

Understanding face perception by means of human electrophysiology

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Electrophysiological recordings on the human scalp provide a wealth of information about the temporal dynamics and nature of face perception at a global level of brain organization. The time window between 100 and 200 ms witnesses the transition between low-level and high-level vision, an N170 component correlating with conscious interpretation of a visual stimulus as a face. This face representation is rapidly refined as information accumulates during this time window, allowing the individualization of faces. To improve the sensitivity and objectivity of face perception measures, it is increasingly important to go beyond transient visual stimulation by recording electrophysiological responses at periodic frequency rates. This approach has recently provided face perception thresholds and the first objective signature of integration of facial parts in the human brain.

Introduction

The human face is a complex multidimensional visual pattern with which everyone is familiar, making it particularly well suited for studying visual perception and the processes underlying perceptual integration of component parts into a meaningful whole. A human face conveys a wide variety of information about an individual (identity, sex, age, mood, etc.) and human adults attain a high degree of proficiency at extracting this information without formal training. A face can be detected in a visual scene shortly after 100 ms [1], and one or two gaze fixations suffice for categorizing a face as familiar [2]. Hence, face perception, which is the construction of a visual representation – an internal image of a face – in the human brain (see [Glossary](#)), is a process generally accomplished by 200 ms after stimulus onset. These characteristics make an understanding of the operations underlying face perception difficult to achieve.

Human electroencephalography (EEG) is the recording on the scalp of electrical currents created by postsynaptic neuronal activity. Following the presentation of a face, successive responses of negative and positive polarity – depending on the orientation of the neural sources – are recorded. If these small changes in EEG activity occur at roughly the same time from trial to trial (time locking) and

with the same polarity (phase locking), averaging over multiple trials extracts this signal from background EEG fluctuations (i.e., noise). This leads to well-identifiable ‘peaks’ and ‘troughs’, the event-related potentials (ERPs) [3], or event-related magnetic fields (ERMFs) recorded in magnetoencephalography (MEG). As illustrated in this review, recording of ERPs, and EEG in general, provides a wealth of information about both the temporal dynamics and the nature of face perception at a global level of brain organization.

The N170

The sudden onset of a face stimulus elicits a wide (120–200 ms) ERP on the adult human scalp that is most prominent over the visual cortex (occipitotemporal sites) and peaks at approximately 170 ms, termed the N170 ([Figure 1](#)) [4,5]. This ERP reflects a transient increase in EEG amplitude in the range 5–15 Hz [6]. The N170 has a specific signature when evoked by faces compared to nonface familiar object shapes: it is larger in amplitude, often peaks a few milliseconds earlier, shows a more consistent right hemisphere lateralization, and is larger at occipitotemporal sites than at medial occipitoparietal sites ([Figure 1](#)) [5]. The N170 is particularly interesting because it can be recorded

Glossary

Electroencephalography (EEG): recording of electrical activity on the scalp.

Event-related potentials (ERPs): small changes in electrical brain activity related to an event (stimulus, response, cognitive process). ERPs are revealed by averaging many epochs that are time-locked to the event, so that larger EEG fluctuations unrelated to the event (i.e., noise) cancel out.

Face perception: interpretation of a visual stimulus as a face. Face perception includes the ability to detect a face (face detection), for instance in a visual scene, and tell this face apart from other unfamiliar faces (face individualization, or individual face discrimination). Face perception is generally distinguished from face recognition, the ability to determine that a specific individual face has been seen before.

Intermodulation: amplitude modulation of signals containing two or more different frequencies in a system with nonlinearities. The intermodulation between the frequency components leads to additional signals at frequencies that are not just at harmonic frequencies (integer multiples) of either, but also at the sum and difference frequencies of the original frequencies and at multiples of those sum and difference frequencies.

Magnetoencephalography (MEG): recording on the scalp of magnetic fields produced by electrical currents occurring in the brain.

N170: relatively large negative potential evoked by face stimuli over the lateral occipital or occipitotemporal areas. It peaks on average at 170 ms, but with large variability across individuals (130–190 ms). A bilateral weaker component is generally evoked by familiar objects, and a left lateralized N170 is also evoked by visual words and nonwords (letter strings).

SSVEP: a steady-state visual evoked potential, as defined by Regan [60], is a periodic electrophysiological response obtained by presenting visual stimuli at a fixed rate. In ideal conditions, the phase and amplitude of the periodic response remain constant over time, which explains the term steady-state.

