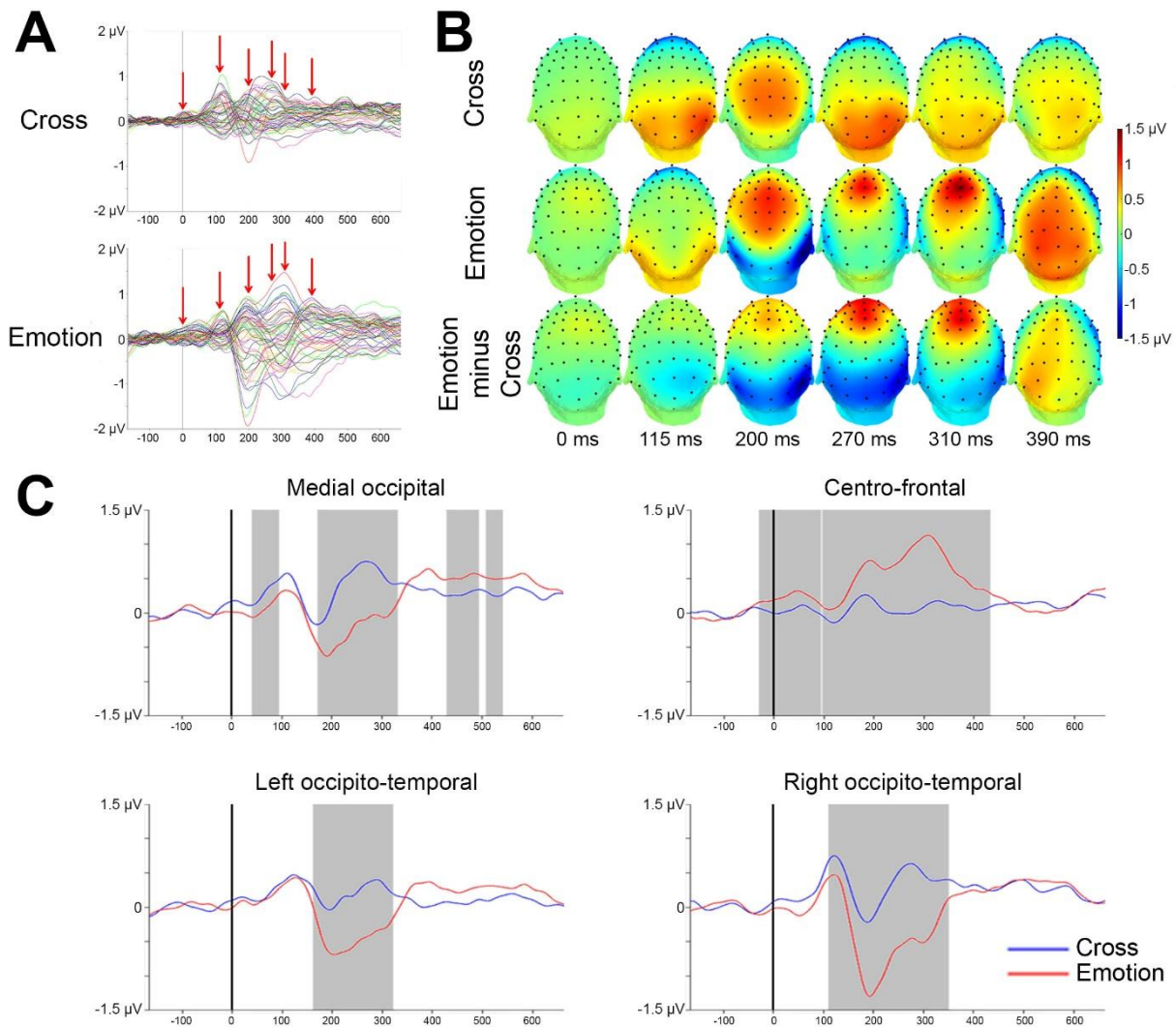


Figure 6. Time course of the differential response to expression, according to task and ROI. **A:** 12 Hz filtered-out grand-averaged EEG waveforms recorded between 167 ms before and 667 ms after the expression onset over the scalp for the cross and emotion tasks, respectively. Only expressions with an intensity of 30% to 100% were considered. The red arrows indicate times illustrated in B. **B:** 3-D topographical maps (posterior view) of the 6 times identified in A for the cross and emotion tasks. The difference between the two tasks (i.e., the *task* effect: expression minus cross) is shown on the third line. **C:** EEG waveforms of the differential responses in the cross and emotion tasks in the four ROIs (response averaged over the 5 ROIs' electrodes). The shaded areas indicate significant differences between the two waves (based on Student's tests, $p < .05$) for at least 16 consecutive bins (i.e., 31.25 ms). These waves indicate that involving the participants in the recognition of emotional facial expressions caused an increase in the response over the centro-frontal region even before the appearance of the stimulus. At the same time, the response over the medial occipital region was also reduced early, with a significant difference from 41 ms. Then, the response in the emotion task started to differ for the cross task from 103–109 ms over the right occipito-temporal region and from 155–161 ms over the left occipito-temporal region, amplifying the second negative component. The left occipito-temporal medial occipital region also showed a significant differential response at the end of processing.

Note that the analysis of the brain response before applying the various filters globally confirms the effects described above (see Supplementary Figure S4A). It also suggests that

participants' engagement in the explicit recognition of the emotion expressed at the expression-specific frequency elicited an anticipatory response (i.e., before face onset) for all faces displayed at 12 Hz in the sequence (see Supplementary Figures S4A and S4B).

Discussion

To summarize the main results of our study, asking participants to be engaged in facial expression recognition displayed at the expression-specific frequency (i.e., 1.5 Hz and harmonics) had several outcomes on the brain response. Mainly, the response to the expression-specific frequency was increased during the emotion task over three regions: the right and left occipito-temporal regions and the centro-frontal region. This effect was larger for 30-50% expression intensities (i.e., below the recognition threshold). The right occipito-temporal region also responded to the base stimulation (i.e., 12 Hz), although it primarily included neutral faces. The influence of task demands on the response over the medial occipital region was less clear, as the brain response decreased at the base frequency but not reliably at the expression-specific frequency. Time domain analysis also revealed the sequence of responses over these four regions, with modulation over the centro-frontal beginning before the stimuli onset, followed by an early reduced response over the medial occipital regions. Finally, the response was amplified over the right and then left occipito-temporal regions.

