Effect of face-related task on rapid individual face discrimination

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ABSTRACT

Human adults can typically visually discriminate the faces of unfamiliar individuals accurately, rapidly, and automatically, i.e. even without the explicit intention to do so. Recent studies have used fast periodic visual stimulation (FPVS) coupled with electroencephalography (EEG) to measure this process with objectivity and high sensitivity during simple non-face related tasks (Liu-Shuang et al., 2014). Here we consider to what extent fast individual face discrimination measured in the human brain with this approach is modulated by a direct face-related task. We recorded 128-channel EEG while participants viewed 70s sequences of a random female face identity (A) repeating at 6 Hz. Female faces of different identities (B, C…), interleaved regularly every 7th image (AAAAAABAAAAAAC…) led to significant periodic responses at 0.857 Hz (i.e., 6 Hz/7) and its harmonics, thereby indexing individual face discrimination. Participants performed two tasks: (1) an orthogonal *Fixation task*, monitoring random colour changes of the central fixation cross, and (2) a *Face task*, detecting male faces randomly replacing a female face. While the implicit Fixation task elicited robust individual face discrimination responses peaking over the (right) occipito-temporal region, the Face task led to significantly greater overall response amplitude (~100% increase). However, this attentional boost strongly reduced response specificity by disproportionately recruiting prefrontal and central parietal regions, thereby blurring the occipito-temporal topography typical of specialized high-level face processing. The individual face discrimination response over face-selective occipito-temporal cortex was modulated by the face-sex task starting from 180 ms onset, followed by activations over prefrontal and central parietal region from 200 ms to 450 ms, respectively. Overall, these findings show that even a robust automatic individual face discrimination response can be further enhanced when explicitly searching for face-related information, albeit with a decrease in response specificity.

1. Introduction

In the human species, recognizing people's identity by their face is critical for social interactions. A key aspect of individual face recognition is the ability to discriminate between different but highly similar visual patterns that constitute individual faces, even when these faces have not been encoded before in memory, i.e., are unfamiliar to us. Indeed, if our visual system was unable to respond differently to different unfamiliar faces, we would not be able to accurately tell apart new people and recognise them during subsequent meetings. Measuring unfamiliar face discrimination ability in humans is challenging because performance at explicit behavioural tasks, like the Benton Facial Recognition Test (BFRT; Benton and Van Allen, 1968; Rossion and Michel, 2018 for an electronic version of the test) or other more recent tests (e.g., Duchaine et al., 2007; Burton et al., 2010; Logan et al., 2016; Fysch and Bindemann, 2017) can be influenced by many factors beyond the face processing functions, such as task understanding, visual search, motivation, decisional processes or fluctuations of attention. This makes it difficult to compare individual face discrimination ability between different individuals, and in particular to assess and compare this ability across development and in clinical populations. Moreover, explicit behavioural tasks lack validity for estimating individual face identity discrimination ability in real world situations at two levels at least. First, since these tests rely on explicit instructions and behavioural responses, they do not measure *automatic* individual face discrimination. This is unfortunate because in real life circumstances, typical human adults discriminate individual faces automatically, i.e. without the intention to do so and without being able to suppress this visual discrimination process. Second, these tasks do not measure *rapid* individual face discrimination, i.e. forcing the visual recognition system to perform this function at a single glance.

To overcome these issues, recent studies have taken advantage of

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the brain's property to synchronize its electrophysiological activity to the temporal frequency of a stimulus (Adrian and Matthews, 1934; Regan, 1966; Norcia et al., 2015 for review). Specifically, by coupling frequency-tagging or fast periodic visual stimulation (FPVS) with human electroencephalography (EEG), one can obtain objective and sensitive measures of rapid and automatic unfamiliar individual face discrimination (since Rossion and Boremanse, 2011; Alonso-Prieto et al., 2013). A key paradigm for this endeavor is based on a periodic *oddball-like* stimulation, in which robust individual face discrimination measures can be obtained within a few minutes in every typical adult tested (Dzhelyova and Rossion, 2014a, 2014b; Liu-Shuang et al., 2014, 2016; Xu et al., 2017). In this paradigm, each stimulation sequence is composed of a randomly selected unfamiliar face identity repeated at a periodic rate, usually 6 Hz (i.e., 6 images/second), allowing only a single fixation on each face image. Different unfamiliar face identities are interleaved at regular intervals within the repeated identity (e.g., 1 change of identity every 5 faces, or 1.2 Hz). While EEG responses recorded at 6 Hz reflect common visual processing of all visual stimuli, responses at exactly 6 Hz/5 and its harmonics (1.2 Hz, 2.4 Hz, etc.) can be taken as an index of rapid individual face discrimination (i.e., discrimination based on the perception of idiosyncratic physical features of the faces). The validity of this measure has been shown in previous studies by showing that it resists large changes of stimulus size (all studies cited above; Dzhelyova and Rossion, 2014a for systematic manipulations of this parameter), but is largely reduced following picture-plane stimulus inversion and contrast-reversal (Liu-Shuang et al., 2014), two manipulations that completely preserve low-level visual differences between facial images but selectively disrupt individual face recognition (Galper, 1970; Yin, 1969). Moreover, the rapid individual face discrimination response is selectively abolished in a well-known case of prosopagnosia following brain damage (Liu-Shuang et al., 2016). In neurotypical human adults, this individual face discrimination response can be objectively identified and quantified, as it is measured only at experimentally pre-defined frequencies of interest, and is associated with a high signal-to-noise ratio (SNR) (see Rossion, 2014). Most importantly with respect to the issue raised above, this individual face discrimination response is obtained during severe stimulation time constraints (i.e., one fixation per change of face identity) and even when there is no instruction to the observers to explicitly attend to individual faces (Dzhelyova and Rossion, 2014a, 2014b; Liu-Shuang et al., 2014, 2016; Xu et al., 2017).

