From coarse to fine: Interactive feature processing precedes local feature analysis in human face perception

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ABSTRACT

Face perception depends on a dynamic interplay of a "holistic" Interactive Feature Processing (IFP) and a Local Feature Processing (LFP) style. However, it is unclear whether features are processed locally before they are integrated into a holistic percept (Fine-to-Coarse strategy), or whether local feature processing occurs only after a holistic percept is established (Coarse-to-Fine strategy). The present Event-Related Potentials study investigates whether IFP precedes LFP (Coarse-to-Fine) or vice versa (Fine-to-Coarse).

Participants matched target features within face pairs (here the eye region), in which distracter features (nose and mouth) called for the same or a different response (congruent and incongruent, respectively). Psychophysical results replicated previous findings. That is, dissimilar target features are locally processed (LFP), which minimizes interference from surrounding incongruent distracters. Conversely, an IFP mode is elicited when similar target features are embedded in dissimilar contexts. In IFP mode, incongruent distracters interfere with the processing of similar target features, thereby deteriorating task performance. Face inversion, which preserves input properties but disrupts high-level face perception, annihilated these incongruency effects.

Psychophysical observations were reflected at the neural level. The IFP and LFP modes of face perception elicited distinct time-courses in occipito-temporal cortex. IFP was affected by inversion as soon as 176 ms post-stimulus onset (coinciding with the N170 peak). In contrast, the first robust indications of LFP occurred 120 ms later, at 296 ms. Thus, the contribution of IFP to high-level face perception appears to temporally precede LFP. Moreover, results showed that the IFP and LFP modes did not only operate in distinct time intervals, but also in different brain areas: activity associated with the IFP mode was right-lateralized, whereas the LPF mode engaged the left hemisphere.

In sum, interactive "holistic" encoding of facial features temporally precedes their local analysis. This agrees with models suggesting a Coarse-to-Fine strategy for face perception, in line with generic descriptions of visual perception in which global scene analysis precedes the examination of local details.

1. Background

Holistic theory of face perception posits that faces are automatically perceived as integrated wholes ('Gestalt') rather than as a collection of independent features (e.g., Maurer, Le Grand, & Mondloch, 2002; Sergent, 1986; Tanaka & Farah, 1993). This is illustrated by the difficulty for human observers to process a single feature in isolation of the facial context in which it is embedded (Sergent, 1984). Support for such *Interactive Feature Processing* (*IFP*) comes from whole-part (e.g., Tanaka & Farah, 1993) and composite illusion (e.g., Hole, 1994; Young, Hellawell, & Hay, 1987) paradigms (see Rossion, 2008 for review). The latter paradigm entails a visual illusion in which two identical top halves of faces are perceived as being different, when their bottom halves belong to different faces. This illusion perpetuates when subjects realize the top halves are identical and bottom halves should be ignored, providing compelling evidence that face features are automatically integrated into an undecomposed whole representation. Though robust when viewing upright faces, the engagement of IFP vanishes when faces are viewed upside-down (Farah, Wilson, Drain, & Tanaka, 1998; Goffaux, 2009; Rhodes, Brake, & Atkinson, 1993). Since consistent evidence shows that inversion affects the processing of faces more than other visual categories, the disruption of IFP by inversion

was taken to support the notion that the specialization of (upright) face processing resides in a particularly strong engagement of IFP. The supremacy of IFP for upright face processing has however been challenged by findings that the latter also depends on *Local Feature Processing* (*LFP*), i.e., the independent, local processing of features (e.g., Burton, Schweinberger, Jenkins, & Kaufmann, 2015; Cabeza & Kato, 2000; Leder & Carbon, 2005; Matthews, 1978; Sergent, 1984). The fact that inversion disrupts discrimination performance even when features are presented in isolation (Goffaux, 2012; McKone & Yovel, 2009; Rakover, 2012) further indicates that LFP contributes to the specialization of upright face processing (Burton et al., 2015; Nemrodov, Anderson, Preston, & Itier, 2014; Sadr, Jarudi, & Sinha, 2003).

Recently we used a congruency paradigm (Farah et al., 1998; Goffaux, 2009; Goffaux, 2012; Goffaux, Schiltz, Mur, & Goebel, 2013; McKone & Yovel, 2009) to explore the flexible interplay between interactive and local visual mechanisms when processing upright faces (Goffaux, 2012; Goffaux et al., 2013). In such a paradigm, participants are instructed to match a set of target features (e.g., eyes and brows) in pairs of faces while ignoring the surrounding distractor features (e.g., nose and mouth). Target and distractor features vary either congruently (either both the same or both different; Fig. 1A) or incongruently (targets are identical while distractors differ or vice-versa; Fig. 1A), and the strength of IFP is assessed by comparing target discrimination performance in congruent versus incongruent conditions (Farah et al., 1998; Goffaux, 2009, 2012). In Goffaux (2012), we parametrically varied the discriminability of the target features and showed that the strength of IFP as indexed by congruency effect size decayed monotonically as a function of target dissimilarity within a pair. That is, the more similar the target features, the stronger the IFP. Although interactive processing is often highlighted as an instant and automatic component of face perception, our paradigm revealed that the relative contribution of IFP versus LFP depends on the discriminability of local features. This finding suggests that IFP contribution to upright face processing may be to enlarge the perceptual integration window whenever the local input provided by facial features is ambiguous. Our recent fMRI study (Goffaux et al., 2013) indicated the high-level face-selective Fusiform Face Area (FFA) as the main cortical site for the flexible engagement of IFP and LFP depending on local discriminability (see also Arcurio, Gold, & James, 2012; Harris & Aguirre, 2010). The local processing of feature fine details (LFP) on the other hand, recruited other brain regions (Occipital Face Area, the Lateral Occipital Complex, and early visual cortex).

While the question of *"where"* IFP and LFP are implemented in the human visual system is documented, the question of *"when"* IFP and LFP operate has been far less explored; despite its potential to clarify how the human visual system codes the complex information carried by faces. Are features locally processed before they are integrated into a holistic percept? In other words, does LFP precede IFP? Or vice versa? That is, does IFP occur before features are examined at the local level? Two opposing frameworks have been put forward to explain the time course of face processing. The view that local cues must be fully processed before IFP can occur is predominant in the field of vision research (e.g., Haxby, Hoffman, & Gobini, 2000; Jiang et al., 2006; Ullman, 2007). This framework defends the notion of a *Fine-to-Coarse (FtC)* processing mode, in which local cues are decoded first and only subsequently glued into a holistic representation. However, several findings suggest that face perception may rather adhere to a *Coarse-to-Fine (CtF)* strategy, in which facial features are initially processed interactively based on the rapid extraction of the coarse face structure and individual features are only extracted later, based on the slower extraction of fine feature details (e.g., Farah et al., 1998; Goffaux et al., 2011; Goffaux & Rossion, 2006; Rossion, 2008; Sergent, 1986). A CtF modus operandi for face processing is suggested by two lines of evidence: 1) IFP is driven by the low spatial frequencies (SF) of the face image whereas LFP relies on the processing of the high SF (Goffaux & Rossion, 2006; Goffaux, Hault, Michel, Vuong, & Rossion, 2005; Goffaux, 2009). 2) Low SF are integrated earlier than high SF in the brain regions responding preferentially to faces (Goffaux, Gauthier, & Rossion, 2003; Goffaux, Jemel, Jacques, Rossion, & Schyns, 2003; Goffaux et al., 2011) Together, these findings imply that IFP precedes LFP. Nevertheless, the latter hypothesis has still to be empirically tested. The present Event-Related Potentials (ERP) study investigates whether IFP precedes LFP (Coarse-to-Fine) or vice versa (Fine-to-Coarse) by comparing temporal differences between neural markers of IFP and LFP. Note that the correlational measures employed here do not allow causal inferences. Therefore, "temporal precedence" should be interpreted in the strict sense (i.e., without implying any causal dependencies between IFP and LFP).