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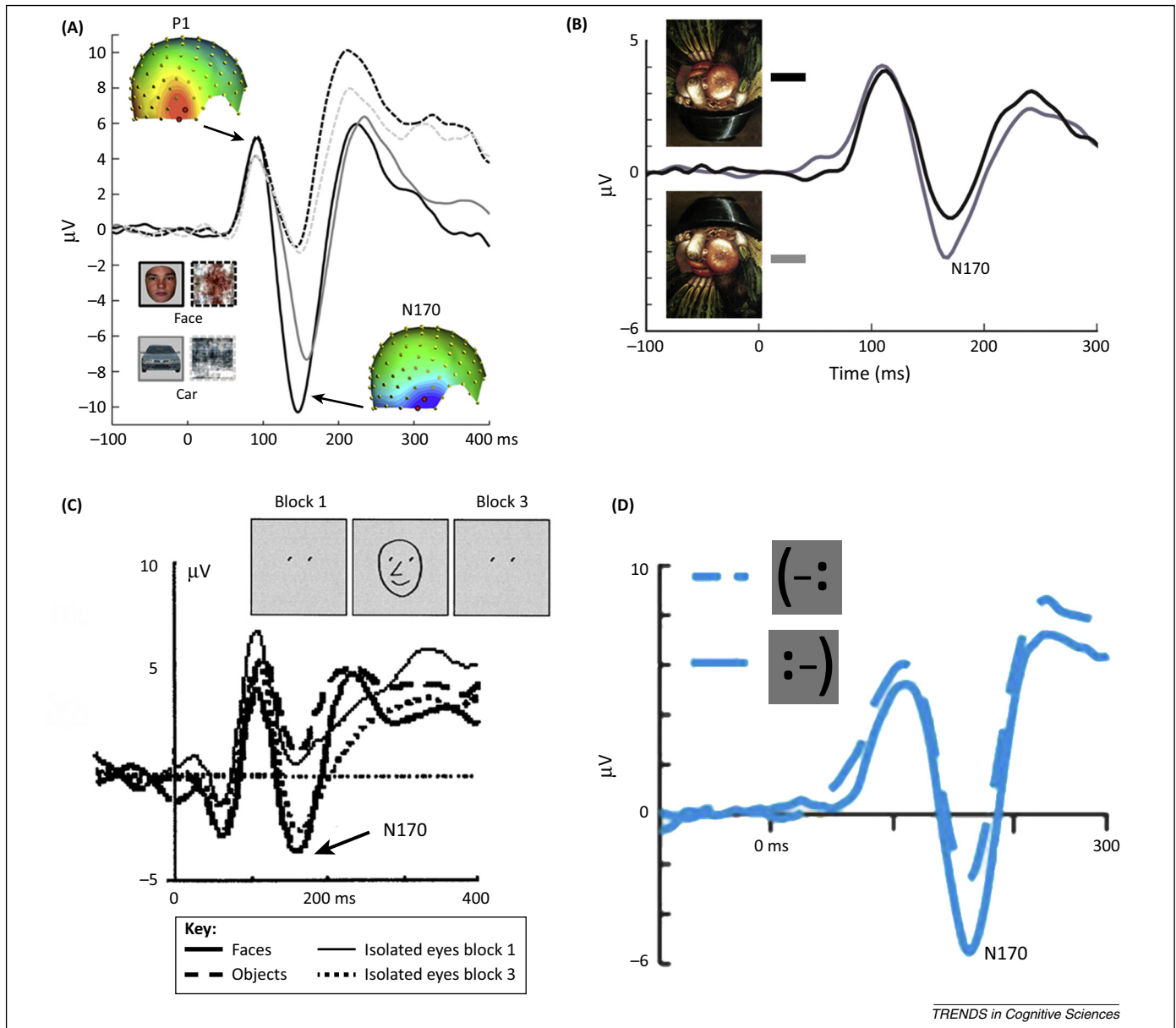


Figure 1. Responses based on perceptual knowledge start after 100 ms and the N170 event-related potential (ERP) component reflects interpretation of the stimulus as a face. (A) Grand averaged ERP response to four types of stimuli for the two electrodes highlighted in red over the right occipitotemporal cortex. The N170 is a large negative potential occurring between 100 and 200 ms, and is significantly greater in response to faces than for other familiar object categories (cars). There is virtually no N170 for meaningless stimuli that are matched for low-level visual properties to faces or cars (i.e., stimuli on the right, with phase information scrambled but the power spectrum preserved). An early visual ERP (P1) is also greater in response to faces than to cars, but this 'face sensitivity' is fully accounted for by low-level properties: it is also observed for phase-scrambled faces when compared to phase-scrambled cars (see also [82,83]). Adapted from [14] with permission. (B) Grand averaged data for right occipitotemporal electrodes. The same painting (the Vegetable Gardener by Arcimboldo) elicits a much greater N170 response when it is presented in an upright orientation because it is perceived as a face. Adapted from [16] with permission. (C) Isolated dots elicit an N170 response only after human observers see these dots in schematic faces, which primes their interpretation of the dots as the eyes of a face. Adapted from [20] with permission. (D) The character combination :-:) known as an emoticon and used to indicate a smiling face in digital communication, elicits a conspicuous N170 response that is substantially reduced if the same physical stimulus is reversed to (-:) and is thus not interpreted as a face. All the waveforms were extracted from either a single channel or a region of interest over the right occipitotemporal cortex. Adapted from [18] with permission.

independently of a face-related task, or even of any behavioral task, as long as the stimulus is fixated. In addition, this time window precedes potential saccadic eye movements, which take ~200 ms to initiate. Hence, the N170 time window is usually free of eye movement artifacts and corresponds to the time between the first two fixations on a face, which are usually sufficient for recognition [2,7]. Moreover, the N170 is a relatively large response that can generally be identified by averaging over a few tens of trials despite the poor signal-to-noise ratio (SNR) of ERPs. By contrast, post-

200-ms ERP components that have been related to higher-level nonspecific aspects of face processing (e.g., N250r [8,9]) may be contaminated by eye movements, can overlap with electrophysiological responses elicited by general cognitive, decisional, and motor processes, and are more difficult to define spatially and temporally.