An outstanding issue is whether such a robust neural index of automatic individual face discrimination can nevertheless be modulated by increasing the attentional focus on the face stimuli, if so to what extent and along which spatio-temporal course. Clarifying these questions is important because it extends our understanding of the relationship between face-related task modulation and face perception (i.e., whether actively expecting or searching for faces increases identity detection). In general, experimental studies have shown that selectively attending to faces leads to improved behavioural performance and increased neural activation. For instance, Boutet et al. (2002) found a significant advantage in individual face encoding when their participants were asked to pay attention to the faces rather than a house picture on 50% transparency displays. Similarly, Jackson and Raymond (2006) reported that the recognition of unfamiliar faces was susceptible to temporal attention effects (attentional blink). At the neural level, face-selective responses in the middle fusiform gyrus of the ventral ocipito-temporal cortex are stronger when participants pay attention to the face stimuli (while ignoring superimposed non-face objects), or perform a face instead of a house matching/recognition task (Baldauf and Desimone, 2014; Clark et al., 1996; Furey et al., 2006; Haxby et al., 1994; O'Craven et al., 1999; Wojciulik et al., 1998; Yi et al., 2006). The time-course of these effects of attention remain controversial however, with some studies finding a modulation of face processing only after 200 ms of stimulus onset (Engell and McCarthy, 2010; Lueschow et al., 2004), while other studies showed that the early stages of face

processing indexed by N170 was strongly modulated by selective attention (Mohamed et al., 2009). Importantly, none of the above studies on attentional modulation have isolated a neural response specifically reflecting (fast) individual face discrimination.

To investigate attentional modulation of rapid and automatic individual face discrimination captured by FPVS-EEG, we instructed participants to complete two types of behavioural tasks: either (1) detect the colour change of a central fixation cross (**Fixation** Task), which is the typical orthogonal task used in such studies (e.g., Dzhelyova and Rossion, 2014a; Liu-Shuang et al., 2014) or (2) detect target male faces that were randomly embedded among the female faces in each sequence (**Face** Task). A face sex task was used because it requires paying attention to the visual characteristics of the face identities that are presented in the sequence. However, unlike a face identity task, a face sex task remains orthogonal to the measure of interest (individual face discrimination) and does not introduce contaminating decisional components every time there is a periodic change of face identity in the sequence. We expected to find a significant individual face discrimination response over face-selective regions (i.e., occipito-temporal cortex, with a right hemispheric dominance), in line with previous studies (see above). However, we also predicted an increase of the individual face discrimination response in the Face Task relative to the Fixation task. By spacing out the changes of identity in the stimulation sequences (i.e., every 7 stimuli or 0.857 Hz, every 1167 ms), we were also able to analyse the data in the time-domain to clarify the time-course of explicit face-task modulations.

2. Material and methods

2.1. Participants

Eighteen Caucasian participants were recruited in this experiment, with two individuals excluded due to excessive muscular artefacts. The final sample consisted of 16 participants (8 females; mean age, 22.5 years). All participants had normal or corrected-to-normal vision. None reported to have a history of neurological or psychiatric disorder. All participants gave their written consent prior to the experiment. The Biomedical Ethical committee of University of Louvain approved the study.

2.2. Stimuli

We used full-front coloured photographs of 30 female and three male adult Caucasian faces with a neutral expression, taken under standardized conditions with respect to lighting, background, and distance from the camera. All stimuli were cropped around the outline of the face (removing hair, ears, and neckline) while preserving the overall shape of the face. They were overlaid on a square greyscale background, sized to 400 × 400 pixels. Stimuli were displayed at a distance of 80 cm and subtended approximately 9.3° visual angle, with faces themselves subtended 3.7° × 4.8° visual angle on average. The stimulus set has also been used in previous studies (Dzhelyova and Rossion, 2014a, 2014b; Liu-Shuang et al., 2014, 2016).

