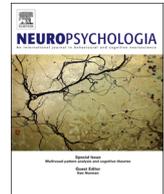




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Neural and cognitive face-selective markers: An integrative review

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ABSTRACT

Faces elicit robust and selective neural responses in the primate brain. These neural responses have been investigated with functional MRI and EEG in numerous studies, which have reported face-selective activations in the occipital-temporal cortex and an electrophysiological face-selective response that peaks 170 ms after stimulus onset at occipital-temporal sites. Evidence for face-selective processes has also been consistently reported in cognitive studies, which investigated the *face inversion effect*, the *composite face effect* and the *left visual field (LVF) superiority*. These cognitive effects indicate that the perceptual representation that we generate for faces differs from the representation that is generated for inverted faces or non-face objects. In this review, I will show that the fMRI and ERP face-selective responses are strongly associated with these three well-established behavioral face-selective measures. I will further review studies that examined the relationship between fMRI and EEG face-selective measures suggesting that they are strongly linked. Taken together these studies imply that a holistic representation of a face is generated at 170 ms after stimulus onset over the right hemisphere. These findings, which reveal a strong link between the various and complementary cognitive and neural measures of face processing, allow to characterize where, when and how faces are represented during the first 200 ms of face processing.

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1. Introduction

Faces convey very rich information that is critical for intact social interaction including person's identity, age, gender, expression and so on. The importance of faces in our daily social life and the rich information they convey may account for the highly reliable, robust and selective neural responses that they elicit in the primate brain. In this review, I will start by describing these well-established face-selective neural responses that were revealed with event-related potential (ERP) (Fig. 1A) and functional MRI (fMRI) (Fig. 1B) and investigated in thousands of studies. In particular, I will evaluate their associations to well-known face-selective cognitive effects such as the face inversion effect, holistic face processing and the left-visual-field (LVF) superiority for faces (Fig. 1C–E, respectively). I will then highlight studies that have examined the associations between these neural face-selective measures and assessed the extent to which they reflect the same neural mechanisms. Overall, these studies have expanded our understanding of the neural architecture of the face processing system by providing data with both the high spatial resolution that is enabled by fMRI and the high temporal resolution that can be measured with EEG. Furthermore, by combining these measures with neural stimulation techniques we can examine a causal

relationship between them with the high spatial and temporal resolution that transcranial magnetic stimulation (TMS) provides. These findings have enabled us to describe the course by which faces are processed and represented in the occipital-temporal cortex during the first 200 ms of face processing. The research that Shlomo conducted, in particular on the role of the face-selective N170 component in face processing, has significantly contributed to our current understating of these face-selective mechanisms as will be underlined in this review.

2. Are face-selective neural markers associated with face-selective cognitive markers?

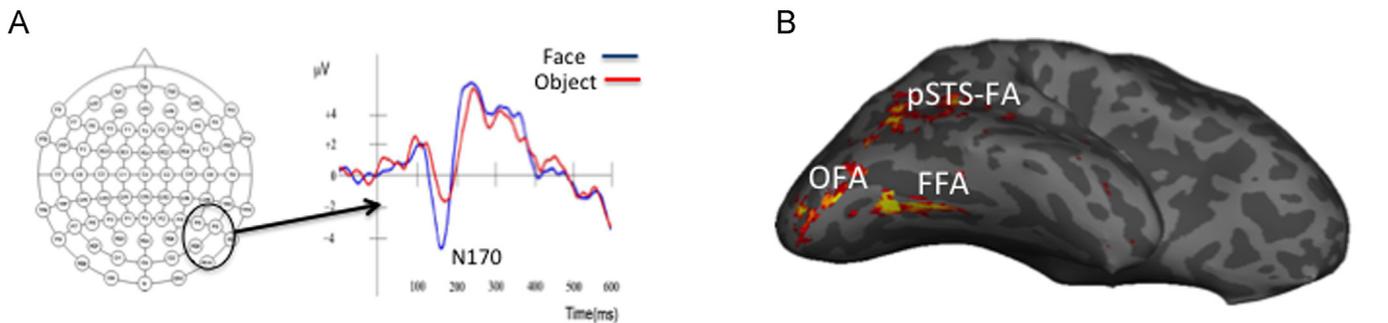
2.1. Event-related potentials: the face-selective N170 component

The seminal study published by Bentin et al. (1996) was the first to report and systematically characterize the face-selective N170 ERP component (Fig. 1A). This study, which by now has been cited by over 1900 papers, reports a negative event-related potential component that peaks 170 ms after stimulus onset at occipital-temporal sites and is larger for faces than any other non-face stimuli (for an extensive review see Rossion and Jacques (2008)). The amplitude of the N170 is larger over the right than the left hemisphere, consistent with the right hemisphere superiority in face perception that will be discussed below.