Visual representation of facial expression over the right occipito-temporal region

Consistent with previous studies (see Dzhelyova et al., 2017; Leleu et al., 2018; Matt et al., 2021), we found a clear response over the right occipito-temporal region during the orthogonal cross task (i.e., implicit emotion recognition task) that was further amplified in the emotion task. This response was primarily stimulus-driven, since it increased gradually along with expression intensity (i.e., with the amount of perceptual differences between the expressive and the neutral face) throughout the sequence, even after expression recognition was completed, and up to the highest intensity. Enhancement of this response, when participants were involved in expression recognition, further indicated an additional operation of top-down processes, especially for the intensities that

preceded effective recognition. Another top-down influence was evident for nonexpressive faces, i.e., the neutral faces displayed at the base frequency. In that case, the effect was not stimulus-driven, since the task effect was the same regardless of intensity, even when the difference between the "expressive" face and the neutral face was null.

The right occipito-temporal response, recorded in both the cross and the emotion tasks as well as in previous studies, probably reveals the extraction of an expressive representation of the face. Such a response likely stems from the activity of the core system of facial information processing (Duchaine & Yovel, 2015; Haxby, Hoffman, & Gobbini, 2000), more specifically the superior temporal sulcus involved in the processing of facial movements and expressions (Harris, Young, & Andrews, 2012; Puce et al., 1998, 2003; Srinivasan, Golomb, & Martinez, 2016) or the lateral fusiform gyrus, whose activity is also modulated by facial expression (Buchel & Dolan, 2000; George, Driver, & Dolan, 2001; Kawasaki et al., 2012; Morris et al., 1998; Vuilleumier et al., 2001). In support of a role in the representation of facial expression, time-domain analysis indicates a large second component over the right occipito-temporal region, which peaks at approximately 200 ms, similar to previous FPVS-EEG studies (Dzhelyova et al., 2017). Both temporal and topographical characteristics of this component match the latency and topography of expression responses reported with other EEG approaches and associated with integration of visual information within an expressive representation (e.g., Puce et al., 2003; Rossi, Parada, Kolchinsky, & Puce, 2014; Schyns, Petro, & Smith, 2007). The third component could reflect the categorization of facial expressions into discrete emotion categories (Leleu et al., 2018), again in a time window that corresponds to that reported with other approaches (e.g., Luo et al., 2010; for a review and discussion, see Calvo & Nummenmaa, 2016).

In summary, we found that (i) the task effect was mainly observed for the low intensities preceding the intensity that allowed recognition and that (ii) a response to neutral faces displayed at the base frequency also occurred. Taken together, these findings suggest that the involvement in

expression recognition especially prompted the right occipito-temporal regions to extract an expressive representation when bottom-up information was too weak to trigger this process automatically and efficiently. This pattern of results may reflect a mechanism of gain control over the flow of information that reaches the occipito-temporal regions, increasing SNR in the visually evoked response, as reported in regions involved in color processing, for example (e.g., Brouwer & Heeger, 2013). Similar phenomena have been reported for faces, houses or words, where attending to a specific category increased the response of category-specific areas in the ventral temporal cortex, especially with regard to ambiguous stimuli (Furey et al., 2006; Kay & Yeatman, 2017).

Time domain analyses further allowed us to specify the time course of the task-related top-down modulation, showing a significantly more negative differential response over the right occipito-temporal region in the emotion task that lasted from approximately 100 to 350 ms after stimulus onset, peaking at approximately 200 ms, corresponding to the time window of the second component. This result is consistent with previous EEG studies investigating top-down modulation in visual selective attention tasks (e.g., Hillyard & Anllo-Vento, 1998; Kastner & Ungerleider, 2000) and typically reporting an enhanced neural response starting from 80 ms after stimulus onset, with an amplified response over the N1 ERP component lasting approximately 200 ms for stimuli with relevant or attended features according to task demands. Amplification of the second component over occipito-temporal regions has also been reported when attention is focused on face processing using the FPVS-EEG approach (Quek et al., 2018b; Yan et al., 2019).

Overall, the involvement of participants in expression recognition promoted the extraction of an expressive representation in the dedicated occipito-temporal regions by fostering the integration of bottom-up information. This resulted in a more uniform response to the different expressions. The variations in topography or amplitude observed between the different expressions in the cross condition, variations also reported in other studies using an implicit task (e.g., Dzelhyova et al., 2017;

Leleu et al. 2018; Matt et al., 2021), are reduced when the participants direct their attention to the expression to recognize it.

Top-down task monitoring over centro-frontal regions

The centro-frontal region response in the emotion task gradually increased along with the expression's intensity, getting stronger until the intensity was sufficient for recognition (i.e., approximately 50% of the intensity of the expression). It then stopped increasing, returning to a level close to that observed in the cross task. Moreover, the task effect arose even *before* the occurrence of the expression and was significant throughout the processing, up to more than 400 ms after stimulus onset. The earlier occurrence of a centro-frontal response to task demands makes it a good candidate as a neural marker for early task-related top-down modulation of expression detection. It is also a candidate for indexing the response of brain regions involved in task monitoring in the course of facial expression recognition; that is, the regions underlying this response not only have a role in the detection of the expressive face but also at later stages of its processing. The strong correlation between the centro-frontal region activity and all the other responding regions (which do not correlate with each other) further supports such a monitoring role.