2.3. Design & procedure

Stimuli were presented at the frequency of 6 Hz (6 images per second; SOA = 167 ms), using a custom Java-based stimulation software. Stimuli were presented through square-wave contrast modulation between 0 and 100% (off/on), with a 75% duty cycle (Retter and Rossion, 2016). Specifically, at each 167-ms stimulus presentation cycle, the image was presented at 100% contrast during the first 125 ms (i.e., 15 × 8.3 ms screen frames) and at 0% contrast for the next 42 ms (5 × 8.3-ms frames) (Fig. 1). Note that this presentation mode differs from previous studies with this paradigm, in which a sinusoidal contrast modulation was used (Dzhelyova and Rossion, 2014a, 2014b; Liu-
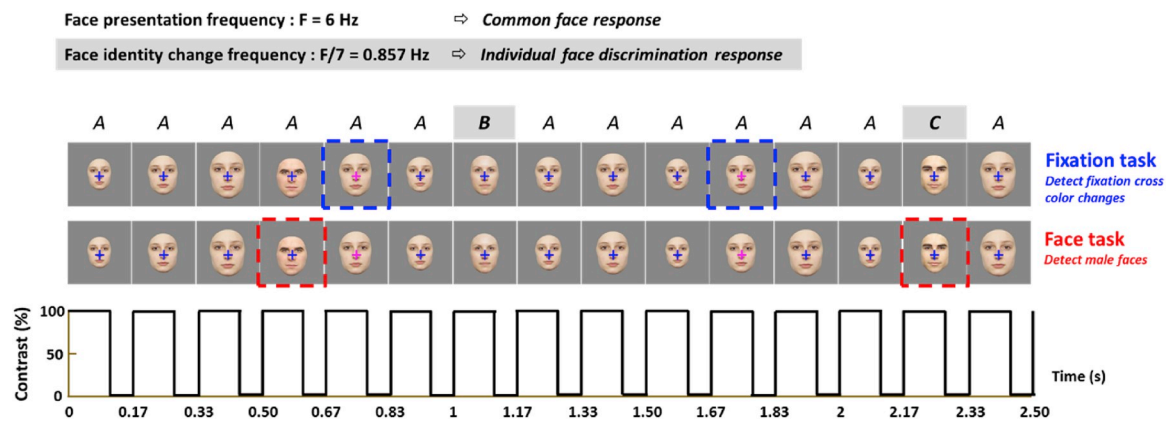
Fig. 1. Schematic illustration of the experimental design. Images were presented through square-wave contrast modulation (75% duty-cycle) at a fixed rate of 6 images per second (6 Hz), with large size variations occurring randomly at each stimulation cycle to minimize pixel-wise discrimination effects. The 70s stimulation sequences contained different female faces (B, C …) interleaved at regular intervals (1/7) among a repeated identical female face (A). Two types of targets were present concurrently within each sequence: the central blue fixation cross turning red, and male faces replacing female faces (in this example, the male face replaced one of different identity female faces). Each of these target types randomly occurred 6 times within each sequence. Participants were given two different behavioural tasks in an alternated order: detect fixation colour changes, or detect the appearance of a male face. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Shuang et al., 2014, 2016; Xu et al., 2017). The square-wave contrast is used here for optimizing the measure of temporal dynamics of the face discrimination response (i.e. clear onset of the stimuli) and is not expected to change the magnitude and nature of the response (see Retter and Rossion, 2016 for direct comparison of square-wave and sinewave stimulation in FPVS). Within each 70s stimulation sequence, a randomly selected female identity was repeated (A) and interleaved with different female face identities (B, C…) every 7th image (AAAAAAB-AAAAAAC…). Thus, face identity changed periodically, at a frequency of 6 Hz/7 = 0.86 Hz. At every stimulation cycle, image size randomly varied between 80 and 120% in order to minimize pixel overlap between consecutive stimuli and ensure that the individual face discrimination response generalizes across image changes.

This experiment had two task conditions. In the orthogonal **Fixation** task, participants were required to attend to the central fixation cross, and to respond when they detected a random colour change of cross (from blue to red, lasting 200 ms). In the **Face** task, participants were required to attend to the face images and respond whenever female faces were randomly replaced by one of the three male faces. The male faces could either replace the repeated female face (i.e., face A, in the above example) or any of the different identity female faces (i.e., B, C, D…). On average, target male faces replaced the different identity female faces 13% of the time. There were 6 targets for each of the Fixation and the Face tasks, and participants responded by pressing the spacebar on a keyboard. Critically, both types of targets were presented concurrently within a same sequence so that visual stimulation was held constant, with only task instruction varying between conditions. Each task condition was repeated 6 times, resulting in a total of 12 stimulation sequences (70s each with 60 oddball identity-change events; total testing time = 15–20 min, including breaks). The two tasks were presented in alternating order and the starting condition was counterbalanced across participants. There was no order effect in either the behavioural performance or the EEG signals.

2.4. EEG acquisition

The experiment was run in a quiet and low-lit room. The stimulation sequences were presented on an LED monitor (BenQ XL2420T) with a 1600 × 900 screen resolution and a 120 Hz refresh rate. Stimuli were presented centrally on the screen. High-density 128-channel EEG was acquired with the ActiveTwo Biosemi system (Biosemi, Amsterdam, The Netherlands) at a 512 Hz sampling rate. The magnitude of the offset of all electrodes, referenced to the common mode sense (CMS), was held

below 30 μV. Vertical and horizontal electrooculogram (EOG) was recorded using four additional flat-type active-electrodes: two electrodes above and below the participant's right eye and two lateral to the external canthi.