For all these reasons, hundreds of studies have focused, entirely or largely, on the N170 evoked by faces [5] and its positive counterpart observed on the vertex (the vertex positive potential) described in early studies [10]. In MEG,

Box 1. Single-trial approaches to the temporal dynamics of face perception

Rather than computing an average measure across trials, relatively recent studies have correlated the EEG amplitude of every single trial with the visual stimuli. This information is then used, for instance, to derive the construction of visual categories over time [84] or to reveal the elements of face stimuli driving the EEG response (reverse correlation) [72,73]. Although these single-trial approaches have sometimes been pitted against standard ERP approaches for face perception, single-trial EEG studies that have contrasted faces and controlled nonface objects without *a priori* definition of a time window have essentially rediscovered the N170 time window [29,85–87]. Prediction of behavioral performance by EEG amplitude across trials of the N170 time window has also been reported [29,87] but this prediction holds only for specific tasks and stimulus variations, and is better for late responses [29] or the whole time course [85]. A limitation of single-trial approaches is their quite different implementations, and their increase in computational and statistical sophistication (e.g., principal component analysis to reduce computational load, corrections for multiple comparisons). In addition, some of these approaches require thousands of trials [72,73], which seriously limits their practical application. Nevertheless, they can be useful in specific cases to understand the nature of ERP differences. For instance, denoising of single trials, estimation of local minima of the N170 time window, and correcting for latency jitter of the trials for averaging can significantly improve SNR [30]. Comparison of the outcome of this procedure with the average N170 response has recently revealed that the source of the decrease in averaged N170 amplitude with added noise is due to an increase in latency jitter between trials [30]. Thus, this approach can sometimes complement rather than replace standard ERP analyses.

a similar component, the M170, is also observed [11]. Although EEG and MEG are sensitive to different sources of brain activity [12], there are no consistent functional dissociations between the N170 and M170, and this review treats the two components indifferently. Over recent years there has been increasing emphasis on single-trial analyses in face perception studies, in particular during the N170 time window (Box 1). However, the main and most consistent contributions to our understanding of face perception come from averaged ERP measures, as discussed in the following sections.

Beyond physical features: the N170 marks the interpretation of a stimulus as a face

The N170 is the earliest marker of high-level visual processes: a face and a meaningless nonface stimulus matched for low-level visual properties elicit the same waveform up to the onset of the N170 time window, but there is virtually no N170 component for the meaningless stimulus (Figure 1A) [13,14]. Most importantly, the N170 is not merely triggered by the physical characteristics of the stimulus, but rather depends on our knowledge and past experience of what is a 'face'. For instance, the N170 is enhanced when an ambiguous two-tone Mooney face or a reversible painting by Giuseppe Arcimboldo is consciously perceived as a face (Figure 1B) [15,16]. In the same vein, objects consciously interpreted as face-like (pareidolia) increase the N170 [17,18]. However, the N170 is not increased for stimuli that are similar to faces according to a computational model if humans do not interpret these stimuli as faces [19]. Strikingly, a pair of shapes elicits an N170 response only after observers have been primed to

interpret these shapes as schematic eyes (Figure 1C) [20]. Most recently, it has been shown that the character combination:-) (known as an emoticon and used to indicate a smiling face in digital communication) elicits a conspicuous N170 response that is substantially reduced if the exact same stimulus is reversed to (-: and is thus not interpreted as a face (Figure 1D) [21]. Collectively, these observations indicate that the N170 is a correlate of the interpretation of a visual stimulus as a face. This electrophysiological activity is not only a brain 'response', but necessarily involves perceptual knowledge derived from experience of what is a face, incorporating both bottom-up and top-down processes. This view allows a better understanding of the recent observations that mental imagery [22] and even auditory semantic information [23] can modulate the N170. More generally, these observations strongly support the indirect view of visual perception, according to which perception is an active process and a search for the best possible interpretation of what an individual is seeing [24,25].

The N170 indexes perceptual awareness of a face

According to the indirect view of perception, a visual percept is an unconscious inference from sensory data and knowledge derived from experience [24,25]. Does this mean that the N170 does not reflect perceptual awareness of a face? The N170 certainly depends on attention and is reduced if the face appears at an unattended location [26]. Reducing face visibility by adding noise [27,28] or gradual phase-scrambling [29] also reduces the N170 either linearly [27] or with a sigmoid function [29]. Most interestingly for the issue of perceptual awareness, an N170-like component has recently been identified in response to consciously invisible faces during ocular suppression [30]. However, this component was wider and less lateralized, suggesting a relative failure of early interpretation of the stimulus as a face. Besides this, studies using backward masking all revealed correlation between the N170 and conscious reports of face perception [28,31–33]. Although this correlation does not imply that perceptual awareness *per se* emerges before 200 ms, it challenges the view that correlates of consciousness emerge only at relatively late latencies (after 200 ms [34]) when incoming information is made globally available to multiple brain systems [35].