Past studies took advantage of the high temporal resolution of the ERP technique to investigate the time course of IFP. Face inversion disrupts IFP more robustly than LFP, while largely preserving stimulus properties (Rossion, 2008). Therefore, past studies attempted to track
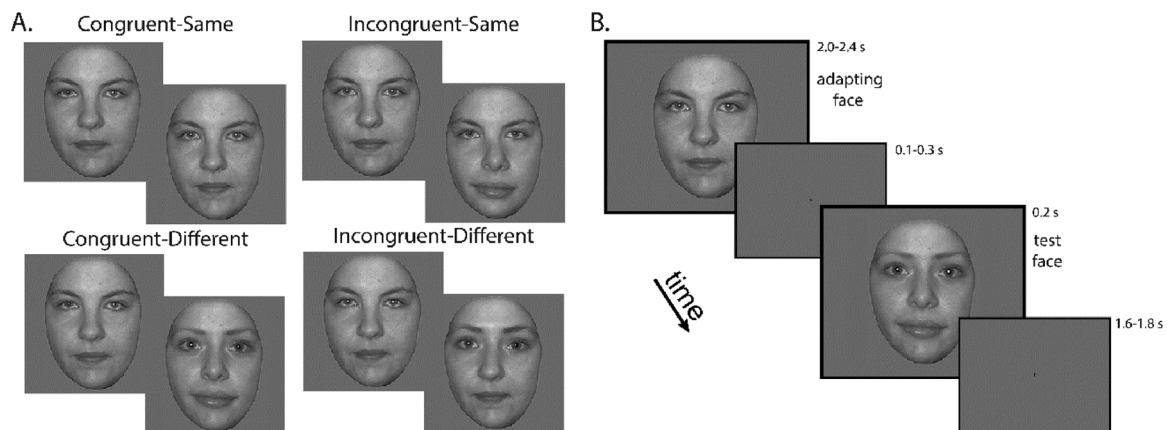
Fig. 1. Congruency paradigm. A. Experimental conditions. In face pairs, subjects had to discriminate the target region (same/different), i.e., the eyes and eyebrows, while ignoring the context of other features (i.e., distracters: nose and mouth). In congruent conditions, both the target and distracter features lead to an identical decision, while they call for opposite responses in incongruent conditions. *Interactive Feature Processing (IFP)* is illustrated by the observation that the dissimilar noses and mouths of the faces in *Incongruent-Same* pairs increases the difficulty to detect that the eyes are the same compared to when all features are similar as in Congruent Same condition. In contrast, the *Incongruent-Different* condition engages a *Local Feature Processing (LFP)* strategy, which prevents incongruent influences of the surrounding features. Note that the test face is shown for 200 ms only (and subsequently to the adapting face and blank screen, see B), which amplifies the illusory incongruency percept in Incongruent-Same pairs much stronger than in the present visualization. B. Timeline of the stimulus sequence (congruent-different condition). After presentation of the adapting and test face, subjects indicated whether the eyes of the two faces were similar or different.

the spatiotemporal dynamics of IFP, by comparing ERPs to upright and inverted faces. Several of these studies reported inversion-related modulations of the occipito-temporal N170 and frontocentral Vertex Positive Potential (VPP) components around 170 ms after stimulus onset (Jacques, d'Arripe, & Rossion, 2007; Jemel, Coutya, Langer, & Roy, 2009; Rossion et al., 2000; Goffaux, Gauthier et al., 2003; Goffaux, Jemel et al., 2003; Itier & Taylor, 2002). However, since inversion affects both IFP and LFP, its influence on neural responses to faces cannot be taken to purely reflect a disruption of IFP. Several recent studies manipulated IFP more systematically, for example, by comparing ERP waveforms induced when face top and bottom halves are aligned versus misaligned in the composite paradigm (inducing and disrupting IFP, respectively; Jacques & Rossion, 2009; Letourneau & Mitchell, 2008). Caharel et al. (2013) used Arcimboldo faces (i.e., paintings in which various objects are arranged to give a global impression of a face) while others compared neural responses to upright and inverted Mooney faces (i.e., two-tone transformation of blurred face images that wipes out local feature cues and therefore encourages IFP strategies; Eimer, Gosling, Nicholas, & Kiss, 2011; George, Jemel, Fiori, Chaby, & Renault, 2005; Latinus & Taylor, 2005; see also Carbon & Leder, 2005 for psychophysical investigations using Thatcherized faces). These studies confirmed the early emergence of IFP in the N170 time window. However, considering the drastic alterations these past studies applied to the face stimulus in order to activate or disrupt IFP, the findings are difficult to interpret solely on the basis of IFP (dis)engagement. For example, by destroying the upright face structure, the misaligned condition used in the composite paradigm not only extinguishes IFP but also profoundly disrupts the activation of the more general mechanisms tuned to the upright face structure. By cutting faces in halves (or parts such as in the whole-part paradigm) artificial sharp edges are introduced in the image. These sharp edges differently affect the processing of low versus high SF ranges, thereby also influencing IFP and LFP (Goffaux, 2009; Morrone, Burr, & Ross, 1983; see also Harmon & Julesz, 1973). Therefore, it is difficult to disentangle the contribution of genuine IFP and unwanted stimulus-driven processes in, for example, the observed increase in N170 amplitude for misaligned composite faces (e.g., Letourneau & Mitchell, 2008; Jacques & Rossion, 2009) and isolated face parts (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Itier, Alain, Sedore, & McIntosh, 2007). Furthermore, Mooney faces while preserving the low SF component of the whole face template, prevent access to individual (high SF) features. These stimuli therefore cannot be used to address the relative contribution of IFP and LFP to face perception. Here, we adapted the congruency paradigm to the ERP setting in order to circumvent these limitations. Importantly, this paradigm enables the selective assessment of IFP versus LFP mode, via the manipulation of feature similarity (Goffaux, 2012). Moreover, it also preserves the whole face configuration across all conditions, unlike the composite and whole-part paradigm

Similar to our fMRI study (Goffaux et al., 2013), we embedded the congruency paradigm in a neural adaptation framework (see also Jacques et al., 2007; Jacques & Rossion, 2009; Kovacs et al., 2006). Participants viewed pairs of face stimuli in which the target features, i.e., the eyes and brows, were either identical or different, and embedded either in congruent or incongruent contexts of distracter features (i.e., nose and mouth; Fig. 1A). In agreement with our past findings, the Incongruent-Different condition (i.e., different targets combined with identical distracters) was expected to evoke weak congruency effects due to LFP engagement and, consequently a more veridical representation of target features. In contrast, the Incongruent-Same condition (i.e., identical targets embedded in different distracters) was expected to activate the IFP mode indexed by strong congruency effects, causing faces to look different even though the eyes are strictly identical (thereby mimicking the composite illusion effect; Young et al., 1987).