2.5. Behavioural analysis

Response times (RTs) were calculated relative to the onset of target faces. Analyses were conducted on the median of correct RTs. Responses were considered correct if they occurred between 150 ms and 3000 ms following target onset. Keypresses recorded outside this time-window were labelled as incorrect as our current paradigm does not enable the dissociation between misses or false alarms. We compared the overall response accuracy, correct response times, and number of incorrect keypresses across conditions.

2.6. EEG analysis

2.6.1. Preprocessing

EEG data was analysed as in previous studies using this approach (e.g., Liu-Shuang et al., 2014; Retter and Rossion, 2016), with an open source software Letswave 5 (https://www.letswave.org), running in MATLAB R2013a (MathWorks, USA). EEG data was first band-pass filtered between 0.05 and 100 Hz with a 4th order zero-phase Butterworth filter and then downsampled to 256 Hz to reduce computational load. The data sequence was then segmented for each stimulation sequence relative to the starting event code, with an additional 2 s before and after each sequence (each epoch spanned from −2 to 76 s relative to the event code corresponding to the sequence start). Individual channels with artefacts (i.e. channels with unstable signal or containing muscular artefacts exceeding ~100 μV during multiple stimulation sequences) were interpolated by their three neighbouring channels. The maximum interpolated channels for each participant was 6 (average 3 ± 2). For four participants who blinked more than 0.2 times/s on average during the sequences (Retter and Rossion, 2016), prior to channel interpolation, a single component accounting for blink artefacts was removed, based on an independent component analysis (ICA) applied on the EEG data. The cleaned up data was then re-referenced to the average of all 128 channels.

2.6.2. Frequency-domain analysis

In order to avoid spectral leakage, the pre-processed EEG data were re-segmented into epochs with an integer number of cycles of face

identity change frequency (i.e., 0.857 Hz = 0.167 s per cycle). The first and last 2 s of each presentation sequence were discarded to remove eye-movements and transients related to the abrupt onset and offset of the flickering stimuli. The resulting cropped epochs were 68.84 s long and contained 59 face identity change cycles. A Fast Fourier Transform (FFT) was applied to the epochs averaged by condition and the amplitude spectra were extracted, with a frequency resolution of 0.0145 Hz (1/68.84s). However, to calculate task reliability, FFT was also applied separately to the odd and even stimulation epochs of each task.

To define significant periodic EEG responses at the relevant stimulation frequencies, the spectral amplitude of each participant was averaged across all conditions and all channels, and transformed into z-scores. The z-scores at a given frequency were calculated by subtracting the mean amplitude of 20 neighbouring frequency bins (10 bins on each side) from that frequency, divided by the standard deviation of the 20 neighbouring bins. The neighbouring bins did not include the two immediately adjacent frequency bins (in case of residual spectral leakage; Jacques et al., 2016; Rossion et al., 2012; Liu-Shuang et al., 2014). A conservative threshold of z-scores > 3.1 (*p* < .001, one-tailed, signal > noise) was used as the cut-off (Jacques et al., 2016).

Having selected the relevant range of frequency harmonics, responses were quantified by first applying a baseline-correction to the raw amplitude spectra, i.e. subtracting from each selected frequency the mean amplitude from the 20 surrounding frequency bins (excluding immediately adjacent bins). Then, the baseline-corrected amplitudes were summed at the frequency harmonics of interest. The individual face discrimination response was quantified as the sum of the first 9 harmonics of 0.857 Hz (0.857 Hz, 1.714 Hz, 2.571 Hz, 3.428 Hz, 4.285 Hz, 5.142 Hz, 6.856 Hz, and 7.713 Hz, excluding the 7th harmonic 6 Hz), while the common face response was quantified as the sum of the first 8 harmonics of 6 Hz (6 Hz, 12 Hz, 18 Hz, 24 Hz, 36 Hz, 42 Hz, and 48 Hz) see Retter and Rossion (2016) for validation of the quantification procedure through summation of amplitudes across harmonics). Henceforth, we refer to these summed and baseline-corrected responses when mentioning the individual face discrimination response or the common face response.

2.6.2.1. Task modulation analysis. To measure the effect of task modulation on face discrimination response, we first examined the overall effect over across 128 scalp channels. Next, since the individual face discrimination response was mainly located over occipito-temporal (OT) regions, consistent with previous studies (Dzhelyova and Rossion, 2014a, 2014b; Liu-Shuang et al., 2014, 2016; Xu et al., 2017), we defined bilateral OT regions-of-interest (ROIs) in the right (P8, P10, PO8, PO10, PO12) and the left hemisphere (P7, P9, PO7, PO9, PO11) to examine more specific effects of task modulation. Statistical analyses were carried out using repeated-measured ANOVAs and Greenhouse-Geisser corrections were applied to degrees of freedom whenever the assumption of sphericity was violated. Pairwise t-tests were used for post-hoc comparisons and the Bonferroni correction was applied for multiple comparisons. We also indexed the percentage response amplitude change with the formula: (Face-Fixation)/Fixation*100, to examine the relative extent to which the Face task boosted the response amplitude compared to the Fixation task.