From coarse- to fine-grained face representations by 200 ms

Although the N170 reflects the conscious interpretation of a stimulus as a face, this does not imply that it corresponds to a single 'face detection' stage of face processing [4]. Indeed, face detection can be partly based on low-level information extracted before the N170 onset (Box 2, Figure 1) [14,36]. In addition, the N170 absence does not necessarily prevent behavioral face detection if the behavioral report is based on a slow and detailed analysis of a degraded stimulus [37]. More generally, face detection is a global perceptual decision process and there is no reason to expect it to be based on a particular stage rather than continuous accumulation of evidence in the (visual) system.

Rather than a single process, many processes are probably engaged during this N170 time window, as suggested

Box 2. Controlling for low-level visual cues in electrophysiological studies of face perception

Comparison of electrophysiological responses for pictures of faces versus other objects for different face categories (e.g., males vs females) or for individual faces requires careful attention to low-level visual differences between the stimulus sets. For instance, if one stimulus set has a higher stimulus versus background contrast than the other set, this factor may (partly) account for electrophysiological differences between the two sets and make the findings difficult to interpret. Researchers have used two opposite procedures to deal with this problem. The first procedure, control by elimination, controls for all low-level visual differences by eliminating them: colorless stimuli are equalized for luminance, internal contrast, and even spatial frequency differences [6,13]. However, natural low-level cues can be used by the visual system to distinguish faces from other objects [88], faces of different ethnic groups, male and female faces (differing in skin color, [89]), or even individual faces (e.g., a Caucasian face with dark eyebrows is more contrasted than the same face with blond eyebrows). Hence, controlling by elimination degrades the stimuli and makes them highly artificial, removing a wealth of potentially diagnostic information for face categorization. At the other extreme, all the stimuli can be left intact to preserve naturalness and take this into account when interpreting electrophysiological differences between different stimulus sets [84,87]. A limitation of this procedure is that the differences observed may be due to the specific stimulus set used in the experiment rather than the real categories. Therefore, a large set of variable images should be used, with many exemplars for each category. In addition, control conditions can be used to help in isolating naturally diagnostic differences. For instance, high-level visual information can be disrupted by adding phase-scrambled stimuli (Figure 1A) [14] or inverted faces [48,65,67] to the design and testing if the responses resist these manipulations. This control-by-generalization procedure, which is often preferable, can also be done by introducing low-level variations that are orthogonal to the question of interest, for instance by introducing a change in size and/or position between images of the same category [48,65–67].

by multiple sources overlapping in time that are recorded intracerebrally in the ventral and lateral occipitotemporal cortices between 100 and 200 ms (Box 3) [38–40]. One hypothesis is that these processes concern finer-grained categorization of faces (i.e., gender, expression, race, eye gaze direction, identity). However, direct comparison of the N170 evoked by different face categories usually leads to null effects, or small and inconsistent differences across studies [41–44]. This is not surprising because the scalp N170 response reflects global activation of the face perception system: there is no reason to expect it to differ reliably and consistently for different categories of faces (e.g., the same face with different expressions, faces of different ethnic origins).

A powerful alternative approach for assessing the N170 sensitivity to face categories is the ERP repetition paradigm [45,46]. Repetition of the same face identity with a brief delay reduces the N170 response, and this repetition suppression/adaptation effect emerges significantly at the peak of the N170 rather than at its onset [47,48]. This effect cannot be accounted for in terms of low-level image-based cues: it is found across size changes, resists a substantial degree of viewpoint-change [49], and is not found for inverted faces ([48]). There is also evidence that this effect is based on 3D shape cues as opposed to surface-based cues (color, texture [50]) and is greater for same-race than for other-race faces [51], indicating a perceptual basis for the difficulty in recognizing faces from another ethnic group

Box 3. Neural sources of electrophysiological markers of face perception

Responses to transient stimulation of a face, or to fast (>3 Hz) periodic face stimulation, are usually recorded on the scalp over bilateral occipitotemporal cortices, with a right hemispheric dominance (Figures 1–3). Researchers have attempted to localize the sources of these responses, and of the N170 and M170 in particular, using a variety of source localization algorithms [5,90–92]. However, source localization of scalp responses is an ill-posed problem [12], and no hypothetical advantage of MEG over EEG for source localization has been demonstrated, at least in this area of research. Source localization of EEG/MEG activity is particularly challenging for face perception because this function is widely distributed across the whole ventral occipitotemporal cortex and superior temporal sulcus, as evidenced by functional magnetic resonance imaging (fMRI) in humans [93,94]. Many of these sources are certainly activated in parallel during face perception, making the exact localization of these sources an intractable problem for scalp recording studies, even when simultaneously recording fMRI [95]. Beyond fMRI, which measures indirect sources of brain activity, intracerebral recordings of electrophysiological responses to faces in epileptic patients can help in identifying the sources of face perception in the human brain. These recordings are performed via either subdural grids on the cortical surface (electrocorticography, ECOG, [38,40]) or depth electrodes (stereotactic EEG, SEEG, [39]). Low- (N170/N200) and high-frequency (>30 Hz, gamma-range) responses to faces have been recorded with both approaches over multiple sites of the ventral and lateral occipitotemporal cortex [38–40,96]. Although the spatial coverage of ECOG is wider, SEEG has the advantage of recording from smaller contacts, both in cortical gyri and sulci. Thus, SEEG can identify potentials of opposite polarities (e.g., N170/P170, [39,97]) and provide more information for localizing the generators of electrical currents, and can also be used to perform more focal electrical stimulations to elicit specific impairments in face perception [97]. Recent studies have taken advantage of these intracerebral implants to record the activity of single neurons in the human brain [98]. For technical reasons, these microelectrode recordings are performed mainly in medial temporal lobe structures, and although these studies have identified neurons coding for abstract concepts (including people), there is no evidence yet of a human analog of visual neurons that respond selectively to faces as found in the monkey inferotemporal cortex [99,100].