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Face-selective neural markers



Face-selective cognitive markers

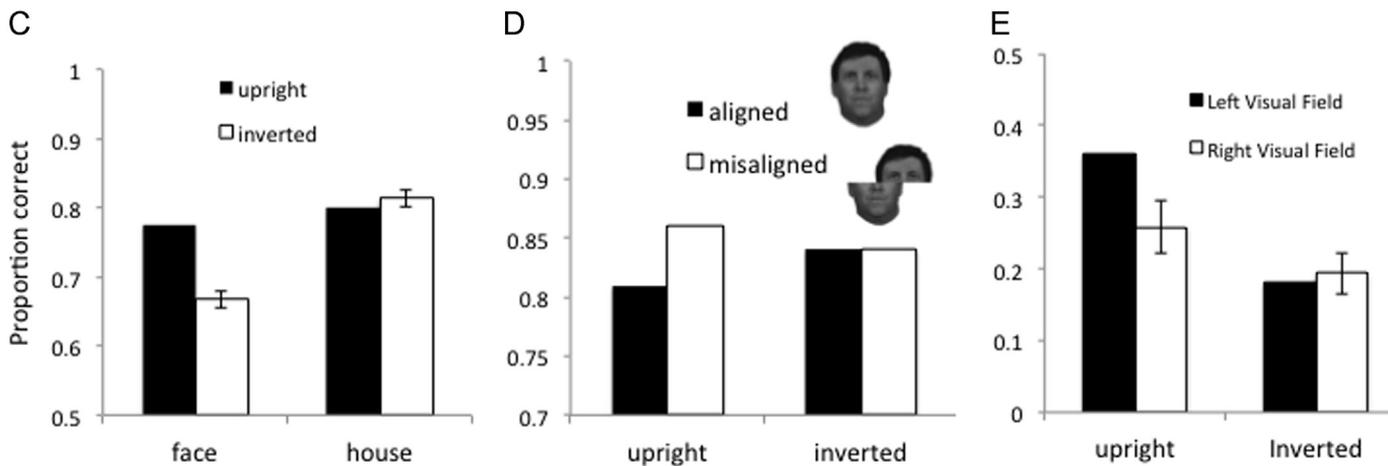


Fig. 1. Neural and Cognitive Face-selective markers: Face-selective neural markers: (A) *Face-selective ERP component*: Faces elicit higher ERP response than non-faces at 170 ms after stimulus onset (N170) at occipito-temporal electrodes. The figure shows ERPs from right occipito-temporal electrodes. (B) *Face-selective fMRI activations*: Faces typically elicit three face-selective fMRI activations in the occipital lobe (Occipital Face Area–OFA) the fusiform gyrus (Fusiform Face Area–FFA) and the posterior superior temporal sulcus (pSTS-FA). Cognitive face-selective markers are demonstrated by illustrative figures of the typically reported behavioral effects: (C) *Face Inversion Effect*: Stimulus inversion results in larger drop in performance for faces than for non-face objects (Data published in [Yovel and Kanwisher, 2008](#)). (D) *Composite Face Effect*: Recognition of inconsistent half faces is better when they are misaligned than aligned due to the holistic representation that is generated for aligned faces. This effect is not found for inverted faces (Data published in [Robbins and McKone, 2007](#)). (E) *Left Visual Field Superiority*: Performance level is higher for faces presented in the left visual field than the right visual field for upright but not inverted face (Data published in [Yovel et al. \(2005\)](#)).

Unlike functional MRI studies, which require a functional face localizer (presentation of faces and objects) to independently define the voxels that are face-selective, it is already known which scalp electrodes show a face-selective N170 response. Thus, the examination of the functional profile of the face N170 is typically done by measuring the peak of the response between 140 and 200 ms after face onset in the occipital-temporal electrodes. Hundreds of studies since the publication of the first N170 paper by Bentin and colleagues have examined the nature of the face representation that is generated at this relatively early stage of visual processing. Whereas several studies have claimed that the N170 reflects an early structural encoding stage, which does not represent the identity of the face ([Bentin and Deouell, 2000](#); [Eimer, 2000](#)), other studies, using neural adaptation techniques, have claimed that some information about face identity is represented at 170 ms after stimulus onset ([Jacques and Rossion, 2006](#); [Vizioli et al., 2010](#)). Here I will focus on studies that suggest that the N170 is associated with other face-selective measures revealed in behavioral experiments. The N170 component has shown to be related to several known face-selective cognitive effects. This includes the *face inversion effect*, *holistic face processing* and the *left visual field superiority* found for faces.

2.1.1. Face inversion effect

The face inversion effect refers to the much better recognition that we have for upright than upside down faces ([Fig. 1C](#)). This effect has been shown to be larger for faces than any other non-face stimulus ([Yin, 1969](#)). The response of the N170 to inverted faces is consistently larger and slightly delayed relative to upright faces. Importantly, similar to the behavioral face inversion effect, the effect of inversion on the N170 amplitude and latency is also face specific ([Rossion and Gauthier, 2002](#); [Rossion et al., 2000](#)). For example, unlike faces, the N170 amplitude for inverted cars was less negative than the response to upright cars. Furthermore a smaller latency difference was found between upright and inverted cars relative to the effect of inversion on the latency to faces ([Boehm et al., 2011](#)).

Rossion and colleagues have asked whether the N170 face inversion effect is associated with the behavioral face inversion effect by measuring the magnitude of the N170 face inversion effect and examining its correlation across individuals with the magnitude of the behavioral face inversion effect ([Jacques and Rossion, 2007](#)). In this study they presented a face in 10 different in-plane orientations and showed that behavioral performance for the rotated faces decreases as a function of the rotation from upright to

upside-down orientation. The same pattern was found for the amplitude and latency of the N170 and these electrophysiological and behavioral modulations as a function of in-plane face rotation were correlated.

In a second study, which also supports the idea that the N170 is associated with the face inversion effect, Jacques et al. (2007) applied a design that was similar to fMR-adaptation in an ERP study. In an earlier study Jacques and Rossion found a larger N170 response to a face that was preceded by a different identity face than to a face that was preceded by a same identity face (Jacques and Rossion, 2006), indicating sensitivity to face identity information at the N170 latency. This effect was absent for inverted faces (Jacques et al., 2007). These findings suggests greater sensitivity to differences in face identity for upright than for inverted faces, in accordance with the better performance level for upright than inverted faces, which is demonstrated in behavioral studies. These findings are also consistent with fMRI studies that examine the face inversion effect in face-selective areas (e.g., Yovel and Kanwisher, 2005) that will be discussed below.