2.6.2.2. Scalp topography analysis. Visual inspection suggested potential topographical differences between the individual face discrimination responses of the two task conditions. We quantitatively evaluated this by first applying a scalp normalization transformation (McCarthy and Wood, 1985). More precisely, for each participant in each task, the individual face discrimination response on each electrode was rescaled by dividing it by the mean square root of the sum of squares of amplitudes over all 128 electrodes (see also Barceló et al., 2000; Dzhelyova et al., 2017; Jacques et al., 2016). This computation enabled the comparison of the relative response

topographies independently from any overall amplitude differences between conditions. Next, we identified any significant topographical distribution changes between task conditions by means of a cluster-based permutation *t*-test using the FieldTrip toolbox (5000 permutations with the Monte Carlo method, minimum 3 neighbourhood channels, *p* < .05, two-tailed, for both the cluster statistic and the permutation test, using the percentile cut-off of the maximum of summed t-statistics within clusters) (Maris and Oostenveld, 2007). Note that the scalp normalization transformation was only applied to the response amplitudes in the frequency-domain.

2.6.2.3. Reliability analysis. To further explore the data and examine whether adding a task would affect the stability of responses across participants, we analysed the reliability of response patterns. We computed the Pearson correlation of the individual face discrimination response in odd and even stimulation sequences for each task, over the face-selective OT ROIs.

2.6.3. Time-domain analysis
We also investigated the temporal dynamics of the individual face discrimination response with a time-domain analysis (Jacques et al., 2016; Retter and Rossion, 2016). Re-referenced preprocessed data were first low-pass filtered with a 30 Hz cut-off (4th order Butterworth filter), then cropped into an integer number of cycles of the face identity frequency (2–70.84 s, 17624 bins = 59 face presentation cycles). Data were then notch-filtered (FFT filter, width = 0.05 Hz), selectively removing the face presentation frequency (6 Hz) up to its 5th harmonic (30 Hz). Sequences were then segmented into smaller epochs of 1.167 s (7 face presentation cycles), time-locked to the onset of face identity changes, with a 167 ms pre-stimulus (*ABAAAAA*). Epochs were finally averaged and baseline-corrected (−167 ms – 0 ms). This analysis was conducted first in individual participants and then averaged at the group-level.

To determine which time-windows showed significant effects of task, we also ran a cluster-based permutation *t*-test on the post-stimulus onset time-points (0–1000 ms, all other parameters same as above). This analysis was done on baseline-corrected waveform amplitudes. Video clips were created to show the time-course of the face-task modulation effect on face processing (movie 1).

3. Results

We first describe participants' behavioural performance across the Fixation and Face task before reporting the EEG data. After quantifying the relevant individual face discrimination and common face responses according to the procedures presented above, we explore task modulation effects on these responses. Finally, we focus on the temporal dynamics of the task modulation effect on the individual face discrimination response.

3.1. Behavioural performance

We first inspected the behavioural performance across our two task conditions. Table 1 shows the mean behavioural performances for both tasks in terms of Accuracy, RTs, and Incorrect keypresses. Participants were slightly less accurate ($t_{(15)} = 2.50$, *p* < .05) when responding to

Table 1
Behavioural performance (Accuracy, RT, Incorrect keypresses) for both tasks. Standard deviations of the means are shown in the parentheses.

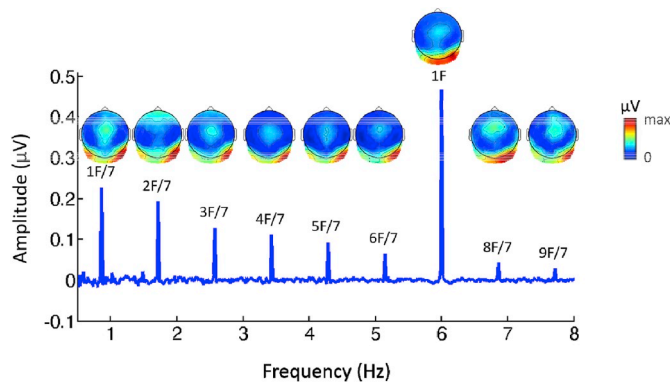|	Fixation Task	Face Task
Accuracy (%)	97.1 (± 4.2)	92 (± 7.3)
RT (ms)	430 (± 37)	493 (± 42)
Incorrect keypresses (count)	0.94 (± 1.6)	9.63 (± 8.8)

Fig. 2. Grand-averaged amplitude spectrum across conditions and across all 128 electrodes. There were large significant peaks at the face identity change frequency (0.857 Hz and its harmonics) and at the face presentation frequency (6 Hz and its harmonics). Only consecutively significant responses (*z-score* > 3.1, *p* < .001, one-tailed) were taken into account for analysis. 2-D scalp topographies are shown above each frequency of interest, with their colour scale adjusted to the maximum value of each frequency. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

male faces compared to the fixation colour change, although the performance was high and near ceiling in both tasks (i.e., 97.1% vs. 92%). Participants were also significantly slower ($t_{(15)}$ = 4.96, *p* < .001) when responding to male faces compared to the fixation colour change. There was no speed-accuracy trade-off. In addition, on average, participants also made more incorrect keypresses in the Face task than in the Fixation task ($t_{(15)}$ = 3.99, *p* < .001).