(the other-race face effect [52]). This repetition effect is important because it arguably reflects the most difficult type of visual discrimination between face stimuli, requiring the coding of identity. Hence, there are good reasons to expect this ERP repetition paradigm to reveal clear sensitivity of the N170 to other face categorizations (e.g., facial expression, gender, social categories of faces; Box 4 [5]).

In summary, ERP studies of face perception show that a face is initially encoded with a coarse representation based on registration of the visual stimulus with perceptual knowledge or perceptual expectations. This initial percept is rapidly refined, with incorporation of specific information about an individual face before 200 ms.

Use of the N170 as an index of perceptual face knowledge: limitations

Given what has been learned about the N170, this component potentially appears to be an excellent marker of the early involvement of perceptual face knowledge that could be useful in understanding human cognition and its development and pathology [5]. For instance, N170 shows a typical adult-like response profile as early as 5 years of age [53], suggesting that enough experience is accumulated at this age to interpret a visual stimulus as a face. However,

Box 4. Outstanding questions

- Why does N170 correlate with perceptual awareness of a face, even though such correlations are not found until much later latencies for other visual stimuli? Moreover, does this mean that humans are conscious of a face stimulus before 200 ms or that this response is a prerequisite for awareness of a face, which would emerge at a later latency?
- Given the inconsistency and relative failure of studies directly comparing N170 elicited by different faces categories (e.g., different facial expressions, male vs female faces), ERP repetition paradigms should be used more extensively to clarify whether face categories emerge during this time window (e.g., taking into account low-level confounds, N170 to an angry face should be greater when preceded by the same face with a different expression than with the same expression).
- Why do we observe a large N170 component on the scalp at all when there are so many sources of different polarities activated in parallel at this latency inside the human brain (Box 3) [38–40]? In principle, these sources should cancel each other out unless there are dominant negative sources located close to the surface of the scalp electrodes.
- What are the respective contributions of activities observed intracerebrally in the high-frequency (gamma) range in response to faces [96] in comparison to the low-frequency responses (Box 3)?
- Are there specific parts of the face that drive the intermodulation EEG responses indicative of integration? If so, what are these features and can we find intermodulation responses?
- What is the spatiotemporal hierarchy between the representation of a whole face and parts of a face? So far, the timing (i.e., phase) of the intermodulations and of the fundamental responses during part-based frequency tagging stimulation cannot be directly compared, which precludes inferences about the spatiotemporal hierarchy between part-based and integrated representations.

the characteristic N170 response to faces is absent in humans blind from birth who underwent cataract surgery between 2 months and 14 years of age [54]. This suggests that the ability to interpret a visual stimulus as a face – that is, going beyond the physical characteristics of the stimulus – depends on visual experience during early development. Recent studies have also used the N170 to better characterize face recognition impairments following brain damage (acquired prosopagnosia [55,56]) and in congenital/developmental prosopagnosia [57].

Unfortunately, use of the N170 as a tool in ERP studies is limited by at least two factors. First, the poor SNR of ERPs evoked by transient visual events often requires the collection of a large number of trials, for instance to identify the effect of face identity repetition on the N170 [48]. This factor precludes short recording sessions and identification of significant effects at the individual level. Second, there is ambiguity in defining what is an N170 versus an N170-like component [30] and in quantifying this response. These limitations are particularly problematic for studying single cases of prosopagnosia with brain lesions that distort ERP components [56] and in relating ERPs observed on the infant scalp to the N170 observed in older children and adults [58]. They also restrict our understanding of the nature of the wide interindividual differences in face processing recently identified by behavioral studies [59], which constitute a topic of primary importance. Consequently, a challenge in this area of research is to increase the SNR of electrophysiological visual responses to faces to reduce testing times and to rely on approaches that allow

more objective definition and quantification of these responses. This is the main goal of the recently developed approach termed periodic face stimulation, which is briefly described next.