Several regions can be responsible for the centro-frontal response, which may be involved at different stages in processing. In addition, the slight topographical variations in response over time (see Figure 6B) suggest the contribution of different regions depending on processing stage. In previous fMRI studies, several regions were activated when participants were involved in the explicit recognition of facial expression, for example, the ventromedial prefrontal and somatosensory cortical regions (Winston et al., 2003) or the right precentral sulcus, the lower frontal gyrus and part of the fusiform gyrus (Gorno-Tempini et al., 2001). Ventromedial prefrontal and somatosensory cortical activation can be explained by the association between emotion perception and representations of somatic states, while the right precentral sulcus, lower frontal and fusiform gyrus activations were related to general cognitive processes, such as face perception and monitoring

functions. The literature on spatial and selective attention can also shed light on the centro-frontal response recorded here. It has been reported that attention-related modulation originates in frontal and parietal cortices, with a top-down influence on the visual cortex (e.g., Fiebelkorn & Kastner, 2020). Investigations of the effect of participant involvement in face processing reported enhanced responses over the ventral temporal cortex in face-related tasks associated with top-down influence from the intraparietal sulcus (Kay & Yeatman, 2017) or the inferior frontal junction (Baldauf & Desimone, 2014). The top-down modulation of the ventral temporal cortex was suggested to “scale” the bottom-up representation of the stimulus (Kay & Yeatman, 2017). Both the timing and topography of the current centro-frontal response correspond to parameters reported in previous EEG studies during spatial attention tasks (e.g., Itthipuripat, Ester, Deering, & Serences, 2014), which has been related to perceptual decision mechanisms (Hillyard, Squires, Bauer, & Lindsay, 1971; O'Connell, Dockree, & Kelly, 2012). Interestingly, in a recent study, using a gender categorization task in which implicit expectations about the gender of the appearing face caused an increase in alpha/beta power prior to face occurrence, the most pronounced over the central electrodes within occipital, parietal, and frontal regions (Roehle et al., 2021). In this study, alpha/beta power was associated with task-related top-down selection of relevant neural responses and simultaneous reduction of irrelevant responses. Another study, this time on expression, showed that the frontoparietal network exerts top-down control that plays a determining role in the recognition of expressions (especially when they are close to the perception threshold; Kajal et al., 2021). Using the FPVS-EEG approach, it has also been found that drawing attention to all faces in a sequence to detect the occurrence of a male face triggers a response over central parietal and prefrontal regions (Yan et al., 2019), which was construed as reflecting attentional operations associated with response inhibition and task difficulty.

Featural/analytic or language-related mechanisms over the left hemisphere

The voluntary involvement of the participant in expression recognition also resulted in an increase in response over the left occipito-temporal region. Similar to other regions, the response

increased gradually along with the intensity of expressions with a more prominent task effect for low intensities that preceded recognition. Nevertheless, it also increased less linearly with intensity than over its right occipito-temporal counterpart, with a reduction in the increase when a response was reached. Analysis in the time domain indicated that the task effect emerged later than in the other regions, starting from approximately 160 ms, and then affected the second component that peaked at approximately 200 ms. We also noted a shift of in the third component, whose peak went from 310 ms in the cross task to 390 ms in the emotion task, which is centered on the occipital and left occipito-temporal regions at this latency (see last column in Figure 6B). Consequently, the late 390 ms component is mainly located over the medial occipital and left occipito-temporal regions. Together, these observations show that task demands also modulate the response over left occipito-temporal regions, but with a response that is partially different in nature from its counterpart in the right hemisphere.

While the processing of emotional facial expression has long been regarded as a function primarily of the right hemisphere (e.g., Borod, Koff, Lorch, & Nicholas, 1986; Harris et al., 2012), it is not uncommon to observe a left occipito-temporal response, even if it is generally weaker than over the right hemisphere (Sliwinska & Pitcher, 2018; for examples in FPVS-EEG studies, see Dzhelyova et al., 2017; Leleu et al., 2018; Matt et al., 2021). The nature of the contribution of the left hemisphere is unclear. Some authors have proposed that it operates a more analytic or featural processing of the face and facial expressions, with the right hemisphere processing more holistically (e.g., Calvo & Beltrán, 2014; see also Lobmaier, Klaver, Loenneker, Martin, & Mast, 2008; Maurer, O'craven, Le Grand, Mondloch, Springer, Lewis, & Grady, 2007; Scott & Nelson, 2006). In ERP studies, left featural vs. right holistic effects were observed on component N170 (Calvo & Beltrán, 2014; Scott, & Nelson, 2006) within a time window close to the second component in our study. Another possibility is the involvement of the left hemisphere in language-related mechanisms (see Adolphs, 2002; Bowers & Heilman, 1984; Burt & Hausmann, 2019; Stone, Nisenson, Eliassen, & Gazzaniga, 1996), while the

right hemisphere performs visual representations of facial expressions. Naming facial expressions therefore requires the response and coordination of both hemispheres.

Top-down mechanisms stemming from the explicit task of recognizing emotional expression favored the extraction of an expressive representation in left occipito-temporal areas (whether analytical, verbal, or of another type), especially when the information flow was poor (i.e., low expression intensity). This modulation might be associated with the activity of centro-frontal regions, as suggested by the correlation in the response of the two regions and the temporal anteriority of the centro-frontal response. In this way, task-related top-down modulation of the ventral temporal cortex (more specifically, face-specific regions) initiated in the intraparietal sulcus was reported in the left hemisphere (Kay & Yeatman, 2017). Note that the influence of task demands emerges later in the left hemisphere than in the right hemisphere, reinforcing the hypothesis that the expression representation extracted there is of a different nature. In particular, the response of the left hemisphere could depend more on the implementation of task-related processes: As has been indicated above, task-related top-down modulation was reported mainly on the left hemisphere (Kay & Yeatman, 2017). Expectations also modulate the N170 amplitude, but only in the left hemisphere (Roehe et al., 2021). Furthermore, this last modulation was associated with increased prestimulus alpha/beta power, still with a predominance in the left hemisphere.

The task effect also resulted in the emergence of a later component, peaking at approximately 390 ms, lasting several tens of milliseconds over the occipital and left occipito-temporal regions, with a significant effect over the mO (but only a trend over the IOT; see Figure 6B and 6C). It has been suggested that the left hemisphere is particularly involved in the naming of facial expressions following processing performed in the right hemisphere (e.g., Rapcsak, Comer, & Rubens, 1993). This left-sided third component could be related to the verbal labeling of facial expression prior to naming required by the task; such timing is consistent with that proposed for access to conceptual knowledge about emotion (>300 ms: Adolph, 2002). In our view, an influence of

the motor response on this component seems unlikely, as this response occurred only once during the emotion recognition sequences (while up to 48 stimulations with the expressive face were averaged, knowing that trials exceeding an amplitude of +/- 100 microvolts were discarded). Moreover, the effect occurred only in the left hemisphere, whereas participants had to respond with both hands.