All conditions were tested at upright and inverted orientations. Since inversion preserves image spectral properties, it offers an interesting control for low-level differences between the Incongruent-Same and Incongruent-Different condition, and allows isolating the high-level mechanisms at stake in each condition. We contrasted IFP and LFP time courses by comparing the spatiotemporal profile of their respective inversion effect. In the Incongruent-Same condition, the emergence of the face inversion effect was taken as a temporal marker for the emergence of IFP (e.g., Jacques et al., 2007). Inversion was also expected to non-negligibly disrupt LFP in the Incongruent-Different condition, in agreement with past findings (Goffaux, 2012; Itier et al., 2007; McKone & Yovel, 2009; Nemrodov et al., 2014; Rakover, 2012). We expected IFP to emerge in the N170 window, in line with the onset of holistic processing in the composite face illusion (Jacques & Rossion, 2009). The FtC framework predicts that faces are first processed at a local level, and therefore that the inversion effect on LFP arises before the inversion effect on IFP. In contrast, a CtF mode of face processing engages LFP only after IFP processing. Our results indicate that IFP occurs at an earlier stage than LFP therefore suggesting that faces are processed according to a CtF strategy.

2. Methods

2.1. Participants

Nine healthy participants with normal or corrected-to-normal visual acuity (4 males; 21–30 years old; 1 left-handed) gave their written informed consent to participate for financial compensation or course credits. All procedures were approved by the ethics committee of the Faculty of Psychology and Neuroscience of Maastricht University.

2.2. Stimuli and task design

Stimuli were similar to Goffaux (2009). For a full description see Goffaux (2009). In short, twenty grayscale front-view photographs (6.8° × 5.0° visual angle) of Caucasian faces (half males) with neutral expression served as stimuli. The inner features of each face (eye-–eyebrow further jointly referred to as 'eyes', nose, and mouth) were pasted onto a generic, gender-specific face shape (thereby equalizing face contours between the adapting and test face). Features were combined to create twenty gender-matched sets of four face types (Fig. 1A): face "A" (same congruent), face "B" (different congruent), face A with nose-mouth region of face B, and face A with eye–eyebrow region of face B (different incongruent). These four face types were presented equally often for each face set. Note that in congruent conditions, both the eye–eyebrow region as well as its surrounding features led to an identical decision, whereas they activated opposite responses in incongruent conditions.

2.3. Procedure

Each trial started with the presentation of the adapting face (2.0–2.4 s), followed by a short interval of about 200 ms (0.1–0.3 s; Fig. 1B). Subsequently, the test face was presented (0.2 s) and subjects had to indicate whether the eye-eyebrow region of the adapting and test face was similar or different by pressing the left or right button of a 2-button response pad, respectively (response mapping reversed across subjects). They were instructed to focus on the eye-eyebrow region and ignore other face features. After circa 1.7 s (1.6–1.8 s) in which only a fixation cross was shown at the center of the screen, the next trial started. Each participant received 60 randomized trials of each face stimulus condition (3 repetitions of each face stimulus set), leading to 480 trials in total. Thus, each face appeared equally often in each of the target similarity and congruency conditions in the conditions and in half of the trials, the second face had the same eye–eyebrow region as the adapting face. Moreover, all faces were equally often shown in upright and inverted orientation. Both the adapting and test face were presented upright or inverted within a trial, and all faces were

presented at the center of the screen. Conditions were randomized across trials. Participants took a short break every ten minutes. During the break, they received information about their average reaction time (RT) and accuracy. Prior to the experiment, subjects practiced the task (20 trials). During practice, response feedback was provided on each trial. A high tone (250 ms, 1000 Hz) indicated a correct response, a low tone (500 Hz) an error. At the end of the practice block, participants were informed about their mean accuracy and RT.

Subjects were comfortably seated in front of a 21-inch LCD monitor (60 Hz refresh rate) in a dimly lit room. They were instructed to maintain a fixed viewing distance from the monitor and experimenters monitored this throughout the measurements. Furthermore, they were instructed to maintain fixation at the fixation cross during the whole trial and to respond as accurately and fast as possible.

2.4. Behavioral data analysis

Behavioral reaction times and accuracy were subjected to separate repeated-measure ANOVAs with Orientation (upright, inverted), Congruency (congruent, incongruent), and Target Similarity (same, different) as factors. Only correct reaction times between two standard deviations above and below subject- and condition-specific means were included (outliers were excluded from further analyses). Statistical procedures (e.g., corrections for potential assumption violations, corrections for Type I & II errors, effect sizes) were otherwise similar to those for ERP peak analyses and are further explained in the last paragraph of the next section.

2.5. Electrophysiological recording and processing

The electroencephalogram (EEG) was recorded (sampling rate 500 Hz; band-pass filter of 0.01–200 Hz; Brain Products amplifier, Munich, Germany) from 32 Ag/AgCl scalp electrodes (extended International 10/20 system) with reference electrodes placed at the mastoids. Signals were collected using the left mastoid as reference and re-referenced off-line to the average activity of all electrodes. Horizontal and vertical electro-oculograms (EOG) were recorded with bipolar electrodes placed at the external canthii and above and below the left eye. Electrode impedance was kept below 10 kOhm for all electrodes.

EEG data of correct response trials (with RT between 0.1–2 s) were epoched (from -100 to 500 ms, relative to stimulus onset of the second face), filtered (0.01–30 Hz Zero Phase Shift 12 dB/oct Butterworth band-pass filter) and baseline-corrected (75 ms pre-stimulus interval) using Vision Analyser (Brain Products, Munich, Germany). Artefacts from horizontal eye movements and blinks were reduced with the algorithm of Gratton, Coles, and Donchin (1983). Trials with artifacts (samples exceeding ± 50 μV, steep gradients [50.00 μV per sampling point or 50 μV per epoch] or low activity [0.5 μV over 100 ms interval]) were excluded from subsequent analyses. Finally, all epochs of a condition were averaged per subject for further time course and peak analyses. Rarely (3 cells in total), a combination of too many artefacts and behavioural errors resulted in a too low number of individual epochs to compute the average. These missing values were replaced with condition-specific medians. The number of epochs did not differ statistically between conditions (p > 0.4; partial-η^2 = 0.11).

2.6. Electrophysiological data analysis

We focused ERP analyses on the main, early components of face perception, i.e., the well-studied N170, and the peak preceding (P1) and succeeding (P2) the N170. Peak latencies and mean peak amplitudes (50 ms window) were extracted at global peak-maximum from each condition-specific average at occipito-temporal (PO7, PO8) electrodes in the P1 (70–160 ms), N170 (130–200 ms), and P2 (190–270 ms) interval, in line with previous face processing EEG studies (e.g., Peters,

van den Boomen, & Kemner, 2017; Peters, Vlamings, & Kemner, 2013; Goffaux, Gauthier et al., 2003; Goffaux, Jemel et al., 2003). PO7 and PO8 were selected because they are the scalp locations where face ERPs are the most prominent (e.g., Bentin et al., 1996; Rossion, 2008). Peak amplitudes and latencies were submitted to separate repeated-measure ANOVAs with Orientation (upright, inverted), Congruency (congruent, incongruent), Target Similarity (same, different), and Hemisphere (left, right) as factors. Interactions were further tested with three-way ANOVAs and Bonferroni-corrected t-tests.