2.1.2. *Holistic face processing*

The idea that faces are processed holistically is prevalent in the face processing literature and refers to the finding that face parts are processed interactively, rather than independently, when presented in the context of a face (Maurer et al., 2002). One of the most common tasks that has been used to measure holistic processing is the *composite face task*. In the composite face task, subjects are asked to recognize a familiar face by naming or to perceptually match the upper or lower half of an unfamiliar face that is combined with the complementary half face of a different identity. Performance is better when two upright halves are misaligned than when they are aligned, a difference that has been termed the *composite face effect* (Fig. 1D). The lower performance for aligned stimuli is believed to reflect the fusion of the two halves into a single holistic representation in which the parts from the two halves are processed interactively (Young et al., 1987). The composite face effect was shown to be present for upright but not inverted faces in a seminal paper by Young et al. (1987) (see also, Robbins and McKone, 2007 in Fig. 1D) and later was also shown to be smaller or absent for non-face stimuli such as dogs (Robbins & McKone, 2007) or cars (Cassia et al., 2009).

To reveal whether the face representation that is generated at 170 ms after stimulus onset is holistic, the sensitivity of the N170 to the composite face effect has been assessed. Jacques and Rossion (2009b) presented pairs of different faces, same faces and faces that differed in the bottom but not the top halves. They found highest N170 amplitude to the different faces, and lowest for same faces. Consistent with a composite face effect, the N170 for faces that differ in the bottom but not the top half was intermediate. Importantly, the difference in the N170 amplitude to the aligned composite faces was absent for misaligned faces suggesting it does not reflect image-based differences but the holistic representation that is generated for aligned but not for misaligned faces. Interestingly, the N170 composite effect was found only over the right occipito-temporal electrodes and not over the left hemisphere. This result is consistent with the findings that showed a behavioral composite effect when faces are presented in the left visual field and not the right visual field (Ramon and Rossion, 2011), and relates to the left visual field superiority for faces, which will be discussed next.

2.1.3. *Left visual field superiority*

The superiority of the right hemisphere for face recognition was suggested during the first half of the 20th century by neuropsychological studies, which found that unilateral right hemisphere damage was much more likely to lead to prosopagnosia

than unilateral left hemisphere damage (for review see, De Renzi et al., 1994). Confirmation to this idea came from studies with split-brain patients, which showed better recognition for faces presented in the left visual field (LVF), which directly projects to the right hemisphere, than for faces presented in the right visual field (Levy et al., 1972; Levy-Agresti and Sperry, 1968). The LVF superiority has been also repeatedly reported in neurologically intact individuals in numerous laterality studies that briefly presented faces to the right or left of a fixation cross (Fig. 1E). Similar to split-brain patients, neurologically intact individuals showed more accurate and faster recognition for faces presented in the left than the right visual field (e.g., Hellige and Jonsson, 1985; Levine et al., 1988; Levine and Koch-Weser, 1982; Sergent, 1985).

An important finding which demonstrates that the LVF superiority is specific for upright faces, was reported in studies that presented upright and inverted faces in the left and right visual field (Leehey et al., 1978). These studies revealed that the LVF superiority is absent for inverted faces, that is to say that inverted faces are processed equally well in both visual fields. These findings link the face inversion effect to face processing in the LVF suggesting that the face inversion effect originates at the right hemisphere.

ERP correlates of the LVF superiority were examined by Yovel et al. (2003). The study presented subjects with left and right hemifaces (a half face on one side of fixation and a low contrast half face attached to it on the other side) that when presented briefly followed by a mask generates a percept of a complete face. Consistent with the LVF superiority effect, behavioral data show better recognition for left hemifaces than right hemifaces. The N170 latency, but not amplitude, varied as a function of the face stimulus in a manner consistent with behavioral measures showing faster response times to left hemifaces than right hemifaces. A similar pattern was found for the ERP amplitude in 220–280 ms and 400–600 ms after stimulus onset with higher amplitude to left hemifaces than right hemifaces. Interestingly, the difference in amplitude to left and right hemifaces at these later latencies was correlated with hemispheric asymmetry of the N170 amplitude. In other words, the greater the right hemisphere superiority to complete faces, as reflected by larger right than left N170 amplitude, the higher is the amplitude to left than right hemifaces at later latencies (220–280 ms and 400–600 ms).

In summary, the N170 is a robust face-selective neurophysiological marker that is strongly associated with the most well-established face-selective behavioral effects including the face inversion effect, holistic processing and the right hemisphere superiority for faces. This suggests that a holistic face-selective representation is generated already at 170 ms after stimulus onset, primarily over the right hemisphere. In the next section I will examine the association of these behavioral measures with face-selective neural responses revealed with fMRI and later on their association with the N170 response.