3.2. EEG response quantification in the frequency-domain

Considering the average across all 128 channels and across the two task conditions, significant responses were observed at the face presentation frequency (i.e., 6 Hz) up to its 8th harmonic (48 Hz) and at the face identity change frequency (i.e., 0.857 Hz), up to its 9th harmonic (7.713 Hz) (Fig. 2). Responses at face presentation rate reflect general visual processing of all face stimuli (i.e., faces against a uniform visual field), while responses at the face identity change frequency reflect the discrimination between the repeated face identity and the different inserted face identities.

3.3. Task modulation on individual face discrimination responses

3.3.1. Task-related response amplitude differences

First, we compared the overall individual face discrimination response, averaged across 128 channels, between the two tasks to

examine any global effects of task modulation (Fig. 3). A paired *t*-test showed a significant difference, $t_{(15)}$ = 8.57, *p* < .001, reflecting a 107% amplitude increase from the Fixation task to the Face task (0.58 ± 0.09 vs. 1.2 ± 0.11 μV). This task modulation effect was found in all participants. Next, we focused on examining more specific effects of task modulation over the OT ROIs, as this region showed the maximum face discrimination responses (OT ROIs: 2.09 ± 0.93 μV; all scalp channels: 0.89 ± 0.37 μV). Based on visual inspection, a right hemisphere dominance was present for most of the participants in both the Fixation task (12/16) and the Face task (13/16).

A two-way repeated ANOVA with *Hemisphere* (Left, Right) and *Task* (Fixation, Face) as within-subjects factors was conducted on the individual face discrimination response (Fig. 3). The results showed significant main effects of both factors (*Task*: $F(1,15)$ = 29.08, *p* < .001, partial η^2 = 0.66; *Hemisphere*: $F(1,15)$ = 16.87, *p* < .001, partial η^2 = 0.53), and also a significant interaction of *Task* × *Hemisphere*, $F(1,15)$ = 13.36, *p* < .01, partial η^2 = 0.47. Further analyses showed that for both hemispheres, the response in the Face task was larger than that in the Fixation task (Left: $t_{(15)}$ = 3.79, *p* < .001; Right: $t_{(15)}$ = 6.27, *p* < .001). However, when we directly compared task modulation between hemispheres using the percentage response change index, the pairwise *t*-test showed no difference between the left and right hemispheres, $t_{(15)}$ = 0.42, *p* > .1.

In summary, we found that paying attention to face sex substantially increased the individual face discrimination response over all channels, including over the right and left OT regions. However, we note that the percentage response increase in the Face task compared to the Fixation task is larger over all scalp channels (107% response increase) than over the right and left OT regions (65.7% and 55% response increase, respectively). Thus, it appears that task modulation effects are also driven by additional regions beyond the OT area. We therefore examined in further detail the *relative* amplitude differences across all scalp channels between the two tasks.

3.3.2. Task-related scalp topography changes

To isolate the qualitative changes brought by the explicit Face task, scalp topographies were normalised such that the mean amplitude was equalised between the two task conditions (McCarthy and Wood, 1985; see Methods). Fig. 4 shows the resulting normalised topographical maps and the relative spatial distribution of the individual face discrimination response in each task condition. The difference map between conditions highlights the involvement of anterior and central channels rather than posterior channels in the relative amplitude changes observed in the Face task; a pattern that is consistent within individual observers (Fig. 4B). Next, we ran a cluster-based permutation test (see Methods) which showed significant differences in the topographical distribution of responses between the Fixation and Face tasks over a prefrontal region (channels FPz, Afpz, Fp1&2, AF3&4, AF7&8, AFF5&6) and a right parietal region (channels C2, C4h, CCP2h, CCP2, CCP4,
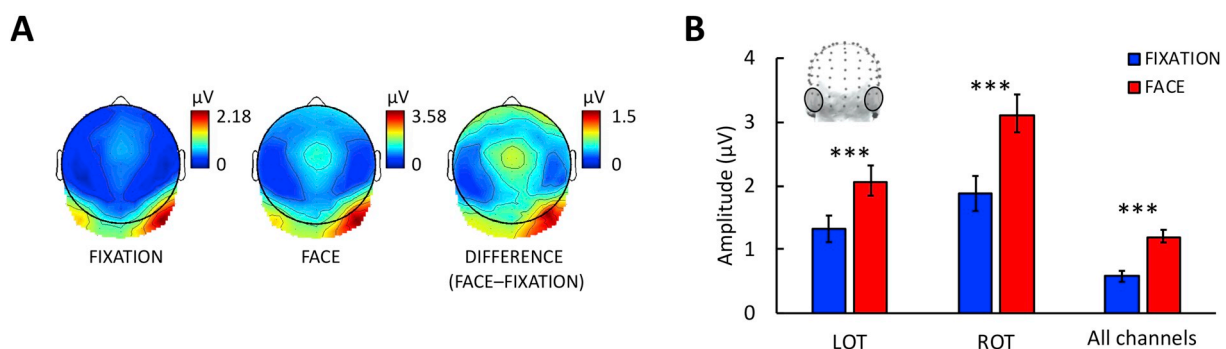