To gain more fine-grained insights in the fast temporal dynamics of IFP and LFP, we estimated differences between condition-specific ERPs at each time point in these windows (see also Jacques et al., 2007; Jacques & Rossion, 2009). The significance of the difference between conditions was assessed using permutation tests (n = 5000 permutations with randomly shuffled condition labels). Two-tailed Tmax (Blair & Karniski, 1993) was used to control for multiple comparisons, which is similar to Bonferroni correction, but more powerful when conditions might be correlated (Westfall & Young, 1993). Permutation tests were computed per electrode pool (and PO8 to compare findings with Jacques et al., 2007) and at each time point. Electrode pools averaged responses in electrodes clustered as a function of their anterior-posterior (Frontal F, Central C, Posterior P) and hemispheric (Left L, Midline M, Right R) location. This resulted in 9 electrode pools: FL (Fp1, F3, F7, FC5, FC1), FM (Fz), FR (Fp2, F4, F8, FC2, FC6), CL (C3, CP5, CP1, T7), CM (Cz), CR (C4, CP2, CP6, T8), PL (P7, P3, O1, PO7), PM (Oz, POz, Pz), PR (P4, P8, O2, PO8).

ANOVA results were Greenhouse-Geisser corrected. Main effects are not discussed when they interact with other factors. Instead, interactions and subsequently performed Bonferroni-corrected paired t-tests are described. Note that Bonferroni-adjusted (Bf-adj.) p-values larger than 1 are reported as p = 1.000. Bf-adj. p-values (corrected for one- or two-tailed tests) smaller than 0.05 (alpha) are considered significant. Main effects (of non-interacting factors) and interactions that are not reported did not reach significance. Effect sizes of F tests were estimated using partial eta squared (partial-η^2). Partial eta squared estimates the magnitude of a given effect, by quantifying the percentage of variance explained by the underlying factor when excluding the contribution of inter-subject variance. Cohen's d effect sizes were calculated for t-tests. Finally, we assessed whether obtained null-findings reflect a veridical absence of the studied effect by applying tests of equivalence. In essence, testing equivalence reverses the null and research hypothesis of traditional significance tests, i.e. by rejecting H_0 (different means) in favour of H_a (same means). In the present study, equivalence testing is especially valuable to assess whether experimental effects are truly eliminated by face inversion. Therefore, we tested equivalence of each pair of inverted face conditions for which a null-finding (p > 0.05) was obtained with traditional t-testing. The subject-specific means of the psychophysical or ERP peak values of each pair were submitted to a Two One-Sided Test of Equivalence for Paired-Samples (TOST-P; δ = 1 s.d; Mara & Cribbie, 2012), one of the few equivalence tests available for testing dependent samples in repeated-measure within-subjects designs. All statistical analyses were performed in SPSS 24 (SPSS INC, Chicago, IL) and Matlab (R2016a; www.mathworks.com).

3. Results

3.1. Behavioral results

Participants performed the task accurately (mean accuracy of 89.0%; s.d. 6.1%) and fast (mean RT of 811.1 ms; s.d. 100.8 ms). For accuracy, an interaction between Orientation and Congruency was revealed (F(1,8) = 12.4, p = 0.008; partial-η^2 = 0.61). Subsequent t-tests revealed that accuracy was better for congruent than incongruent faces when presented in upright orientation (t(8) = 2.5; Bf-adj. p = 0.040; Cohen's d = 0.80; one-tailed), but not when faces were inverted (t

(8) = 0.5; Bf-adj. p = 1.000; TOST-P: t(8) = 2.8, p = 0.01). Given that the Orientation x Congruency interaction tended to be influenced by Target Similarity (F(1,8) = 4.4, p = 0.070; partial-η^2 = 0.35), we further examined how Similarity affected this interaction. In line with previous results (Goffaux, 2012, Goffaux et al., 2013), we expected the upright face congruency effect to be stronger for same than different target features. Indeed, the accuracy difference between the Congruent-Same and Incongruent-Same condition congruency effect was substantial (mean difference = 10.7%) for upright trials (t(8) = 2.3; Bf-adj. p = 0.049; Cohen's d = 0.75; one-tailed). In contrast, such a congruency effect was not significant in upright Different trials (mean accuracy difference = 3.1%; t(8) = 1.2; Bf-adj. p = 0.52; Cohen's d = 0.34). Note that the congruency effect is more than twice as large in the Same compared to Different condition. Moreover, inverted faces did not induce any congruency effects (all Bf-adj. p's = 1.0; all Cohen's d's < 0.22). Together, these findings provide corroborating evidence that Target Similarity has a pivotal influence on how forcefully Congruency interferes with the accurate processing of upright faces.

Mean RT results were in line with the accuracy pattern: An interaction between Orientation and Congruency (F(1,8) = 6.3, p = 0.037; partial-η^2 = 0.44) was observed and posthoc tests revealed that for upright faces, responses to congruent faces were on average 41 ms faster than to incongruent ones (t(8) = 2.8; Bf-adj. p = 0.025; Cohen's d = 0.92; one-tailed). However, similar to accuracy, this congruency effect disappeared when faces were inverted (t(8) = 0.4; Bf-adj. p = 1.000; TOST-P: t(8) = 16.4, p < 0.0001).

3.2. ERP component results

3.2.1. P1 & N170

P1 peak latency was faster for same compared to different eyes (F(1,8) = 11.3; p = 0.010; partial-η^2 = 0.59). In contrast, P1 amplitude was not influenced by any of the factors (all p's > 0.112).

The N170 peaked on average around 174 ms post-stimulus onset (Fig. 3). N170 peak latency showed an interaction between Orientation and Target Similarity (F(1,8) = 7.2; p = 0.028; partial-η^2 = 0.47). However, none of the subsequent posthoc comparisons survived Bonferroni-correction.

N170 amplitude was almost twice as large on PO8 as on PO7 (F(1,8) = 28.9; p = 0.010; partial-η^2 = 0.78). In addition, faces elicited larger N170 peaks when presented in inverted compared to upright orientation (F(1,8) = 12.2; p = 0.008; partial-η^2 = 0.60). Furthermore, N170 peaks were larger for incongruent compared to congruent faces (F(1,8) = 6.0; p = 0.040; partial-η^2 = 0.43). The three-way interaction between Orientation, Congruency and Similarity was not significant (F(1,8) = 0.3; p = 0.878; partial-η^2 = 0.03). However, Orientation did show tendencies to interact with both Similarity (F(1,8) = 5.2; p = 0.051; partial-η^2 = 0.40) as well as Hemisphere (F(1,8) = 3.7; p = 0.092; partial-η^2 = 0.31). These interactions were further explored per hemisphere. At PO7, none of the effects reached significance (all p's > 0.084). In contrast, PO8 N170 peaks were larger for incongruent compared to congruent faces (F(1,8) = 6.0; p = 0.040; partial-η^2 = 0.43). Although Congruency and Target Similarity had no interactive influence on the PO8 N170 amplitude (F(1,8) = 1.1; p = 0.711; partial-η^2 = 0.18), Similarity did interact with Orientation at PO8 (F(1,8) = 5.4; p = 0.048; partial-η^2 = 0.40). Subsequent t-tests confirmed the expected neural adaptation for upright faces: the N170 amplitude was reduced when targets were the same rather than different (mean difference = 2.1 μV; t(8) = 2.4; Bf-adj. p = 0.045; Cohen's d = 0.79; one-tailed). In stark contrast, same and different targets elicited virtually identical N170 response amplitudes in inverted conditions (mean difference = 0.05 μV; t(8) = 0.1; Bf-adj. p = 1.000; TOST-P: t(8) = 4.0, p = 0.002).