2.2. *Functional MRI: face-selective areas in the occipital-temporal cortex*

Since the first reports by Kanwisher et al. (1997) and McCarthy et al. (1997) of a face-selective area in the ventral part of the mid-fusiform gyrus, hundreds of fMRI studies have investigated brain regions showing a face-selective response. These studies typically report three face-selective areas in the occipito-temporal cortex including the Occipital Face Area (OFA) in the inferior lateral occipital cortex, the Fusiform Face Area (FFA) in the mid-fusiform gyrus and the face-selective area in the posterior superior temporal sulcus (pSTS-FA) (for review see Kanwisher and Yovel (2006)) (Fig. 1B). Importantly, fMRI-guided single unit recording studies in monkeys suggest that nearly all visually-responsive

neurons in monkey face-selective areas revealed with fMRI show a strong face-selective response (Freiwald et al., 2009; Tsao et al., 2006). Similar to the N170, the face-selective areas defined with fMRI are also associated with the face-selective behavioral effects reported above – the face inversion effect, holistic processing and the LVF superiority effect, as detailed below:

2.2.1. *Face inversion effect*

The effect of face inversion on the response of face-selective areas was weak and inconsistent in the first experiments that investigated it. Several studies found no difference between the response of the FFA to upright and inverted faces or found a small effect (Aguirre et al., 1999; Epstein et al., 2006; Kanwisher et al., 1998). In later studies, the difference between the FFA's response to upright and inverted faces was larger and more consistent (Brants et al., 2011; Gilaie-Dotan et al., 2010; Mazard et al., 2006; Yovel and Kanwisher, 2004, 2005). Furthermore, in studies that have used the more sensitive measure of fMR-adaptation (Grill-Spector and Malach, 2001), a clear difference between the representation of identity of upright and inverted faces has emerged. Specifically, in an fMR-adaptation study the fMRI signal that is measured to pairs/blocks of different identity faces is compared to the signal to pairs/blocks of identical faces. A higher response to different than same faces reflects discrimination of identity information. Studies that employed fMR-adaptation revealed higher response in the FFA to different than same upright faces but no difference between different and same inverted faces (Gilaie-Dotan et al., 2010; Mazard et al., 2006; Yovel and Kanwisher, 2005). This pattern of response is consistent with the better discrimination of upright than inverted faces – the behavioral face inversion effect. Furthermore, correlational analyses of the behavioral and fMRI inversion effects across individuals revealed a strong correlation ($r=0.5$) between the two measures in the FFA (Yovel and Kanwisher, 2005). Interestingly, the pSTS-FA showed higher response to upright than inverted faces but did not show correlation with the face inversion effect that was measured on a face identity task, suggesting that its neural response to upright and inverted faces does not underlie the behavioral effect.

With respect to the OFA, consistent with the similar fMRI response that it showed to upright and inverted faces, a recent TMS study showed similar disruption to processing of upright and inverted faces following stimulation to the OFA. In contrast, stimulation to the nearby non-face object area reduced performance only for inverted but not for upright faces (Pitcher et al., 2011b). Taken together these findings suggest no difference in the representations of upright and inverted faces in the OFA. Based on the finding that upright but not inverted faces are processed holistically (Farah et al., 1998), these findings may further suggest that the holistic representation of upright faces is not generated at early stages of face processing in the lateral occipital lobe (Pitcher et al., 2011c) but only in mid-level stages in the mid-temporal cortex. Direct evidence for this suggestion is reported in studies that employed tasks that directly assessed holistic face processing, as will be discussed next.

2.2.2. *Holistic face processing*

The processing of whole faces and face parts was first investigated in a PET study by Rossion et al. (2000). In this study subjects were asked to either attend to a single face part or the whole face on different blocks (Rossion et al., 2000). Attention to the whole face led to a stronger response in the right FFA relative to the part task whereas the left FFA showed the opposite pattern. These findings are consistent with lateralized behavioral studies, which show better performance in the RVF on a part based task and better performance in the LVF on the whole face task (Hillger and Koenig, 1991).

Later on, the neural correlates of holistic processing were examined in a study that employed an fMRI measure of the composite face task. Schiltz and Rossion (2006) used an fMR-adaptation design in which they compared composite faces with a similar upper half but different lower half with faces that were similar or different on both halves. They found release from adaptation to faces that were similar in the upper but different in the lower half indicating that they were perceived as different stimuli. This effect was absent for misaligned faces as well as inverted faces consistent with the lack of behavioral composite effect in misaligned and inverted faces. Furthermore, the composite effect was larger in the right FFA than in the left FFA, in line with behavioral findings mentioned above that showed larger composite effect for faces presented in the LVF than the RVF (Ramon & Rossion, 2011).

A similar fMR-adaptation paradigm for aligned and misaligned faces was also used to assess whether external (e.g., hair) and internal facial features generate a holistic representation (Axelrod and Yovel, 2010). Behavioral studies show that the representation of the internal features can be modified by changes in the external features (Nachson, 1995; Toseeb et al., 2012). To assess whether the FFA shows evidence for such holistic representation, Axelrod and Yovel presented faces that differ in external features but were similar in internal features and compared the response to faces that were similar in external and internal features. Results showed higher response for different than same external features (see also, Andrews et al., 2010). Importantly, when the external and internal features were misaligned the difference between the two conditions was significantly smaller. These findings suggest that the FFA is sensitive to the identity of the external features but also to their effect on the representation of the internal features, which extends findings that examined holistic processing of internal features alone and demonstrate that similar holistic mechanisms generate an integrated representation of the external and internal facial features.

2.2.3. *LVF superiority for faces*

Yovel et al. (2008) examined the relationship between the LVF superiority and hemispheric asymmetry of face-selective brain areas. They found that this LVF superiority varied across individuals and was associated with asymmetry of the volume of the FFA across the two hemispheres. Thus, a larger bias to recognize the left than the right face in a task performed outside the scanner was associated with a larger volume of the FFA over the right than the left hemisphere, which was measured by a functional localizer. Interestingly, the behavioral study and the fMRI study were conducted in different sessions several months apart, which suggests that this correlation reflects a stable characteristic of hemispheric asymmetry to faces rather than a task induced effect. Although the OFA also shows strong lateralization, it was not associated with the LVF superiority suggesting that it may not contribute to the behavioral LVF superiority.