Modulation of early visual occipital response

The influence of task demands on the response over the medial occipital region was less clear, as the response was reduced at the 12 Hz base frequency but not at 1.5 Hz expression-specific frequency. Time-domain analysis also indicated that the response to the expressive face was reduced from an early stage of processing, from approximately 40 ms up to the first component that peaked at 110 ms. Then, the response at the second and third component levels was amplified and delayed for the third component. Looking at our results and the ROIs we have defined, it is not possible to dissociate the effects observed on the second and third components from those observed over the right and left occipito-temporal regions, respectively. The amplification of the second component at the occipital level is not distinct from that observed over the right occipito-temporal region, while that of the third component is not distinct from that observed over the left occipito-temporal region. On the other hand, the early decrease in response is specific to the medial occipital region. Furthermore, it does not seem to be specific to the face displayed at the expression-specific frequency. Complementary analyses have shown that asking participants to recognize an expression at the specific frequency also affected the response to neutral (baseline) faces with a reduction in the amplitude of the response before the occurrence of each of them (Supplementary Figure S4). This shows that instructing the participants to pay attention to the expression presented at 1.5 Hz to recognize it caused an anticipatory decrease in the occipital response to all faces in the sequence. An occipital response is generally recorded at the base frequency and associated with low-level and early visual processing, achieved in early visual areas (e.g., Dzhelyova et al., 2017). Reduction of the response of early sensory regions is a phenomenon that has been well described in the literature

(see de Lange et al., 2018; Gilbert & Li, 2013). Several cognitive mechanisms have been proposed to explain this phenomenon, mainly related to expectations and attention (e.g., Summerfield & De Lange, 2014). They were associated with feedback from high-level mechanisms to early visual areas that sharpens the stimulus representation in these areas (Kok, Jehee, & De Lange, 2012) or preactivates stimulus-specific activity patterns (Kok, Mostert, & De Lange, 2017). In humans, stimulation of the right medial or dorsolateral prefrontal cortex reduces the P1 component at the occipital sites (Mattavelli, Rosanova, Casali, Papagno, & Lauro, 2013, 2016). Thus, the early medial occipital effect of participant engagement in expression recognition is another potential indicator of the implementation of top-down processes that influence the processing of incoming visual flow, preparing the visual areas to receive information relevant to the task at hand.

Here, we used the FPVS-EEG approach to study the brain response that corresponded to all the mechanisms and processes at work in the recognition of emotional expressions by including them in a single stimulation sequence. For the first time this particular approach provided us with a complete picture of the processes involved in the explicit recognition of emotional expression. The particular sensitivity of FPVS-EEG allowed us to obtain responses with a very good signal-to-noise ratio and a relatively small number of stimulations. It also allowed us to clearly highlight different stages in the explicit recognition of emotional facial expressions, still within the same stimulation sequence. In addition, this method permitted us to propose a topography and timing for the different processes, integrating them into a single model. This approach also had the advantage that the response identified in the frequency domain as well as the components in the time domain directly reflected the targeted processes, they corresponded to the differential response related to the processes evoked at the specific frequency, but not at the base frequency. The frequency domain analyses with the FPVS-EEG approach isolate a specific response whatever its timing (i.e., whenever it occurs and whatever its duration). The time domain analyses further allowed us to assess the timing

of the responses isolated in the frequency domain (onset, offset, duration), independent from classically evoked components (i.e., without disaggregating the effects that occur in a time window covering several components; for example, P100 and N170).

It is worth noting that the emotion and the cross tasks have differences other than engaging in expression recognition versus processing it implicitly and automatically. In particular, the participants' attention was directed to the faces in the emotion task (but not in the cross task) but also to the frequency of interest (1.5 Hz). Moreover, recognizing the expression is a more difficult task than detecting a color change. This is exactly what allowed us to record top-down processes regardless of their nature (mere orientation of attention toward a stimulus/frequency, specific to the processing of facial expressions, related to task difficulty or not) and thus provided a complete picture of the processes involved in the recognition of emotional expression. However, at this stage it remains important to distinguish between effects that are only the result of paying attention to a stimulus and those that result from the intentional engagement of facial information processing mechanisms. It is possible that the effects related to the simple engagement of attention (and not specific to the processing of emotional information) affect the whole response; they could affect the different regions of interest and occur in both the early and late response in the temporal domain (see Quek et al., 2018b; Yan et al., 2019). The early modulation could result from the effect of orienting spatial attention on expressive stimuli at 1.5 Hz, rather than task-relevant processing (e.g., Wolf, Bruchmann, Pourtois, Schindler, & Straube, 2021). Top-down effects related to the mechanisms specific to expression processing could also occur in all regions, but at a later stage. For example, specific task-related modulations were reported approximately 200 ms after stimuli onset (i.e., on P2; Volpert-Esmond, & Bartholow, 2019) or later (e.g., on P300; Sun, Liu, Cui, Wei, & Zhang, 2021; see also Durston & Itier, 2021). The task difficulty should be translated essentially into the mechanisms related to task monitoring, rather at the centro-frontal level and at the time of the elaboration of a representation (i.e., from the second component) or later. In that way, explicit processing of facial expression in tasks of varying difficulty elicits frontal modulations between 250

and 450 ms post-stimulus (Aguado, Parkington, Dieguez-Risco, Hinojosa, & Itier, 2019). However, these hypotheses remain highly speculative and need to be investigated in future studies.

Conclusions

By using the FPVS-EEG approach, we identified brain markers that operate at different stages of recognition of emotional facial expressions when a neurotypical participant is voluntarily engaged in this task. These markers identify stages ranging from the detection of the expression to its recognition through the implementation of mechanisms sustaining the extraction of a visual and verbal expressive representation as well as task monitoring. The involvement of participants in facial expression recognition results in an early response, even before the onset of the expression, over the centro-frontal region, concomitant with a decrease in the response over the occipital region. This reflects the mobilization of expectation and attention mechanisms, which "prepare" the visual areas to receive the expressive information. Then, an expressive representation of the face is extracted over occipito-temporal regions, with task-related top-down influences (indexed over the centro-frontal region) fostering the integration of information in these regions and amplifying their response. Finally, left hemisphere structures are called upon to complete the processing of emotional facial expressions, probably by engaging further visual processing of local information or language-related mechanisms.