3.2.2. P2

P2 peak latency showed an interaction between Hemisphere,
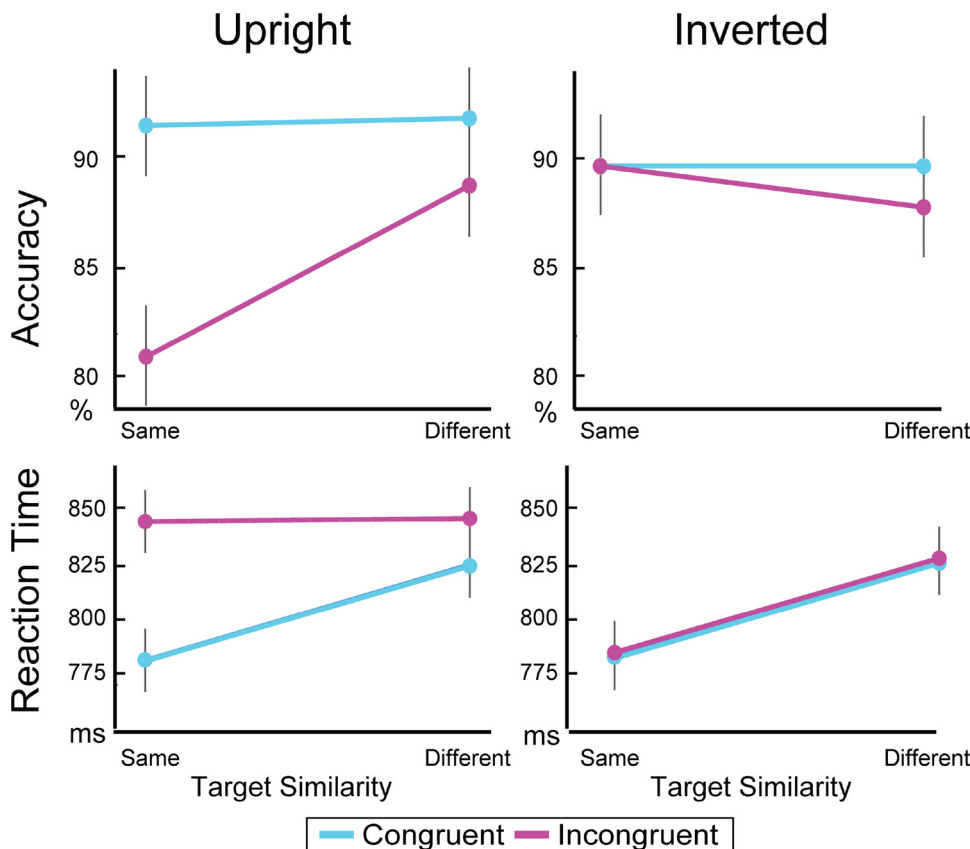
Fig. 2. Normalized mean accuracy (top) and reaction time (RT; bottom) as a function of Target Similarity. Lines represent congruency conditions for upright (left) and inverted (right) faces. Note the low accuracy and high RT in the Incongruent-Same condition for upright but not for inverted faces. Error bars represent 95% within-subjects confidence intervals (Loftus & Masson, 1994).
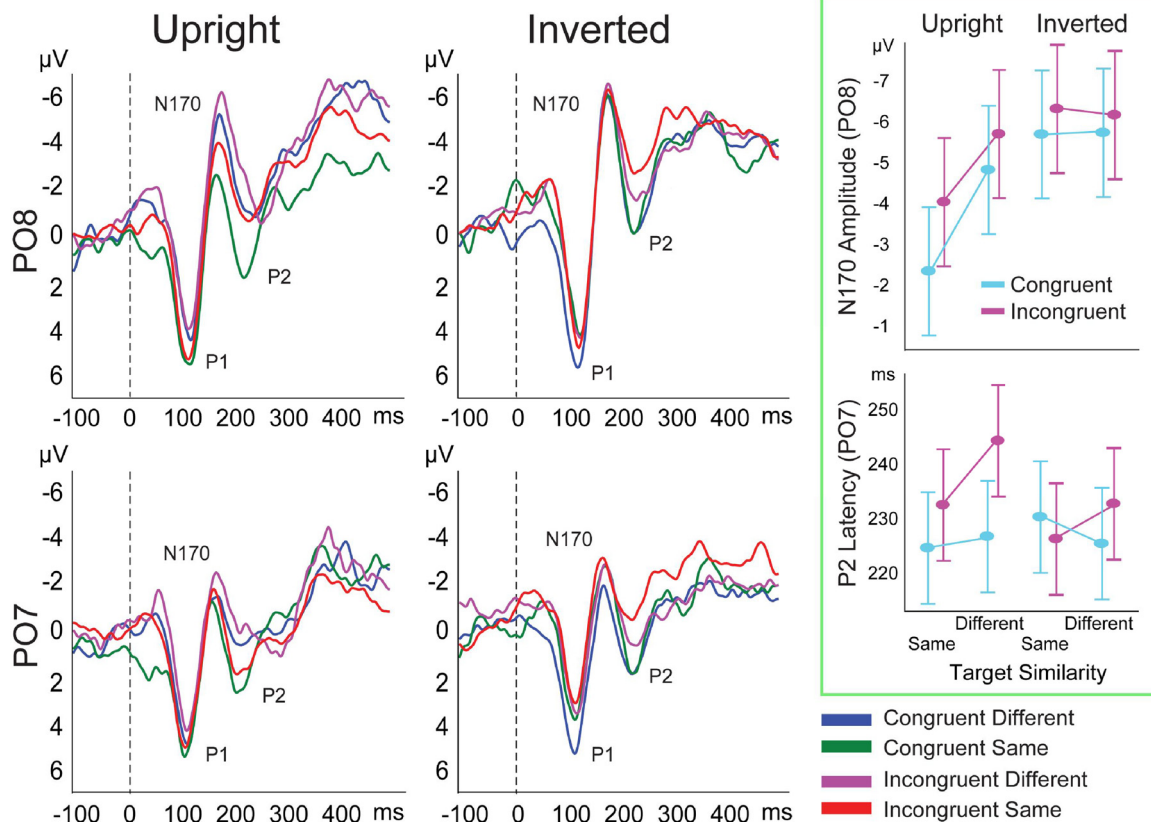
Fig. 3. Grand-averages for upright (left) and inverted (right) test faces at electrodes PO8 (top) and PO7 (bottom). The displayed ERPs are low-pass filtered (20 Hz) for visualization purposes. Notice the differential N170 adaptation for upright faces at PO8 (left panel), which is maximal for faces identical to the adapting face (congruent-same; green line) compared to the partial adaptation in other upright conditions. In contrast, N170 shows no adaptation for inverted faces (right panel). The green inset shows the normalized mean N170 amplitude (at PO8; top plot) and P2 Latency (at PO7; bottom plot) as a function of Target Similarity. Lines represent congruency conditions for upright (left) and inverted (right) faces. Note that the most insightful experimental effects were obtained for the displayed N170 amplitude (Congruency, Similarity × Orientation) and P2 Latency (Congruency × Orientation). Error bars represent 95% within-subjects confidence intervals.