Periodic face stimulation in EEG

In standard ERP studies, the stimuli are presented at relatively slow rates (e.g., one face every 2 s) and the delay between consecutive presentations is usually variable to reduce stimulus expectancy and overlap of components [3]. An alternative approach is to present stimuli at a fixed rate, generating electrophysiological responses at exactly that rate. These periodic responses, so-called steady-state visual evoked potentials (SSVEPs) [60–64], are identified by extracting the frequency spectrum of the EEG by means of a Fourier transform [60]. Visual stimuli can even be presented at a relatively high periodic rate (e.g., 6 stimuli/s, 6 Hz) and thanks to the high dynamic range of EEG, lead to a well identifiable response at this high rate. This response can be identified objectively because it occurs at a specific frequency defined by the experimenter, and it can be quantified directly by comparing the response at that frequency (signal) and at neighboring frequencies (the noise). The periodic stimulation approach, which is relatively immune to artifacts and thus provides high SNR responses, has been used to isolate responses to low-level visual stimuli [61,62] and to measure the effects of spatial and selective attention on low-level visual responses [63,64]. However, recent studies have shown that periodic visual stimulation can capture high-level visual processes, and in particular provide robust indexes of individual face discrimination at fast periodic rates (3–9 face stimuli/s) without requiring any face-related behavioral task and within a few minutes of stimulation [65–67]. As described next, this approach can also provide objective thresholds of face perception that precede decisional processes and motor responses.

Perceptual thresholds for face detection

Presenting phase-scrambled face stimuli at 6 Hz generates a robust 6-Hz electrophysiological response over low-level visual regions (Figure 2A,B) [68]. Phase descrambling for every alternate stimulus reveals three faces per second, which leads to a robust 3-Hz response over the right occipitotemporal cortex associated with face perception (Figure 2). Progressive descrambling of the phase (increasing visibility) can be used to monitor the emergence of the 3-Hz response for a face stimulus in a single brain before behavioral face detection (Figure 2A). Under these conditions, a 3-Hz response emerges abruptly between 30% and 35% phase coherence for the face, and thus provides a perceptual face detection threshold (Figure 2C). Using this high SNR approach, perceptual thresholds can be reliably estimated in single participants from only 15 trials of 20 s and behavioral face detection responses can be predicted across different face trials and participants [68].

Objective evidence for integrated face percepts

An outstanding issue in face perception research is whether the face percept is based on independent facial parts or on an integrated unit, a so-called holistic or configural