Overall, this study further confirms that facial expression recognition does not rely exclusively on bottom-up integration of visual information, but requires the coordination of several structures and mechanisms, and highlights that task-related top-down processes play an important role in the organization of visual perception. The evidence of various top-down effects, which occur at different times during processing and involve distinct brain structures, also supports the hypothesis that the perception and recognition of expressions is a complex phenomenon that reflects a cognitive construct (Barrett, 2012, 2017). This construct involves cognitive monitoring and attentional processes, but it also opens the way to the integration of episodic information related to

the individual's history, multimodal or verbal information, and much more; this complexity and its elements appeared during a single stimulation sequence.

In the present framework, difficulties or deficits in the recognition of facial expressions may thus occur for different reasons. Some are related to the disruption of the upward flow of visual information, preventing or altering the extraction of a visual representation. Others are due to the alteration of top-down or feedback processes, hindering the organization of incoming visual information or the use of language backing. This explains why so many different diseases with varied profiles (e.g., brain-damaged patients, schizophrenia, autism spectrum disorders, depression, various genetic syndromes, and many others) are associated with difficulties in recognizing emotional facial expressions. The approach described here opens a new avenue to better understand the difficulties and specificities of these different populations as well as the way our brains make sense of facial expressions.

References

- Adolphs, R. (2002). Recognizing emotion from facial expressions: psychological and neurological mechanisms. *Behavioral and cognitive neuroscience reviews*, *1(1)*, 21-62.
- Adrian, E. D., & Matthews, B. H. C. (1934). The Berger rhythm: Potential changes from the occipital lobes in man. *Brain*, *4(57)*, 355–385.
- Aguado, L., Parkinson, K. B., Dieguez-Risco, T., Hinojosa, J. A., & Itier, R. J. (2019). Joint modulation of facial expression processing by contextual congruency and task demands. *Brain Sciences*, *9(5)*, 116.
- Baldauf, D., & Desimone, R. (2014). Neural mechanisms of object-based attention. *Science*, *344(6182)*, 424-427.
- Barrett, L. F. (2012). Emotions are real. *Emotion*, *12(3)*, 413-429.
- Barrett, L. F., Adolphs, R., Marsella, S., Martinez, A. M., & Pollak, S. D. (2019). Emotional Expressions Reconsidered: Challenges to Inferring Emotion From Human Facial Movements. *Psychological*

- Science in the Public Interest*, 20(1), 1–68.
- Barrett, L. F., Mesquita, B., & Gendron, M. (2011). Context in emotion perception. *Current Directions in Psychological Science*, 20(5), 286-290.
- Baudouin, J.-Y., Martin, F., Tiberghien, G., Verlut, I., & Franck, N. (2002). Selective attention for facial identity and emotional expression in schizophrenia. *Neuropsychologia*, 40 (5), 518-526.
- Berkovitch, L., Del Cul, A., Maheu, M., & Dehaene, S. (2018). Impaired conscious access and abnormal attentional amplification in schizophrenia. *NeuroImage: Clinical*, 18, 835-848.
- Borod, J. C., Koff, E., Lorch, M. P., & Nicholas, M. (1986). The expression and perception of facial emotion in brain-damaged patients. *Neuropsychologia*, 24(2), 169-180.
- Bowers, D., & Heilman, K. M. (1984). Dissociation between the processing of affective and nonaffective faces: a case study. *Journal of Clinical and Experimental Neuropsychology*, 6(4), 367-379.
- Brouwer, G. J., & Heeger, D. J. (2013). Categorical clustering of the neural representation of color. *Journal of Neuroscience*, 33(39), 15454-15465.
- Büchel, C., & Dolan, R. J. (2000). Classical fear conditioning in functional neuroimaging. *Current opinion in neurobiology*, 10(2), 219-223.
- Burt, D. M., & Hausmann, M. (2019). Hemispheric asymmetries in categorical facial expression perception. *Emotion*, 19(4), 584.
- Calvo, M. G., & Beltrán, D. (2014). Brain lateralization of holistic versus analytic processing of emotional facial expressions. *Neuroimage*, 92, 237-247.
- Calvo, M. G., & Nummenmaa, L. (2016). Perceptual and affective mechanisms in facial expression recognition: An integrative review. *Cognition and Emotion*, 30(6), 1081-1106.
- Cohen Kadosh, K., Cohen Kadosh, R., Dick, F., & Johnson, M. H. (2011). Developmental changes in effective connectivity in the emerging core face network. *Cerebral Cortex*, 21(6), 1389-1394.
- Coll, M. P., Murphy, J., Catmur, C., Bird, G., & Brewer, R. (2019). The importance of stimulus variability when studying face processing using Fast Periodic Visual Stimulation: A novel

- 'Mixed-Emotions' paradigm. *Cortex*, *117*, 182-195.
- Critchley, H., Daly, E., Phillips, M., Brammer, M., Bullmore, E., Williams, S., Van Amelsvoort, T., Robertson, D., David, A., & Murphy, D. (2000). Explicit and implicit neural mechanisms for processing of social information from facial expressions: a functional magnetic resonance imaging study. *Human Brain Mapping*, *9*(2), 93-105.
- Damon, F., Leleu, A., Rekow, D., Poncet, F., & Baudouin, J.-Y. (2020). Expertise for conspecific face individuation in the human brain. *NeuroImage*, *104*, 116218.
- De Heering, A. & Rossion, B. (2015). Rapid categorization of natural face images in the infant right hemisphere. *eLife*, *4*, e06564.
- De Lange, F. P., Heilbron, M., & Kok, P. (2018). How do expectations shape perception? *Trends in cognitive sciences*, *22*(9), 764-779.
- Dobs, K., Schultz, J., Bühlhoff, I., & Gardner, J. L. (2018). Task-dependent enhancement of facial expression and identity representations in human cortex. *NeuroImage*, *172*, 689-702.
- Duchaine, B. C., & Yovel, G. (2015). A revised neural framework for face processing. *Annual Review of Vision Science*, *1*, 393–416.
- Durston, A. J., & Itier, R. J. (2021). The early processing of fearful and happy facial expressions is independent of task demands—Support from mass univariate analyses. *Brain Research*, *1765*, 147505.
- Dzhelyova, M., Jacques, C., & Rossion, B. (2017). At a single glance: fast periodic visual stimulation uncovers the spatio-temporal dynamics of brief facial expression changes in the human brain. *Cerebral Cortex*, *27*, 4106-4123.
- Eimer, M., & Holmes, A. (2007). Event-related brain potential correlates of emotional face processing. *Neuropsychologia*, *45*(1), 15-31.
- Ekman, P., & Friesen, W. V. (1971). Constants across cultures in the face and emotion. *Journal of personality and social psychology*, *17*(2), 124-129.
- Fiebelkorn, I. C., & Kastner, S. (2020). Functional specialization in the attention network. *Annual*

review of psychology, 71, 221-249.