Orientation and Congruency ($F(1,8) = 13.2$; $p = 0.007$; partial-$\eta^2 = 0.62$). Further tests showed that at PO7, congruent faces elicited on average 13 ms faster P2 peaks than incongruent faces for upright faces ($t(8) = 2.7$; Bf-adj. $p = 0.026$; Cohen's $d = 0.91$ one-tailed). In contrast, P2 peak latencies were virtually identical for congruent and incongruent faces when faces were inverted (mean difference = 0.8 ms; $t(8) = 0.22$; Bf-adj. $p = 1.000$; TOST-P: $t(8) = 4.8$, $p = 0.0007$). Congruency did not affect P2 peak latencies at PO8 regardless of orientation (all p's > 0.13).

Congruency also influenced the P2 amplitude: Congruent faces elicited larger P2 peaks compared to incongruent faces ($F(1,8) = 5.5$; $p = 0.047$; partial-$\eta^2 = 0.41$). However, Congruency did not interact with Orientation, and Similarity (three-way interaction: $F(1,8) = 0.07$; $p = 0.936$; partial-$\eta^2 = 0.01$). Finally, Hemisphere had an opposite effect on P2 compared to N170 amplitudes, revealing larger P2 responses in the left compared to right hemisphere ($F(1,8) = 13.7$; $p = 0.006$; partial-$\eta^2 = 0.63$).

In sum, Orientation, Congruency and Target Similarity differentially affected brain responses over time. P1 results showed the expected neural adaptation to face features, as reflected by a shorter peak latency for same compared to different targets. Neural adaptation occurred irrespective of face orientation and congruency. In contrast, neural adaptation of the subsequent N170 was qualified by face orientation: Same targets only elicited smaller (right-lateralized) N170 responses than different targets, when targets were presented in upright faces. The elimination of N170 adaptation when faces were inverted indicates a face-specialized adaptive coding at this second stage of face processing.

Feature congruency influenced N170 and P2 amplitudes, irrespective of orientation. In contrast, congruency effects on the (left) P2 latency were influenced by orientation. Whereas the P2 peaked as much as 13 ms earlier for upright congruent than incongruent faces, this effect was completely abolished (i.e., 0.8 ms congruency difference) by face inversion. In short, these results show that Target Similarity adapts P1 and N170 responses, whereas Feature Congruency affects the N170 and P2 but not the P1. Furthermore, face inversion reduces these effects for some, but not all, peak values. Unfortunately, peak measures of ERP components are relatively crude estimates of fine-grained temporal processes (Luck, 2014), and are not sensitive to off-peak EEG modulations. The emergence, subsequent transitions, and interplay of IFP and LFP, might not coincide with ERP peak latencies. Therefore, we performed point-by-point time course analyses (see also Jacques et al., 2007; Jacques & Rossion, 2009), which allows a precise estimation of temporal differences between IFP and LFP.

3.3. Time courses of interactive (IFP) and local (LFP) feature processing

We assessed the temporal dynamics of IFP and LFP using point-by-point permutation tests. To ensure our tests were sensitive, we first examined whether we could replicate the observation of Jacques and colleagues (2007), that the first significant interaction between adaptation to identity and inversion emerges around approximately 160 ms on right-lateralized occipito-temporal electrodes. To this end, we compared PO8 responses to upright versus inverted presentation of the Congruent-Same and Congruent-Different conditions. In line with Jacques et al. (2007), a first robust inversion effect emerged at 170 ms
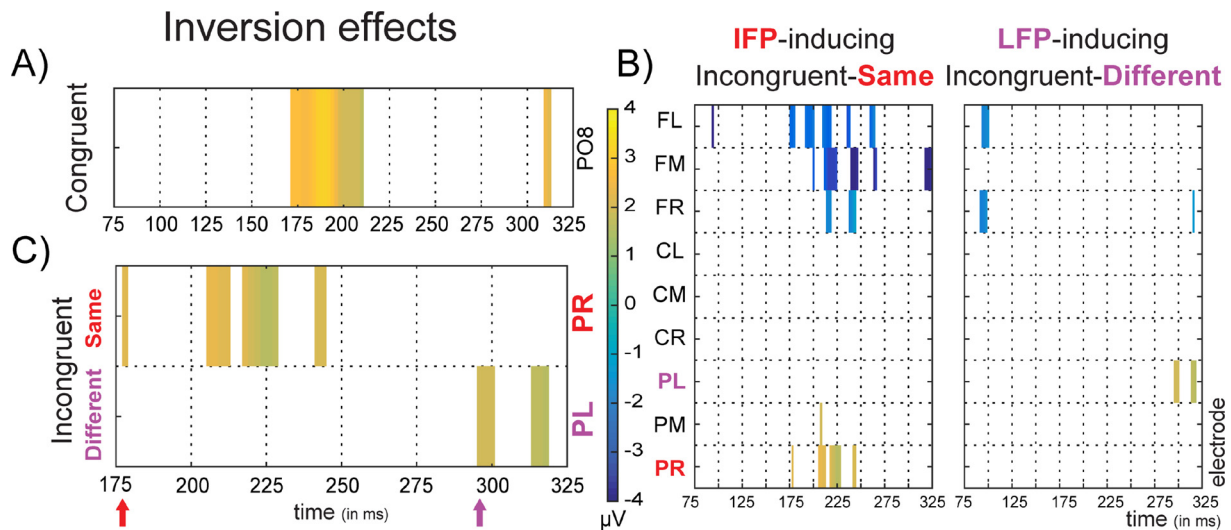
Fig. 4. Statistical plots of Inversion Effects, showing ERP differences between upright and inverted faces per 2 ms time-bin (X-axis) by electrode (Y-axis). Only significant differences (defined by Tmax corrected p-values) are color-coded (scale color bar applies to all panels) as a function of the mean amplitude of the difference between corresponding ERPs. A) General inversion effect congruent faces. Tmax corrected p-values < 0.025. B) Inversion effect in the Incongruent-Same (left) and Incongruent-Different (right) condition per electrode pool. Electrode pools represent average responses in electrodes clustered as a function of their location in frontal (F), central (C) and posterior (P) scalp regions, as well as left hemisphere (L), midline (M) and right hemisphere (R). Tmax corrected p-values < 0.01. C) Close-up of right (PR) and left (PL) posterior electrodes in B), showing the inversion effect in the IFP-Inducing Incongruent-Same (top row) and LFP-eliciting Incongruent-Different (bottom row) condition from 175 to 325 ms. Arrows indicate onset of the inversion effect in the Incongruent-Same (red) and Incongruent-Different (purple) condition.

(Fig. 4A). This effect lasted until 210 ms, thereby encompassing parts of the N170 and P2 time window. A second episode of inversion modulation was observed from 308 to 312 ms.

After establishing the expected inversion effects for congruent faces, we turned to the incongruent conditions. The behavioural results revealed processing differences across Incongruent-Same and Incongruent-Different conditions, which were further unravelled by examining the differences in their neural time courses. At the behavioural level, the Incongruent-Same condition elicited robust IFP during the perception of upright but not inverted faces. At the neural level, the inversion-related disruption of IFP in this condition was reflected by sustained temporal modulations of occipito-temporal and frontal electrode activity (Fig. 4B, left column). The occipito-temporal modulations mimicked the temporal pattern of the Congruent conditions, showing a right-lateralized emergence of IFP in intervals between 176 ms to about 246 ms (Fig. 4B; Fig. 4C, top row). In striking contrast, the LFP-inducing Incongruent-Different condition only showed occipito-temporal inversion effects during two, later, periods (296–302 ms and 314–320 ms) and in the left hemisphere selectively. At frontal sites, the Incongruent-Same condition also showed stronger and more sustained inversion effects than the Incongruent-Different condition. Both conditions showed an unexpected, very brief and early, frontal modulation (Incongruent-Same: 94–96 ms; Incongruent-Different: 92–100 ms). In a later stage, frontal electrodes were again very briefly affected by inversion in both incongruent conditions (Incongruent-Same: 318–324 ms; Incongruent-Different: 316–318 ms). Such short-lasting (i.e., 4 ms on average across conditions) and isolated modulations are likely spurious, or reflect more general differences between processing upright and inverted faces. More importantly, subsequent robust alterations were only revealed for the Incongruent-Same condition: neural responses to Incongruent-Same upright and inverted trials started to differ at left frontal electrodes around 174 ms, followed after 26–40 ms by mid-frontal and right frontal electrodes, until about 268 ms.