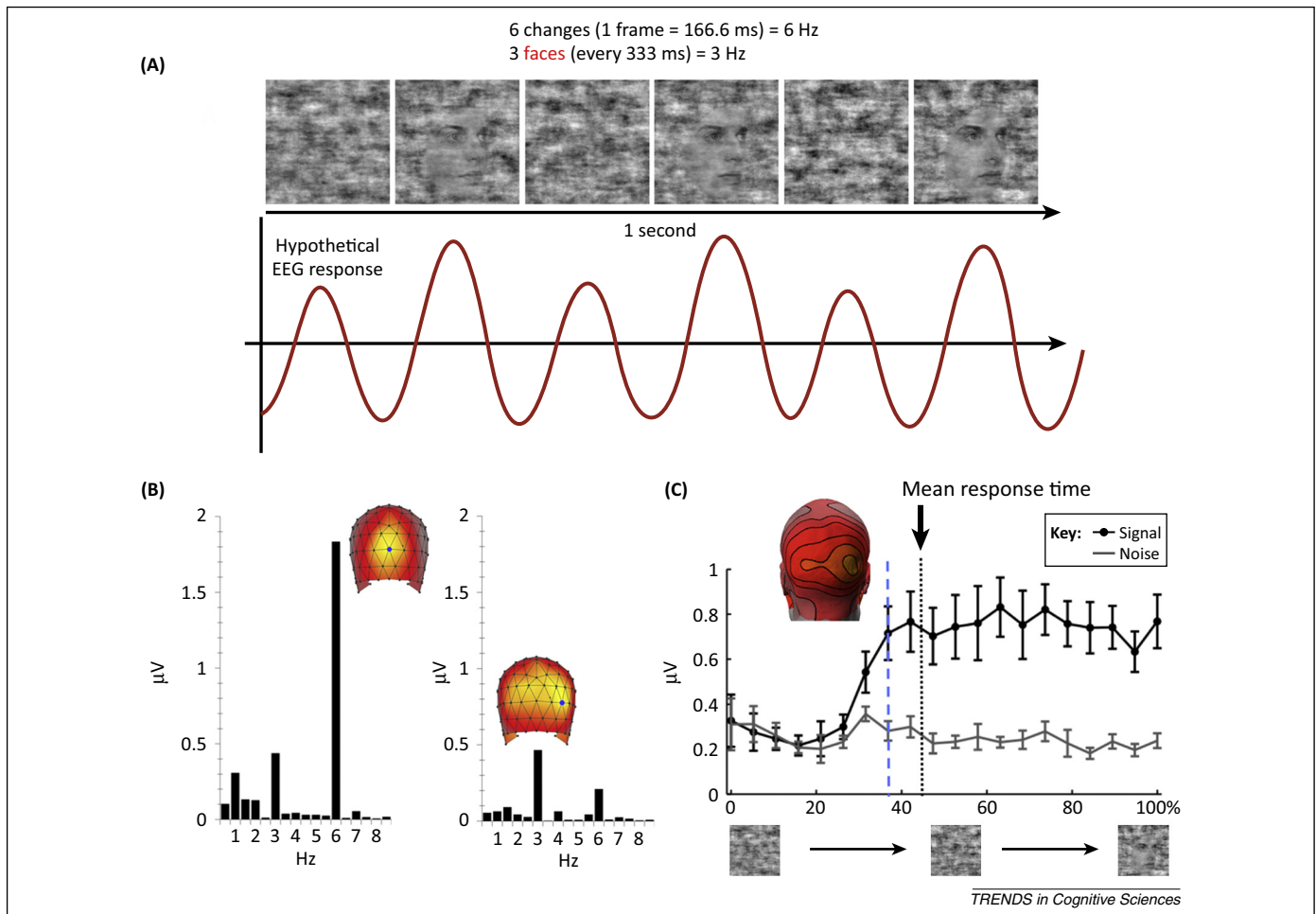
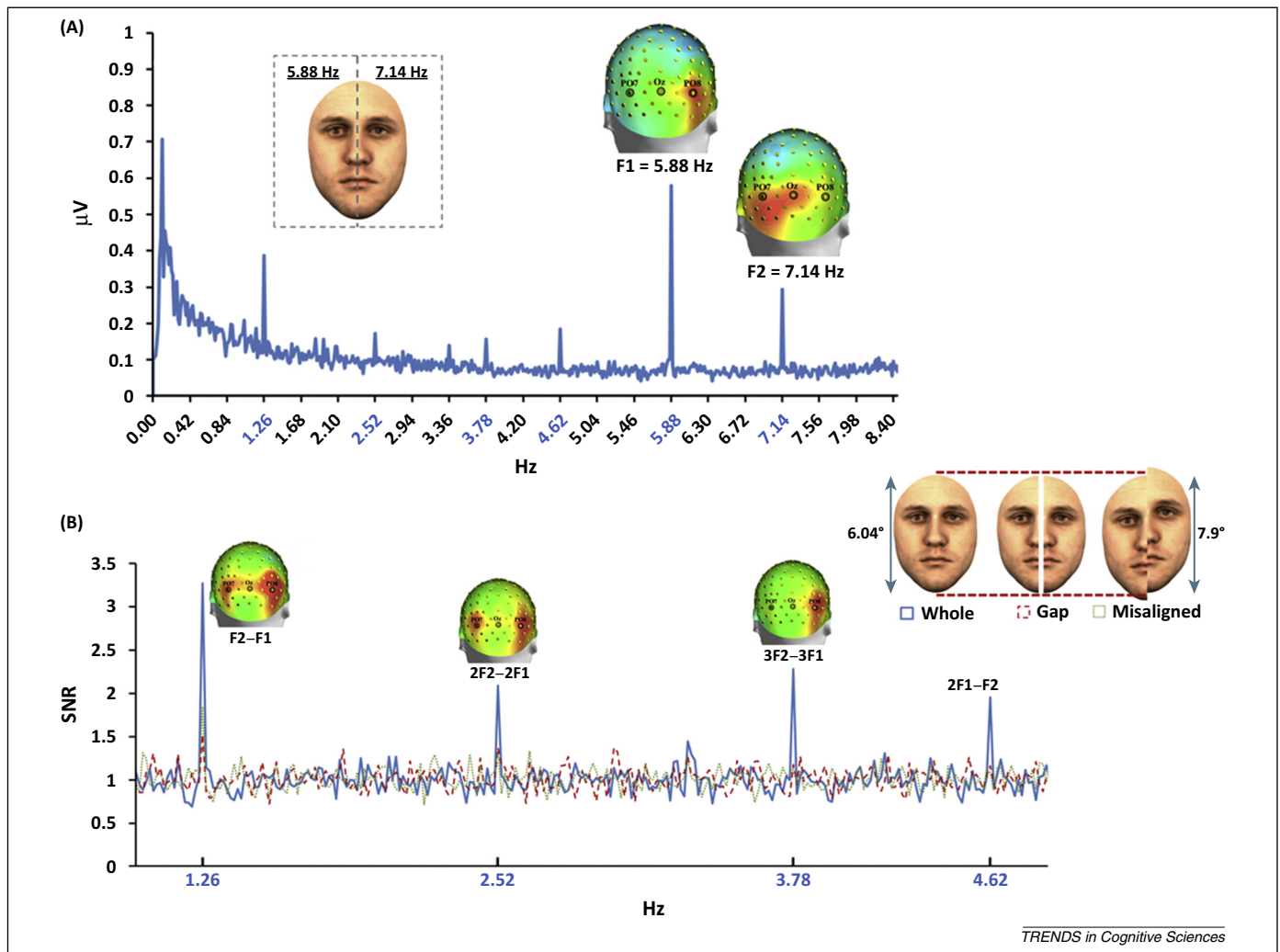