Fig. 3. Effect of task modulation on the individual face discrimination responses. **A.** Group-level 2-D scalp topographies on individual face discrimination responses of both tasks and their difference (= Face task – Fixation task). **B.** Mean individual face discrimination response over Left OT, Right OT, and across all 128 electrodes for both tasks. Error bars indicate standard error of the mean. ***p < .001.
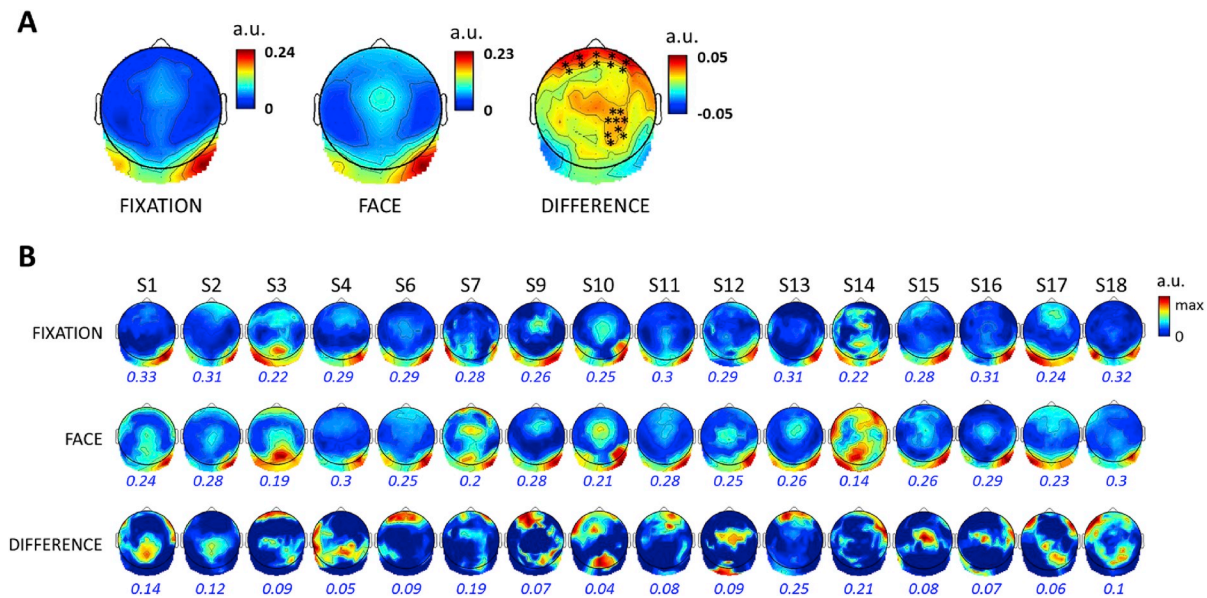
Fig. 4. Task modulation effects on topographically normalised individual face discrimination responses. **A.** Group-averaged normalised 2-D scalp topographies of the individual face discrimination response for each task and the task difference (Face – Fixation). The asterisks on the difference map indicate channels reaching significance in the cluster-based permutation test and indicate relative topographical changes between tasks. Colour scales are adjusted to the maximum value of each task. **B.** Normalised scalp topographies of individual face discrimination responses in the two tasks and their difference in individual participants. The colour scale is adjusted to the range to the maximum value of each individual at each task. The maximum value in relative amplitude change for each topography is shown beneath each plot (in blue colour). a.u. = arbitrary units. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

CPP4h, CPP4, P2, PPO2). By contrast, differences between tasks over OT regions did not reach significance threshold (all $ps > .05$). Overall, analysis based on normalised amplitudes indicates that the explicitly face-related task led to a change in the relative activation between scalp channels displaying the individual face discrimination response, with a substantial increase over prefrontal and parieto-central regions and a relative (non-significant) decrease over occipito-temporal regions.

3.3.3. Within- and between-task reliability

The reliability analysis showed that the within-task correlation across participants was 0.91 ($p < .001$) and 0.97 ($p < .001$) for the Fixation task and the Face task, respectively. The between-task reliability was also significant but reduced, $r = 0.74$ ($p < .001$).

To compare the within- and between-task reliability, we first transferred the correlation coefficients into z-scores, using Fisher r-to-z transformation (Fisher, 1915, 1921). The results showed that the within-task reliability across the two tasks was not significantly different, *z-score* = 1.44, $p = .15$ (two-tailed), and there was no significant difference between the Fixation within-task and the between-task coefficients, *z-score* = 1.47, $p = .14$ (two-tailed). However, the within-task reliability for the Face task was significantly more reliable than the between-task reliability, *z-score* = 2.91, $p < .01$ (two-tailed).