In summary, inversion started to affect occipito-temporal processing of congruent faces in the N170 window. The same was true for Incongruent-Same faces. In stark contrast, Incongruent-Different faces were only much later affected by inversion, with the first occipito-

temporal effect only arising at 296 ms (i.e., 120 ms after inversion onset in the Incongruent-Same condition). In addition to this temporal difference between IFP and LFP at occipito-temporal sites, IFP related modulations were lateralized to the right hemisphere whereas LFP related modulations were confined to the left hemisphere. Finally, IFP was affected by inversion over longer and more sustained periods of time than LFP, for both occipito-temporal as well as frontal locations.

4. Discussion

The present study investigated the time courses of Interactive (IFP) and Local (LFP) Feature Processing in face perception using a congruency paradigm. Participants matched target features within face pairs, in which distracter features were similar or dissimilar, thereby inducing congruency effects. IFP was operationalized as the inability to match target features without being distracted by task-irrelevant surrounding features. Our past and present psychophysical results show that when targets are not locally distinguishable (Incongruent-Same condition), an IFP mode is adopted, leading to deteriorated performance by incongruent distracter information. In contrast, the Incongruent-Different condition (i.e., different targets combined with similar distracters) elicited an LFP mode. Our recent fMRI study (Goffaux et al., 2013) showed that the IFP and LFP modes engage different occipito-temporal brain areas. The present results provide further insights by showing that these two processing modes operate in distinct time intervals. IFP modulated occipito-temporal EEG responses to faces about 120 ms earlier than LFP. This temporal precedence indicates that facial features are first processed interactively ("holistically"), before local analyses of fine feature details occur - in line with Coarse-to-Fine (CtF) models of perception.

4.1. Incongruency of face features deteriorates behavioural performance in upright faces

Previous studies showed that accuracy and perceptual sensitivity (Goffaux, 2009; Goffaux, 2012; Goffaux et al., 2013) decrease when a face part has to be discriminated in an incongruent compared to congruent context. This congruency effect disappears when faces are

inverted. The present behavioural results corroborate these findings and extend them to RT. Importantly, similar to Goffaux (2009, 2012), and Goffaux et al. (2013), congruency was influenced by target discriminability: Participants reached similar accuracies in the Incongruent-Different condition (i.e., face pairs with dissimilar target features embedded in the same context) as the Congruent-Different condition. This suggests that the detection of a local feature difference promotes LFP and consequently prevents incongruent surrounding information from affecting performance. In striking contrast, incongruent surroundings resulted in a substantial drop in accuracy in the Incongruent-Same compared to Congruent-Same condition. This indicates that target and surrounding features are interactively processed (i.e., IFP) when features cannot be discriminated at a local level. This latter congruency effect was not present for inverted faces, corroborating previous studies showing disruption of IFP by inversion (e.g., Goffaux, 2009). Note that these effects are not specifically related to the processing of the eyes, as Goffaux (2009) observed similar differences between Incongruent-Same and Incongruent-Different when the nose and mouth were target features and eyes served as distractors. To pinpoint at which neural processing stage IFP and LFP occur and result in such differential performance, we studied these two modes with high temporal resolution using EEG. Before focussing on the precise time-windows of IFP and LFP processes, we first analysed ERP components to understand how congruency, adaptation, target similarity and inversion modulate the most documented face-related ERP components.

4.2. P1, N170, and P2 are differently affected by orientation, similarity, and feature congruency

Face pairs with same rather than different targets elicited faster P1 and smaller N170 peaks, indicating that visual neurons at early and intermediate processing stages diminished their responses to repeated face features. Such adaptive effects of feature repetition on P1 latencies and N170 amplitudes corroborate previous observations based on repeated photographs of the same face (Jacques et al., 2007; Kovacs et al., 2006). The present results extend these previous findings by showing that repetition of the eye targets (even when embedded in a different face) is sufficient to induce neural adaptation. Indeed, previous studies have revealed that eyes are a relatively important feature of faces (e.g., Walker-Smith, Gale, & Findlay, 1977) and strongly contribute to the emergence of the face-specific N170 (Bentin et al., 1996; Itier, Latinus, & Taylor, 2006; Smith, Gosselin, & Schyns, 2004). Furthermore, the release of adaptation did not differ for one (different eyes embedded in same face) or more (different eyes embedded in different face) divergent features, which suggests the sub-additivity of N170 adaptation. This agrees with previous fMRI studies, which observed that FFA adaptation recovery does not scale with the number of divergent face features (Goffaux et al., 2013; Harris & Aguirre, 2010; Schiltz, Dricot, Goebel, & Rossion, 2010). The similarity between FFA and N170 modulations is consistent with studies showing that FFA is an important neural source for generation of the N170 (Allison, Puce, Spencer, & McCarthy, 1999; Ghuman et al., 2014; Henson et al., 2003).

Two other interesting aspects of these neural adaptation effects deserve mention. Firstly, inversion affected N170 adaptation, but not P1 adaptation. That is, the N170 amplitude was reduced for repeated targets in upright faces only. This shift from orientation insensitivity around 100 ms, to orientation-specific responses around 170 ms, is in line with previous studies suggesting that processing of upright and inverted faces start to diverge from 160 ms on (e.g., Jacques et al., 2007). Secondly, the N170 amplitude was almost twice as large in the right compared to left hemisphere, and neural adaptation was right-lateralized as well. These observations concur with the well-documented theory of right-hemispheric dominance in face perception (e.g., Hillger & Koenig, 1991; Ojemann, Ojemann, & Lettich, 1992; Sergent & Signoret, 1992). The bilateral P1 adaptation effects suggest that hemispheric lateralization only emerges with the onset of face-specialized

processing in the N170 time window. However, the present results should be interpreted in the light of the measured sample size and need to be validated by further research.

Feature congruency influenced both the N170 and the P2 amplitude, regardless of face orientation. In contrast, the congruency effect on P2 latency, was completely eliminated by face inversion. The P2 has been linked to processing of features and their metric relations (Boutsen, Humphreys, Praamstra, & Warbrick, 2006; Halit, de Haan, & Johnson, 2000; Itier & Taylor, 2002, 2004; Milivojevic, Clapp, Johnson, & Corballis, 2003; Pesciarelli, Leo, & Sarlo, 2016). The incongruence between facial features in our study has likely tapped into such inter-feature relational processing, causing a substantial delay in the processing of incongruent face features. Interestingly, slowing down of feature processing by conflicting contextual information was only present for upright faces. Inverting the faces abolished the impact of feature incongruence, suggesting that protracted processing due to incongruent face features is related to observer-dependent constraints rather than input limitations (see also Milivojevic et al., 2003).