Furey, M. L., Tanskanen, T., Beauchamp, M. S., Avikainen, S., Uutela, K., Hari, R., & Haxby, J. V. (2006).

Dissociation of face-selective cortical responses by attention. *Proceedings of the National Academy of Sciences, 103(4)*, 1065-1070.

Fusar-Poli, P., Placentino, A., Carletti, F., Landi, P., Allen, P., Surguladze, S., Benedetti, F., Abbamonte,

M., Gasparotti, R., Barale, F., Perez, J., McGuire, P., & Politi, P. (2009). Functional atlas of emotional faces processing: A voxel-based meta-analysis of 105 functional magnetic resonance imaging studies. *Journal of Psychiatry & Neuroscience, 34(6)*, 418-432.

Gendron, M., Lindquist, K. A., Barsalou, L., & Barrett, L. F. (2012). Emotion words shape emotion

percepts. *Emotion, 12(2)*, 314-325.

George, N., Driver, J., & Dolan, R. J. (2001). Seen gaze-direction modulates fusiform activity and its

coupling with other brain areas during face processing. *NeuroImage, 13(6)*, 1102-1112.

Gilbert, C. D., & Li, W. (2013). Top-down influences on visual processing. *Nature Reviews*

Neuroscience, 14(5), 350-363.

Gorno-Tempini, M. L., Pradelli, S., Serafini, M., Pagnoni, G., Baraldi, P., Porro, C., Nicoletti, R., Umità,

C., & Nichelli, P. (2001). Explicit and incidental facial expression processing: an fMRI study.

Neuroimage, 14(2), 465-473.

Gray, K. L., Flack, T. R., Yu, M., Lygo, F. A., & Baker, D. H. (2020). Nonlinear transduction of emotional

facial expression. *Vision Research, 170*, 1-11.

Habel, U., Windischberger, C., Derntl, B., Robinson, S., Kryspin-Exner, I., Gur, R. C., & Moser, E.

(2007). Amygdala activation and facial expressions: explicit emotion discrimination versus implicit emotion processing. *Neuropsychologia, 45(10)*, 2369-2377.

Hariri, A. R., Bookheimer, S. Y., & Mazziotta, J. C. (2000). Modulating emotional responses: effects of

a neocortical network on the limbic system. *NeuroReport, 11(1)*, 43-48.

Harris, R. J., Young, A. W., & Andrews, T. J. (2012). Morphing between expressions dissociates

continuous from categorical representations of facial expression in the human brain.

- Proceedings of the National Academy of Sciences*, 109(51), 21164-21169.
- Hassin, R. R., Aviezer, H., & Bentin, S. (2013). Inherently ambiguous: Facial expressions of emotions, in context. *Emotion Review*, 5(1), 60-65.
- Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in cognitive sciences*, 4(6), 223-233.
- Hillyard, S. A., & Anllo-Vento, L. (1998). Event-related brain potentials in the study of visual selective attention. *Proceedings of the National Academy of Sciences*, 95(3), 781-787.
- Hillyard, S. A., Squires, K. C., Bauer, J. W., & Lindsay, P. H. (1971). Evoked potential correlates of auditory signal detection. *Science*, 172(3990), 1357-1360.
- Hinojosa, J. A., Mercado, F., & Carretié, L. (2015). N170 sensitivity to facial expression: A meta-analysis. *Neuroscience & Biobehavioral Reviews*, 55, 498-509.
- Hoemann, K., Xu, F., & Barrett, L. F. (2019). Emotion words, emotion concepts, and emotional development in children: A constructionist hypothesis. *Developmental psychology*, 55(9), 1830-1849.
- Itthipuripat, S., Ester, E. F., Deering, S., & Serences, J. T. (2014). Sensory gain outperforms efficient readout mechanisms in predicting attention-related improvements in behavior. *Journal of Neuroscience*, 34(40), 13384-13398.
- Izard, C. E. (1971). *The face of emotion*. New York, NY: Appleton-Century-Crofts Press.
- Kajal, D. S., Fioravanti, C., Elshahabi, A., Ruiz, S., Sitaram, R., & Braun, C. (2020). Involvement of top-down networks in the perception of facial emotions: A magnetoencephalographic investigation. *NeuroImage*, 222, 117075.
- Kanwisher, N., & Wojciulik, E. (2000). Visual attention: insights from brain imaging. *Nature Reviews Neuroscience*, 1(2), 91-100.
- Kastner, S., & Ungerleider, L. G. (2000). Mechanisms of visual attention in the human cortex. *Annual review of neuroscience*, 23(1), 315-341.
- Kawasaki, H., Tsuchiya, N., Kovach, C. K., Nourski, K. V., Oya, H., Howard, M. A., & Adolphs, R. (2012).