In another study, Verosky and Turk-Browne (2012) examined fMR-adaptation for pairs of same and different identity faces presented in the LVF and RVF. They found fMR-adaptation in the right FFA when the two faces were presented in the LVF but no fMR-adaptation in the left FFA when the two faces were presented in the RVF. This is consistent with the right hemisphere advantage in face identification. Interestingly, when the first face was presented in the LVF and the second in the RVF, there was fMR-adaptation in the left FFA. No fMR-adaptation was found in the right FFA if the first face was presented in the RVF and the second in the LVF. These findings suggest that when the right hemisphere receives face information first – information is reliably transferred to the left hemisphere but not the other way around.

In summary, both electrophysiological and fMRI measures of face-selective mechanisms are associated with the face inversion

effect, holistic face processing and the LVF superiority effect, which are the major face-selective behavioral effects. These findings suggest that these neural measures may be associated with one another. The next section will review EEG and fMRI studies, which report such an association.

2.3. Functional MRI and EEG measures of face processing are strongly correlated

Functional MRI and EEG provide complementary information about neural activity, but they have rarely been combined in the study of face processing. Here I will review evidence for the relationship between fMRI and EEG face-selective markers by focusing on the few studies that examined the relationship between the two measures collected with the same paradigm from the same individuals either in separate sessions or simultaneously.

2.3.1. Face-selectivity

As mentioned above, faces elicit a highly selective fMRI and electrophysiological responses (Fig. 1A and B). Whereas electrophysiological measures provide information about face processing with very high temporal but low spatial resolution, functional MRI provides data with high spatial resolution but low temporal resolution. Surprisingly, only few studies have examined the relationship between fMRI and ERP measures of face processing. Horowitz et al. (2004) presented face stimuli with different levels of noise and measured the effect of added noise on the amplitude of the N170 and then in a separate session on the response of the FFA. Results show decrease in amplitude of both neurophysiological measures as a function of the amount of noise. A high correlation between the N170 amplitude and the FFA response across individuals and noise levels was found for faces but not for car

stimuli that underwent the same type of stimulus manipulation. In another study in which ERP and fMRI measures to faces were recorded in the same individuals across two sessions, Iidaka and colleagues reported correlations across individuals between the N170 response to faces and houses and the hemodynamic response in the fusiform gyrus to the same stimuli (Iidaka et al., 2006).

Sadeh et al. (2010) reported for the first time a simultaneous EEG-fMRI study of the face processing system. Subjects were presented with face and chair stimuli. An ERP face-selectivity index was calculated for each individual between 100 and 200 ms after stimulus onset and an fMRI face-selectivity index was calculated for the three occipito-temporal face-selective areas—the OFA, FFA and pSTS-FA. A strong correlation was found between ERP face-selectivity around 170 ms with the mid-temporal areas, the FFA and pSTS-FA, but not with the OFA.

In contrast, OFA face-selectivity was correlated with ERP face-selectivity at 100–110 ms after stimulus onset. The FFA and pSTS-FA face-selectivity indices showed low correlations with face-selectivity in this earlier latency (Fig. 2A shows the FFA and OFA).

These findings are consistent with a TMS study, which showed that stimulation of the OFA at 60–100 ms, but not at the 170 ms latency, after stimulus onset interfered with performance on a face identity matching task (Pitcher et al., 2007). A more recent study, which used double-pulse TMS of 10 ms gap, better localized the stimulation effect on the OFA to 100–110 ms after stimulus onset (Pitcher et al., 2012) (see Fig. 2B). Thus, correlational analyses of simultaneously collected ERP-fMRI markers of face-selective mechanisms revealed that these complementary neural markers are highly correlated. They further demonstrated the advantage of combining these two measures in that they pointed to the latency in which fMRI defined face-selective areas process face