4.3. From Coarse-to-Fine: neural markers of interactive feature processing (IFP) emerge before local feature processing (LFP) markers

To gain more insights into the precise temporal dynamics of face-specialized IFP and LFP, we performed point-by-point permutation tests. By contrasting the ERPs of upright and inverted conditions for each 2 ms time bin, we obtained a high-resolution index of the interaction between inversion and adaptation to facial features (see also Jacques et al., 2007). As expected, the Congruent conditions showed the first inversion effect in the N170 window (at 170 ms) in line with the findings of Jacques and colleagues (Jacques et al., 2007). Our focus of interest was on the two Incongruent conditions: Our past and present psychophysical results indicated that in the Incongruent-Same condition the IFP mode is engaged, leading to strong incongruency conflicts. Furthermore, these results showed that IFP is eliminated by inversion, resolving behavioural deterioration due to incongruent surrounds. In contrast, incongruency effects were weak in the LFP-engaging Incongruent-Different condition, resulting in a lower impact of inversion. These behavioural differences were reflected at the neural level at both occipito-temporal and frontal electrode sites. The inversion-related disruption of IFP (in the Incongruent-Same condition) induced early and long-lasting modulations over the right occipito-temporal electrodes, from 176 ms to 246 ms post-stimulus onset. This period coincides with the N170 and P2 processing windows, and are in line with the observed congruency effects on the N170 and P2 peak. Moreover, the emergence of IFP over occipito-temporal electrodes agrees with fMRI results revealing that the FFA has key roles in both IFP (Andrews, Davies-Thompson, Kingstone, & Young, 2010; Goffaux et al., 2013; Schiltz & Rossion, 2006; Schiltz et al., 2010), as well as in the generation of the N170 (Allison et al., 1999; Ghuman et al., 2014; Henson et al., 2003) and N250 (Schweinberger, Huddy, & Burton, 2004). In stark contrast to the Incongruent-Same condition, no early occipito-temporal inversion effects were observed in the Incongruent-Different condition. In the latter condition, inversion effects occurred at late stages (i.e., > 295 ms after stimulus onset), likely reflecting the inversion-related disruption of detailed but slower feature processing (McKone & Yovel, 2009; Rakover, 2012). LFP plays a key role in establishing facial identity and familiarity (e.g., Burton et al., 2015). Further research could explore how these local feature analyses in relatively late stages contribute to late neural signatures of face identification (between 200–500 ms after stimulus onset; Ghuman et al., 2014; Vida, Nestor, Plaut, & Behrmann, 2017).

In sum, disruption of IFP by inversion of Incongruent-Same faces affected occipito-temporal ERPs in the N170/P2/N250 window (176–246 ms). In contrast, inversion of the LFP-promoting Incongruent-Different faces did not affect processing in this window. Using the same paradigm, an fMRI study observed that FFA activity showed a twice as

large inversion effect for Incongruent-Same compared to Incongruent-Different faces (Goffaux et al., 2013). Together, these findings suggest that the FFA might be particularly important for IFP in a relatively early processing phase (i.e., N170/P2 window). In contrast to the early IFP emergence, the LFP-inducing Incongruent-Different faces only showed occipito-temporal inversion effects in a much later stage, i.e., more than 120 ms later than in the IFP condition. The precedence of the inversion effect in IFP compared to LFP conditions is in line with the presumed CtF-strategy of face perception (Goffaux & Rossion, 2006; Goffaux et al., 2011; Rossion, Dricot, Goebel, & Busigny, 2011; Sergent, 1986).

Interestingly, the early-phase IFP modulations were right-lateralized, whereas the late-phase LFP modulations were left-lateralized. This differential lateralization might indicate that qualitatively different processes might underlie these two face perception mechanisms. However, since other factors such as handedness and gender might have contributed to the observed lateralization differences, these effects should be interpreted with great caution. Further research could further establish the nature of the mechanisms underlying this lateralization. For example, to assess whether such IFP and LFP lateralization holds in other settings and whether it has any relation to the traditional framework of hemispheric dissociation between holistic (right) and feature-based (left) processing of information (Bradshaw & Nettleton, 1981), in particular for the perception of faces (Hillger & Koenig, 1991; Rossion et al., 2000; Yin, 1970).

The stronger impact of inversion on Incongruent-Same compared to Incongruent-Different faces observed at occipito-temporal sites, was replicated at frontal electrodes (Fig. 4B; left panel). These frontal modulations could reflect the VPP, the vertex polarity reversal of the N170 (Jeffreys & Tukmachi, 1992; Jemel et al., 2003, 2009). However, the frontal interval was more temporally extended than the occipito-temporal N170, and also showed a different hemispherical pattern. This suggests that additional processes beyond the N170/VPP have likely contributed to the frontal inversion effects. Fronto-occipital attentional mechanisms might play a role, if the perceptual integration window were adapted depending on local feature saliency. However, such an adaptation has to occur within the brief interval (200 ms) that the test face is on display, since subjects were not able to prepare an optimal spatial focus for the upcoming congruency context (conditions and adaptation face identities were fully randomized and counterbalanced across trials). Conflict monitoring in anterior cingulate cortex (Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999) might also contribute to the observed frontal differences between inversion effects in the two Incongruent conditions. The interfering influence of incongruent distracter features in the upright Incongruent-Same condition requires conflict detection and resolution, which could enhance the frontal N2b (or N2b-related) component as revealed by various conflict processing paradigms (e.g., Folstein & Van Petten, 2008), such as the classic Flanker task (Eriksen & Eriksen, 1974). The observed conflict-related frontal activities are in line with the accompanying poor task performance (Fig. 2). Correspondingly, frontal modulations did not emerge when Incongruent-Different faces were inverted (Fig. 4B; right panel), in accordance with behavioural performance indicating that the incongruent surroundings did not induce such conflicts when target features were different (Fig. 2). Further research could explore the role of attention and conflict processing in IFP and LFP, to establish how executive processes may help to successfully resolve conflicts in feature integration for face perception.

5. Conclusion

Using the congruency paradigm, our previous work revealed that the relative contribution of interactive and local processing to face perception depends on the discriminability of local features (Goffaux, 2012) and that the Fusiform Face Area (FFA) plays a key role in this flexible engagement (Goffaux et al., 2013). The present ERP study extends these findings in the temporal domain. The first neural markers of

Interactive Feature Processing (IFP) emerged early (around 176 ms) at occipito-temporal electrodes. In contrast, the first occipito-temporal indications of Local Feature Processing (LFP) occurred 120 ms later, at 296 ms. This indicates that interactive encoding of facial features occurs before local feature analysis. This temporal difference does not imply any causal relation between IFP and LFP. However, future studies could apply interferential methods (like non-invasive brain stimulation) to investigate causal IFP and LFP dependencies in face processing, and how failing IFP-LFP interactions may contribute to atypical face feature perception, such as observed in Autism Spectrum Disorder (e.g., Deruelle, Rondan, Gepner, & Tardif, 2004). The temporal order of these IFP and LFP modes agrees with models suggesting a Coarse-to-Fine (CtF) strategy for face perception, in which individual features are processed only after a global, so-called holistic, percept is established (Farah et al., 1998; Goffaux et al., 2011; Sergent, 1986; Tanaka & Farah, 1993). This CtF strategy adheres to more generic models of visual perception in which global scene analysis precedes the analysis of local visual information (Ahissar & Hochstein, 2004; Bar et al., 2006; Bullier, 2001).

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