- Processing of facial emotion in the human fusiform gyrus. *Journal of Cognitive Neuroscience*, 24(6), 1358-1370.
- Kay, K. N., & Yeatman, J. D. (2017). Bottom-up and top-down computations in word-and face-selective cortex. *Elife*, 6, e22341.
- Kok, P., Jehee, J. F., & De Lange, F. P. (2012). Less is more: expectation sharpens representations in the primary visual cortex. *Neuron*, 75(2), 265-270.
- Kok, P., Mostert, P., & De Lange, F. P. (2017). Prior expectations induce prestimulus sensory templates. *Proceedings of the National Academy of Sciences*, 114(39), 10473-10478.
- Leleu, A., Demily, C., Franck, N., Durand, K., Schaal, B., & Baudouin, J.-Y. (2015). The odor context facilitates the perception of low-intensity facial expressions of emotion. *Plos One*, 10(9): e0138656.
- Leleu, A., Dzhelyova, M., Rossion, B., Brochard, R., Durand, K., Schaal, B., & Baudouin, J.Y. (2018). Tuning functions for automatic detection of brief changes of facial expression in the human brain. *NeuroImage*, 179, 235-251.
- Leleu, A., Rekow, D., Poncet, F., Schaal, B., Durand, K., Rossion, B., & Baudouin, J.-Y. (2020). Maternal odor shapes rapid face categorization in the infant brain. *Developmental Science*, 23(2): e12877.
- Lobmaier, J. S., Klaver, P., Loenneker, T., Martin, E., & Mast, F. W. (2008). Featural and configural face processing strategies: evidence from a functional magnetic resonance imaging study. *Neuroreport*, 19(3), 287-291.
- Lochy, A., de Heering, A., & Rossion, B. (2019). The non-linear development of the right hemispheric specialization for human face perception. *Neuropsychologia*, 126, 10-19.
- Lundqvist, D., Flykt, A., & Öhman, A. (1998). The Karolinska Directed Emotional Faces (KDEF), 1998. Department of Neurosciences Karolinska Hospital: Stockholm, Sweden.
- Luo, Q., Rossion, B., & Dzhelyova, M. (2019). A robust implicit measure of facial attractiveness discrimination. *Social Cognitive and Affective Neuroscience*, 14, 737-746.

- Luo, W., Feng, W., He, W., Wang, N. Y., & Luo, Y. J. (2010). Three stages of facial expression processing: ERP study with rapid serial visual presentation. *NeuroImage*, *49*(2), 1857-1867.
- Martin, A. B., Yang, X., Saalmann, Y. B., Wang, L., Shestyuk, A., Lin, J. J., Parvizi, J., Knight, R. T., & Kastner, S. (2019). Temporal dynamics and response modulation across the human visual system in a spatial attention task: An ECoG study. *Journal of Neuroscience*, *39*(2), 333-352.
- Matt, S., Dzhelyova, M., Maillard, L., Lighezzolo-Alnot, J., Rossion, B., & Caharel, S. (2021). The rapid and automatic categorization of facial expression changes in highly variable natural images. *Cortex*, *144*, 168-184.
- Mattavelli, G., Rosanova, M., Casali, A. G., Papagno, C., & Lauro, L. J. R. (2013). Top-down interference and cortical responsiveness in face processing: a TMS-EEG study. *NeuroImage*, *76*, 24-32.
- Mattavelli, G., Rosanova, M., Casali, A. G., Papagno, C., & Lauro, L. J. R. (2016). Timing of emotion representation in right and left occipital region: evidence from combined TMS-EEG. *Brain and cognition*, *106*, 13-22.
- Maurer, D., O'craven, K. M., Le Grand, R., Mondloch, C. J., Springer, M. V., Lewis, T. L., & Grady, C. L. (2007). Neural correlates of processing facial identity based on features versus their spacing. *Neuropsychologia*, *45*(7), 1438-1451.
- McCarthy, G., & Wood, C. C. (1985). Scalp distributions of event-related potentials: an ambiguity associated with analysis of variance models. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section*, *62*(3), 203-208.
- Monroe, J. F., Griffin, M., Pinkham, A., Loughhead, J., Gur, R. C., Roberts, T. P., & Christopher Edgar, J. (2013). The fusiform response to faces: explicit versus implicit processing of emotion. *Human Brain Mapping*, *34*(1), 1-11.
- Morris, J. S., Friston, K. J., Büchel, C., Frith, C. D., Young, A. W., Calder, A. J., & Dolan, R. J. (1998). A neuromodulatory role for the human amygdala in processing emotional facial expressions. *Brain*, *121*(1), 47-57.

- O'Connell, R. G., Dockree, P. M., & Kelly, S. P. (2012). A supramodal accumulation-to-bound signal that determines perceptual decisions in humans. *Nature neuroscience*, *15*(12), 1729-1735.
- O'Craven, K. M., Downing, P. E., & Kanwisher, N. (1999). fMRI evidence for objects as the units of attentional selection. *Nature*, *401*(6753), 584.
- Peelen, M. V., Fei-Fei, L., & Kastner, S. (2009). Neural mechanisms of rapid natural scene categorization in human visual cortex. *Nature*, *460*(7251), 94-97.
- Plutchik, R. (1962). *The emotions: Facts, theories, and a new model*. New York, NY: Random House
- Plutchik, R. (1980). A general psychoevolutionary theory of emotion. In *Theories of emotion* (pp. 3-33). Academic press.
- Poncet, F., Baudouin, J.Y., Dzhelyova, M., Rossion, B., & Leleu, A. (2019). Rapid and automatic discrimination between facial expressions in the human brain. *Neuropsychologia*, *129*, 47-55.
- Puce, A., Allison, T., Bentin, S., Gore, J. C., & McCarthy, G. (1998). Temporal cortex activation in humans viewing eye and mouth movements. *Journal of neuroscience*, *18*(6), 2188-2199.
- Puce, A., Syngienotis, A., Thompson, J. C., Abbott, D. F., Wheaton, K. J., & Castiello, U. (2003). The human temporal lobe integrates facial form and motion: evidence from fMRI and ERP studies. *Neuroimage*, *19*(3), 861-869.
- Puce, A., Allison, T., Bentin, S., Gore, J. C., & McCarthy, G. (1998). Temporal cortex activation in humans viewing eye and mouth movements. *Journal of Neuroscience*, *18*(6), 2188-2199.
- Quek, G. L., Liu-Shuang, J., Goffaux, V., & Rossion, B. (2018a). Ultra-coarse, single-glance human face detection in a dynamic visual stream. *NeuroImage*, *176*, 465-476.
- Quek, G.L., Nemrodov, D., Rossion, B., Liu-Shuang, J. (2018b). Selective attention to faces in a rapid visual stream: hemispheric differences in enhancement and suppression of category-selective neural activity. *Journal of Cognitive Neuroscience*, *30*, 393-410.
- Rapcsak, S. Z., Comer, J. F., & Rubens, A. B. (1993). Anomia for facial expressions: Neuropsychological mechanisms and anatomical correlates. *Brain and Language*, *45*, 233-252.
- Regan, D. (1966). Some characteristics of average steady-state and transient responses evoked by