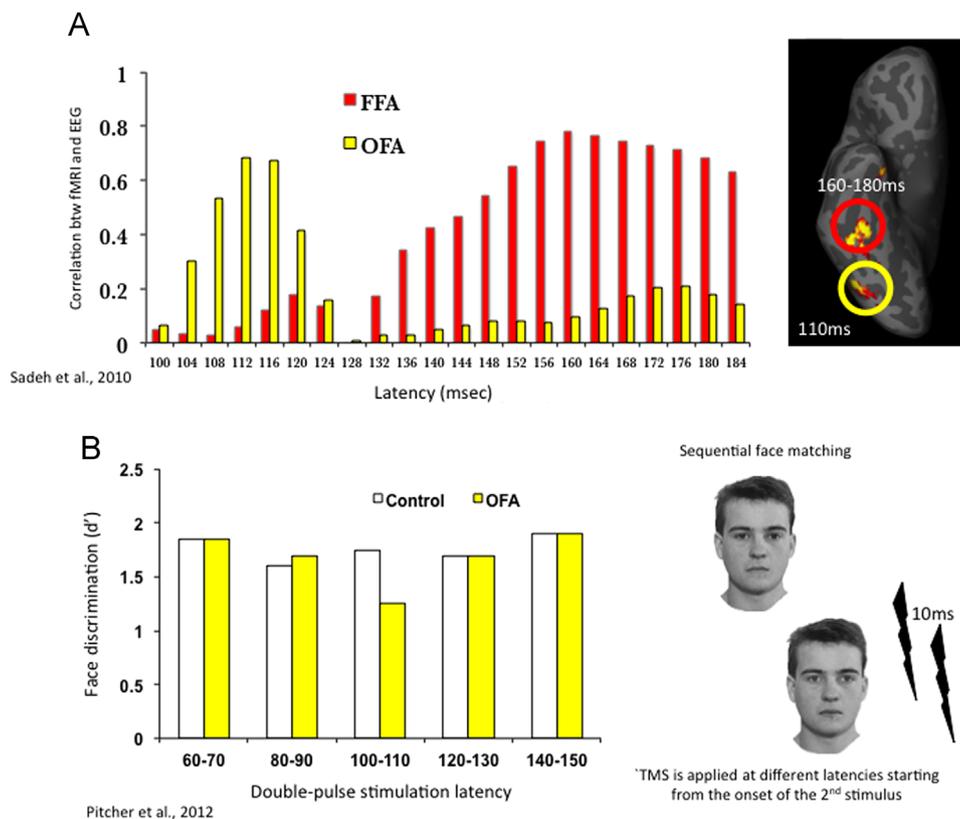


Fig. 2. A. In a simultaneous EEG-fMRI study the correlation between EEG and fMRI face-selective measures revealed that face-selectivity in the FFA was correlated with ERP face-selectivity at about 150–180 ms after stimulus onset at the time window of the N170. Face-selectivity in the OFA was correlated with ERP face-selectivity at 110 ms after stimulus onset (Sadeh et al., 2010). B. TMS to the OFA but not to a nearby non-face selective area (control) impaired performance on a face matching task at 100–110 ms after stimulus onset (Pitcher et al., 2012), consistent with the EEG-fMRI correlation analysis shown in A.

information at high temporal resolution of tens of milliseconds.

Whereas studies that examine the electrophysiological and fMRI responses to faces can only provide correlational information, TMS enable us to infer about a causal link between these measures. In a simultaneous TMS-EEG study [Sadeh et al. \(2011\)](#) stimulated the OFA and the nearby body-selective area, the extrastriate body area (EBA), while subjects viewed images of faces and headless bodies, at 60–100 ms after stimulus onset. All subjects first participated in an fMRI experiment in which their face-selective and body-selective areas were identified with a functional localizer, which included blocks of faces headless bodies and objects ([Downing et al., 2001](#)). Based on these fMRI data, face and body areas were identified in each subject and the body-selective and face-selective lateral occipital stimulation sites were determined with a neuronavigation system. EEG was collected during stimulation and the N170 response was examined as a function of stimulation site (face-area, body area) and stimulus category (face, body). Stimulation of the OFA enhanced the N170 to faces but not to body stimuli, whereas stimulation of the EBA enhanced the N170 to bodies but not to faces (see [Fig. 3A](#)). These findings suggest a causal link between the activation of the occipital face and body-selective areas at 60–100 ms after stimulus onset and the neural response to their preferred stimuli at 170 ms after stimulus onset.

A similar double dissociation between the response of the face and body-selective areas to faces and bodies, has been reported in a TMS study that employed a behavioral face and body matching task and revealed lower performance to faces but not bodies following OFA stimulation, and lower performance to bodies but not faces following EBA stimulation ([Pitcher et al., 2009](#)) (see [Fig. 3B](#)). Whereas the increase in N170 amplitude and lower performance on a behavioral task may seem contradicting, it is noteworthy that increase in amplitude does not necessarily reflect better

performance. In fact, inverted faces show higher amplitude than upright faces but worse recognition rates (see discussion for a possible mechanism for this effect in the next section). The increase in amplitude due to TMS stimulation may reflect increased synchronization, which may interfere the neural response to the stimulus but may still increase the N170 amplitude.

2.3.2. Face inversion effect

As mentioned above, ERP and fMRI measures show a clear and reliable face inversion effect. The mid-temporal face-selective areas, the FFA and pSTS-FA show a higher response to upright than inverted faces. In contrast, object general areas (i.e. the lateral occipital complex – LOC ([Malach et al., 1995](#))) show a higher response to inverted than upright faces ([Yovel and Kanwisher, 2005](#)). The N170 shows increased and slightly delayed amplitude to inverted than upright faces. Two mechanisms have been suggested to account for the increased N170 amplitude to inverted than upright faces. According to the *qualitative hypothesis* increased amplitude for inverted faces reflects the recruitment of additional non-face mechanisms that are not used for the processing of upright faces. Thus, the increased response to inverted faces in the object area may contribute to the increased N170 amplitude to inverted faces. In contrast, the *quantitative hypothesis* suggests the same processes generate the N170 response to upright and inverted faces but that the increased amplitude for inverted faces reflects the greater demands that inverted face processing places on face mechanisms ([Sadeh and Yovel, 2010](#)). To decide between the two hypotheses, [Sadeh and Yovel \(2010\)](#) employed an ERP competition paradigm ([Jacques and Rossion, 2004](#)), which revealed that an inverted face generated greater competition with an inverted face than with an upright face. These findings were consistent with [Eimer et al. \(2010\)](#), which employed an adaptation rather than a competition design and suggests that inverted faces