Figure 2. Perceptual face detection thresholds estimated by periodic visual stimulation in EEG. **(A)** Six stimuli were presented at a fixed rate, with a new phase randomization for every step. The power spectrum was constant during stimulation. Phase information for the face was not random for every other stimulus, so three faces were presented per second. Populations of neurons coding for faces – independently of low-level information – should respond exactly three times per second, leading to a 3-Hz response on the scalp. **(B)** Grand averaged ($n = 10$) EEG spectrum for the stimulation depicted in A. This stimulation leads to a response at exactly 6 Hz in the EEG spectrum. This response is localized over low-level visual areas (medial occipital site, electrode Oz). A 3-Hz response is also present over right occipitotemporal sites, reflecting face perception. **(C)** Time course of the 3-Hz response (signal) compared to the activity in a neighboring frequency bin of the spectrum (3.5 Hz, noise) during a 20-step sequence (20 s) evolving from a fully phase-scrambled face to a clearly visible face stimulus. Face detection emerges in the EEG at phase coherence of approximately 35%, before the behavioral report of face detection. The topographical map was extracted at the level of the blue dotted line (~35% phase coherence), indicating the emergence of face detection over right occipitotemporal electrode sites. Figure adapted from [68] with permission.

representation [69]. Elicitation of the N170 response is similar for various stimuli that have no element in common, such as isolated eyes [4,70] and an eyeless face [71], so it cannot be driven by a specific subpart of the face. Moreover, unlike meaningful shapes that can be formed of simple meaningless elements (e.g., a triangle formed of three connected lines), a facial part such as an eye is meaningful by itself, and may suffice to activate other parts or an entire face representation by completion. Hence, attempts to fractionate the N170 response by presenting face components isolated *a priori* [4,70] or through reverse correlation [72,73] can lead to serious misinterpretations. For instance, EEG/MEG studies using reverse correlation revealed a progressive increase in sensitivity to multiple parts of a face over a wide time window [72,73]. However, this observation can be accounted for by an increase in the size of the receptive field over time and does not provide any evidence of the integration of parts. High-frequency EEG responses (so-called induced gamma-band oscillations) have also been proposed as a correlate of

such integrated face percepts [74–76] but these responses are highly inconsistent across studies in terms of latency, frequency bands, and scalp topography, and have even been associated with small eye movement artifacts [77].

Given these limitations, how can we objectively dissociate part-based and integrated face representations? This issue can be addressed by means of a periodic frequency-tagging approach [63,64,78]. For instance, by flickering the left and right halves of a face at different frequency rates (e.g., left at 5.88 Hz and right at 7.14 Hz) the responses associated with each of these parts can be objectively separated in the EEG frequency spectrum (Figure 3) [79]. Hence, this approach can simultaneously measure the independent EEG response to each face part. Most interestingly, responses corresponding to exact differences between the two input frequencies (e.g., $7.14 - 5.88 = 1.26$ Hz) can be observed (Figure 3). These nonlinear intermodulation (IM) responses between the two frequencies can only arise from neuronal populations that integrate the two inputs nonlinearly [80,81]. They are



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Figure 3. Frequency tagging evidence of visual binding of facial parts. (A) Electroencephalography (EEG) spectrum (grand averaged for 15 participants, right occipitotemporal channel PO8; SNR, signal-to-noise ratio) obtained by flickering the two halves of a face stimulus at different frequency rates (5.88 and 7.14 cycles/s) for 60 s. The response to each face half is contralateral to the side of stimulation. The extremely high frequency resolution was obtained by Fourier transformation of a long EEG recording and is due to the high dynamic range of the method. (B) Intermodulation responses at the exact differences between the two stimulation frequencies (e.g., $F2 - F1 = 1.26$ Hz; $2F2 - 2F1 = 2.52$ Hz). These responses only arise when a population of neurons in the system processes both frequency inputs. Contrary to the responses to each of the parts, these responses are specific to the condition in which the two face halves form a whole integrated face [79]. Figure adapted from [79] with permission.

prominent over right occipitotemporal channels, suggesting the presence of high-level integration processes of the two face halves. Importantly, manipulations that break the whole face into its constituent parts, such as spatial separation by a gap, misalignment, or even inversion, dramatically reduce the IM responses, whereas part-based fundamental frequency responses remain unaffected (Figure 3) [79]. Thus, the IM responses identified in the EEG provide the first objective signature of an integrated (i.e., holistic or configural) face percept.

Concluding remarks

It is often stated that EEG is a particularly important method in cognitive neuroscience because of its high temporal resolution. This is correct, but it is often understood as a way to extract information about successive temporal stages of processing. However, an important message conveyed by this review is that the high temporal resolution of EEG essentially serves other purposes in face perception research. First, it allows isolation of a perceptual process

from a behavioral response to better understand how a stimulus is perceived as a face. In particular, the ERP studies reviewed have shown that the early correlate of perceptual awareness of a face, the N170, incorporates knowledge and past experience. Second, the high temporal resolution of EEG allows tagging of rapidly changing visual processes at periodic rates with high frequency precision. Hence, despite the ambiguity of this periodic visual stimulation approach regarding absolute timing information (Box 4), this approach allows objective isolation and direct quantification of visual responses at relatively high stimulation rates. Thanks to these advantages, this approach has already provided robust signatures of individual face discrimination, perceptual face detection, and visual integration processes. The simplicity of this approach in terms of data analysis and interpretation opens a real avenue for understanding face perception at the level of the individual brain in different human populations, including brain-damaged patients, infants, and individuals with developmental delay.

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