- modulated light. *Electroencephalography and Clinical Neurophysiology*, 20(3), 238–248.
- Rekow, D., Baudouin, J.-Y., Rossion, B., & Leleu, A. (2020). An ecological measure of rapid and automatic face-sex categorization. *Cortex*, 27, 150-151.
- Retter, T. L., & Rossion, B. (2016). Uncovering the neural magnitude and spatio-temporal dynamics of natural image categorization in a fast visual stream. *Neuropsychologia*, 91, 9-28.
- Roehe, M. A., Kluger, D. S., Schroeder, S. C., Schliephake, L. M., Boelte, J., Jacobsen, T., & Schubotz, R. I. (2021). Early alpha/beta oscillations reflect the formation of face-related expectations in the brain. *Plos one*, 16(7), e0255116.
- Rossi, A., Parada, F. J., Kolchinsky, A., & Puce, A. (2014). Neural correlates of apparent motion perception of impoverished facial stimuli: a comparison of ERP and ERSP activity. *NeuroImage*, 98, 442-459.
- Rossion, B., Retter, T. L., & Liu-Shuang, J. (2020). Understanding human individuation of unfamiliar faces with oddball fast periodic visual stimulation and electroencephalography. *European Journal of Neuroscience*, 52(10), 4283-4344.
- Rossion, B., Torfs, K., Jacques, C., Liu-Shuang, J. (2015). Fast periodic presentation of natural face images reveals a robust face-selective electrophysiological response in the human brain. *Journal of Vision*, 15, 1, 18.
- Schettino, A., Porcu, E., Gundlach, C., Keitel, C., & Müller, M. M. (2020). Rapid processing of neutral and angry expressions within ongoing facial stimulus streams: Is it all about isolated facial features? *PLoS One*, 15(4), e0231982.
- Scheuerecker, J., Frodl, T., Koutsouleris, N., Zetsche, T., Wiesmann, M., Kleemann, A. M., Brückmann, H., Schmitt, G., Möller, H.-J., & Meisenzahl, E. M. (2007). Cerebral differences in explicit and implicit emotional processing—an fMRI study. *Neuropsychobiology*, 56(1), 32-39.
- Schyns, P. G., Petro, L. S., & Smith, M. L. (2007). Dynamics of visual information integration in the brain for categorizing facial expressions. *Current biology*, 17(18), 1580-1585.
- Scott, L. S., & Nelson, C. A. (2006). Featural and configural face processing in adults and infants: A

- behavioral and electrophysiological investigation. *Perception*, 35(8), 1107-1128.
- Sliwinska, M. W., & Pitcher, D. (2018). TMS demonstrates that both right and left superior temporal sulci are important for facial expression recognition. *NeuroImage*, 183, 394-400.
- Srinivasan, R., Golomb, J. D., & Martinez, A. M. (2016). A neural basis of facial action recognition in humans. *Journal of Neuroscience*, 36(16), 4434-4442.
- Stone, V. E., Nisenson, L., Eliassen, J. C., & Gazzaniga, M. S. (1996). Left hemisphere representations of emotional facial expressions. *Neuropsychologia*, 34(1), 23-29.
- Streit, M., Ioannides, A. A., Liu, L., Wölwer, W., Dammers, J., Gross, J., Gaebel, W., & Müller-Gärtner, H. W. (1999). Neurophysiological correlates of the recognition of facial expressions of emotion as revealed by magnetoencephalography. *Cognitive brain research*, 7(4), 481-491.
- Summerfield, C., Eger, T., Mangels, J., & Hirsch, J. (2006). Mistaking a house for a face: neural correlates of misperception in healthy humans. *Cerebral Cortex*, 16(4), 500-508.
- Summerfield, C., & De Lange, F. P. (2014). Expectation in perceptual decision making: neural and computational mechanisms. *Nature Reviews Neuroscience*, 15(11), 745-756.
- Sun, M., Liu, F., Cui, L., Wei, P., & Zhang, Q. (2021). The effect of fearful faces on the attentional blink is modulated by emotional task relevance: An event-related potential study. *Neuropsychologia*, 162, 108043.
- Tomkins, S. S. (1962). Affect, Imagery, Consciousness: Vol. 1. *The positive affects*. New York, NY: Springer.
- Volpert-Esmond, H. I., & Bartholow, B. D. (2019). Explicit categorization goals affect attention-related processing of race and gender during person construal. *Journal of experimental social psychology*, 85, 103839.
- Vuilleumier, P., Armony, J. L., Driver, J., & Dolan, R. J. (2001). Effects of attention and emotion on face processing in the human brain: an event-related fMRI study. *Neuron*, 30(3), 829-841.
- Wang, X., Song, Y., Zhen, Z., & Liu, J. (2016). Functional integration of the posterior superior temporal sulcus correlates with facial expression recognition. *Human brain mapping*, 37(5), 1930-1940.

- Wieser, M. J., & Brosch, T. (2012). Faces in context: a review and systematization of contextual influences on affective face processing. *Frontiers in psychology, 3*, 471.
- Winston, J. S., O'doherty, J., & Dolan, R. J. (2003). Common and distinct neural responses during direct and incidental processing of multiple facial emotions. *NeuroImage, 20(1)*, 84-97.
- Wolf, M. I., Bruchmann, M., Pourtois, G., Schindler, S., & Straube, T. (2021). Top-Down Modulation of Early Visual Processing in V1: Dissociable Neurophysiological Effects of Spatial Attention, Attentional Load and Task-Relevance. *Cerebral Cortex*.
- Wronka, E., & Walentowska, W. (2011). Attention modulates emotional expression processing. *Psychophysiology, 48(8)*, 1047-1056.
- Wronka, E., & Walentowska, W. (2014). Attentional modulation of the emotional expression processing studied with ERPs and sLORETA. *Journal of Psychophysiology, 28*, 32-46.
- Wundt, W. (1896). Emotions. In *Grundriss der Psychologie*, 13. Leipzig, Germany: Engelmann.
- Xu, B., Liu-Shuang, J., Rossion, B., & Tanaka, J. (2017). Individual differences in face identity processing with fast periodic visual stimulation. *Journal of Cognitive Neuroscience, 29(8)*, 1368-1377.
- Yan, X., Liu-Shuang, J., & Rossion, B. (2019). Effect of face-related task on rapid individual face discrimination. *Neuropsychologia, 129*, 236-245.