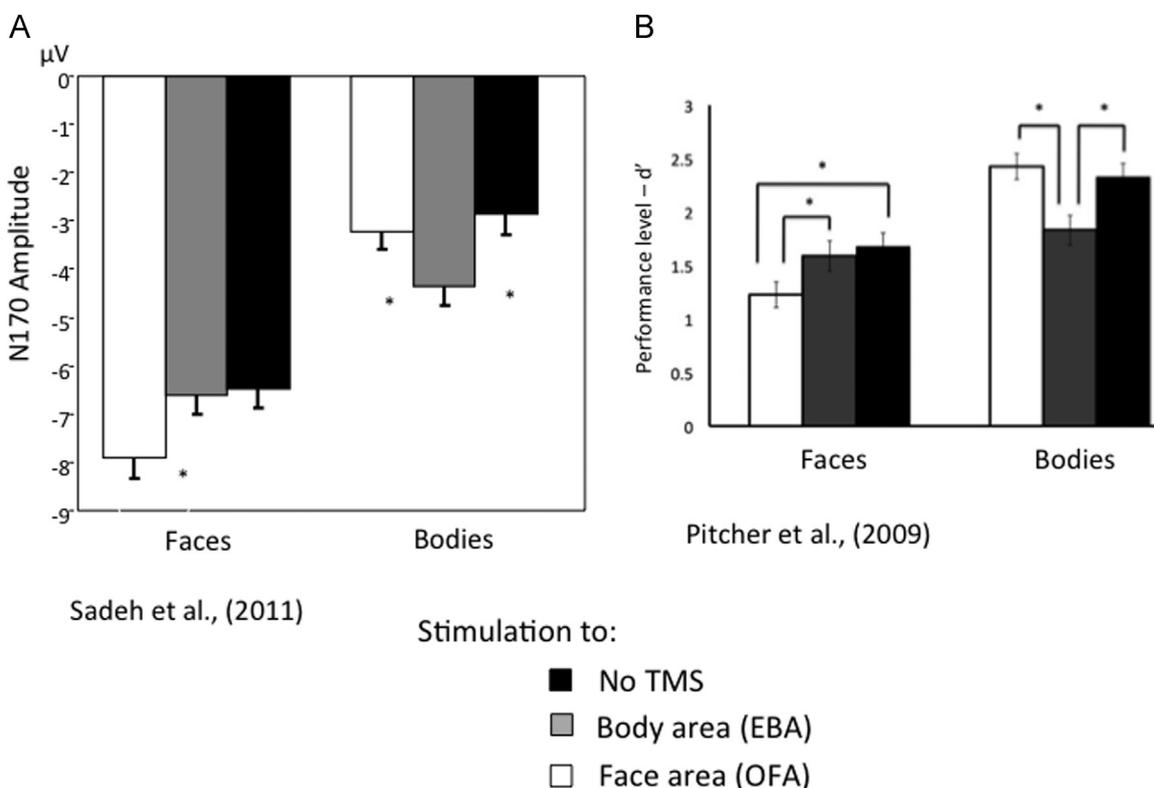


Fig. 3. (A) TMS at 60–100 ms to the occipital face area increased the N170 response to faces but not to bodies, whereas TMS to the extrastriate body area (EBA) increased the N170 to bodies but not faces ([Sadeh et al., 2011](#)). (B) TMS at 60–100 ms to the same areas during a face matching task impaired performance level to faces but not bodies following stimulation of the OFA and to bodies but not face stimulation of the EBA ([Pitcher et al., 2009](#)).

engage mechanisms that do not fully overlap with the mechanisms used for upright faces and are therefore consistent with the *qualitative hypothesis*. However, these findings do not directly show that these additional mechanisms are general object processing mechanisms.

To directly test this question, the N170 and fMRI face inversion effects were measured in a simultaneous EEG-fMRI study. The N170 face inversion effect was calculated for each subject as the normalized difference between the response to upright and inverted faces (Sadeh et al., 2011). In addition, face-selective and object general areas were localized and the difference in their response to upright and inverted faces was measured. A correlational analysis between the fMRI- face inversion effect (i.e. the difference between the response to inverted and upright faces) in the object and face-selective areas and the N170 face inversion effect revealed a very strong correlation with the object areas ($r=0.8$) but not with the FFA. These findings further support the *qualitative hypothesis*, which suggests that inverted faces engage object mechanisms that are not used for the processing of upright faces (see also, Moscovitch et al., 1997; Pitcher et al., 2011b).

The simultaneous fMRI-EEG studies discussed above nicely demonstrate how combining the two methods can provide insight into the temporal characteristics of brain areas and the possible neural generators of ERP signals. In particular, the correlations between the face-selective measures indicate an earlier latency for the occipital face area than for the mid-temporal face areas. The face inversion effect study described above attributed the increased amplitude of the N170 to inverted faces, to activity in object areas rather than the nearby face-area, a finding that cannot be obtained from source localization analysis of EEG data alone (Eimer et al., 2010). These findings therefore do not only further establish the link between the ERP and fMRI face markers but also enhance our understanding of the spatial-temporal architecture of the face processing system.

In summary, whereas direct associations between EEG and fMRI face-selective markers were examined in only a few studies, their findings suggest a close association between them. These associations between the two neural measures are in line with the many studies discussed above which have demonstrated that EEG and fMRI face-selective measures are similarly associated with the face-selective behavioral measures including the LVF superiority, the face inversion effect and holistic effects. This suggests that these neural markers, which have been mostly studied separately, in fact reflect the same mechanisms.

2.3.3. Evidence from intracranial recording

Intracranial recording have the advantage over scalp electrophysiology in that it provides better spatial information about the source of the signal and therefore can complement the data reported from simultaneous fMRI-EEG recording. Of the three types of face-selective measures discussed above, the one that was studied with intracranial recording was the face inversion effect. Intracranial recordings reveal a face-specific response 200 ms after stimulus onset (N200) as was first reported by Allison et al. (1999), McCarthy et al. (1999) and Puce et al. (1999). McCarthy et al. (1999) examined the response to upright and inverted faces at electrodes located in the fusiform gyrus and found no difference between the amplitude to upright and inverted faces, but latency was longer to inverted faces. More recently, Rosburg et al. (2010) have recorded from additional lateral locations including the lateral occipital cortex and the STS. Results show increased amplitude for inverted than upright faces in lateral occipital electrodes but not in electrodes located in the STS and ventral temporal electrodes. The lateral electrodes that showed increased response to inverted faces were located near face-selective and house-selective electrodes. This finding is consistent with fMRI findings reported above that

show stronger response to inverted than upright faces in object areas rather than face areas. The previously mentioned TMS and EEG-fMRI studies of the face inversion effect in fact attribute the larger N170 response to inverted than upright faces to activations in these object areas rather than to face areas. Inconsistent with fMRI findings, intracranial recordings did not find the lower response to inverted than upright faces that it typically reported in the FFA and STS face areas and future studies should address these discrepancies, which may be related to the different tasks used across the different studies. It is also noteworthy that Rosburg and colleagues included scrambled faces in their study and found no differences between the response to these faces than upright intact faces, unlike results reported for the N170 in which the response to intact faces was higher than scrambled faces (Bentin et al. 1996). Thus, the relationship between the intracranial recorded N200 and the N170 is still not conclusive.

In summary, intracranial recording with upright and inverted faces overall reveal stronger response to inverted than upright faces in face and non-face electrodes in the lateral occipital cortex. These findings are consistent with fMRI data that show stronger response to inverted than upright faces in object selective areas. However, there are still discrepancies between the inversion effect reported in the fusiform and STS face-selective areas and lack of effect with intracranial recording in these locations.

2.4. Summary: Neural and cognitive face-selective measures are strongly associated

The review of the literature above demonstrates that cognitive and neural mechanisms of face-selective processing are highly linked. This allows us to portray where, when and how faces are represented during the first 200 ms of face processing. The face-selective N170 was strongly correlated with face-selectivity in the FFA (Sadeh et al., 2010). Furthermore, the face inversion effect was associated with both the N170 and the FFA responses to upright and inverted faces suggesting that the different representations that is generated for upright and inverted faces is manifested 170 ms after stimulus onsets at mid-level stages of face processing in the fusiform gyrus. Furthermore, fMRI studies show similar response to upright and inverted faces in the OFA (Yovel and Kanwisher, 2005) and a TMS study showed that stimulation of the OFA yielded similar interference in the processing of upright and inverted faces (Pitcher et al., 2011a). Thus, at this earlier stage of face processing upright and inverted faces generate similar representations.

In line with these findings, several studies have shown that the representation of faces in the FFA is holistic. This has been demonstrated with the composite face effect discussed above but also with other measures of holistic processing (Harris and Aguirre, 2008, 2010). Similar findings were reported for the N170, which was sensitive to the composite face effect (Jacques and Rossion, 2009a) and has been shown to represent both face configuration as well as face parts (Sagiv and Bentin, 2001). In contrast to the FFA, the OFA has been shown to be sensitive to face parts (Pitcher et al., 2011c). Thus, a holistic face representation is generated at about 170 ms after stimulus onset in the fusiform gyrus.

At this latency the right hemisphere asymmetry to faces emerges. The N170 response to faces but not earlier components show larger amplitude over the right than the left hemisphere (Bentin et al., 1996) and the FFA but not the OFA is associated with the LVF superiority for faces (Yovel et al., 2008). Taken together with findings that show that the representation of faces is more holistic in the right than the left hemisphere (Ramon and Rossion, 2011), we can conclude that the right hemisphere generates a holistic face representation at mid-level stages of face processing about 170 ms after stimulus onset.

The first report of the face-selective N170 by Shlomo Bentin is a significant milestone in the understanding of the neural mechanisms of face processing. As this review portrays, the most fundamental phenomena in face processing are generated during this time window. The N170 is therefore not only *sensitive to faces* but reflects most of what we know about the unique perceptual representation that our brain generates for faces.

2.5. Future directions

The current review focused on neural responses that takes place during the early and mid-stages of faces processing as reflected by the electrophysiological response and TMS effects during the first 200 ms of face processing and fMRI activations in the occipital temporal cortex. However, in recent years face processing research has revealed additional face-selective areas (for review see, Duchaine and Yovel, *in press*). First, it has been suggested that two face-selective areas rather than one reside in the fusiform gyrus (Weiner and Grill-Spector, 2010, 2012). However, we still do not know whether these two areas play different or similar functional roles in face processing. Second, a face-selective area in the anterior temporal cortex is reported in several studies (e.g., Tsao et al., 2008) but its location in an area that suffers from significant susceptibility artifacts (Axelrod and Yovel, 2013) prevents progress on the understanding its functional role in face processing. Third, studies that have started employing dynamic face and object stimuli reveal additional areas, which seem to respond more to dynamic than static faces including the anterior STS and areas in the lateral prefrontal cortex, some of them hardly appear when the standard static face localizer is used (Pitcher et al., 2011a; Fox et al., 2009). These more anterior areas possibly play a role in higher-level stages of face processing and research in the next few years will hopefully reveal what are their functional roles. Thus, future research in face processing should expand to the processing of dynamic faces as well as go beyond the study of perceptual aspects of face processing and integrate it with the contribution of higher-level processes, which include the roles of conceptual and social information in face recognition.

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