3.3.4. Relationship between task difficulty and individual face discrimination

Behavioural results showed that the Face task was more difficult than the Fixation task. Participants were slower and (slightly) less accurate to detect the male target faces among a rapid stream of female faces, compared to the detection of the fixation cross colour change. To examine whether the task modulation effect of the individual face discrimination response was caused by task difficulty, we tested the correlation between the behavioural task difference scores (Face task – Fixation task) with the raw (non-normalised) task effect on the individual face discrimination response. We sampled the individual face discrimination response from several ROIs: bilateral OT, where the strongest responses were located, as well as prefrontal and parietal

regions, which were specifically enhanced during the Face task.

Task difficulty effect on **accuracy** did not correlate at all with the neural individual face discrimination responses over any ROIs (OT: $r = -0.25$, $p > .1$; parietal: $r = -0.3$, $p > .1$; prefrontal: $r = -0.003$, $p > .1$), which is not surprising given that behavioural differences in accuracy rates were small between the two conditions. However, a significant correlation was found over the parietal ROI ($r = 0.63$, $p < .01$) with **RT** difference between the two tasks. Participants for whom RTs increased the most between the Face task and Fixation task showed stronger task-related increase of the individual face discrimination response over the parietal area. Correlations between differential RTs and individual face discrimination responses were not significant on other ROIs (OT: $r = 0.16$, $p > .1$; prefrontal: $r = 0.4$, $p > .1$).

3.4. Task modulation on common face responses

We also tested whether the task also had a general effect on the common face response at 6 Hz and harmonics (12 Hz, etc.), reflecting general visual processing of the image sequence. As typically found in these studies (e.g., Dzhelyova and Rossion, 2014a, 2014b; Liu-Shuang et al., 2014, 2016; Xu et al., 2017), this response was localized over medial occipital channels (Fig. 5), and tested at an occipital ROI (O1&2, Oz, POI1&2, OIz, I1&2, Iz, POO5&6, and POOz). A paired *t*-test showed that the common face response was slightly but significantly larger in the Face task than that in the Fixation task (13% response increase), $t_{(15)} = 2.59, p < .05$ (Fixation: $2.68 \pm 0.94\,\mu V$; Face: $3.01 \pm 1.1\,\mu V$). This response difference was also significant across all 128 channels (6% response increase), $t_{(15)} = 2.23$, $p < .05$ (Fixation: $1.07 \pm 0.28\,\mu V$; Face: $1.18 \pm 1.1\,\mu V$).

We ran multiple correlations to verify whether the task-based modulation effect observed on the common face response shared similar sources with the effect found on the individual face discrimination response. Since each type of response had a distinct topography (bilateral OT for the individual face discrimination response and medial occipital for the common face response), we correlated task difference
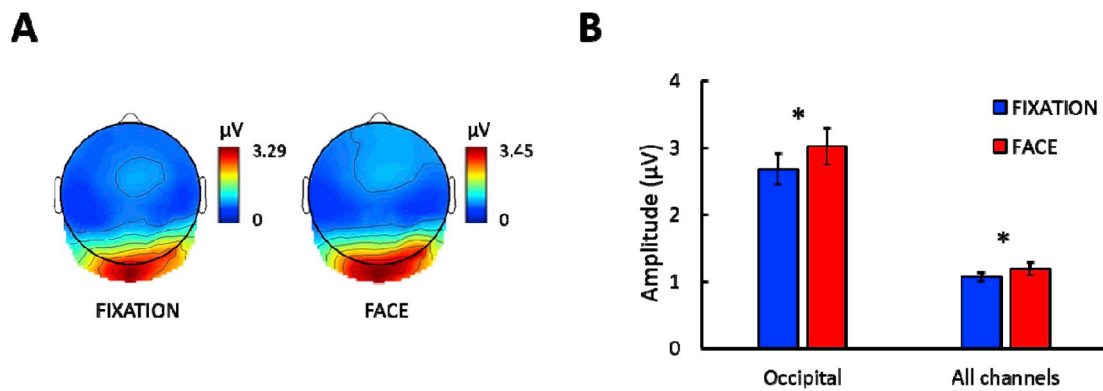
A **B**

Fig. 5. Grand-averaged common face responses. **A.** Two-D scalp topographies of two tasks with colour scaled to the maximum baseline-corrected amplitude value of each task. **B.** Mean baseline-corrected amplitude over the occipital ROI and across all 128 channels as a function of task. *$p < .05$. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

scores within and across these ROIs. Results show no significant correlations between task modulations on individual face discrimination responses and on common face responses either within the occipital ROI ($r = 0.45$, $p = .08$) or the OT ROI ($r = 0.35$, $p > .1$), or across the optimal ROI for each type of response (OT ROI for the individual face discrimination response and occipital ROI for the common face response) ($r = 0.44$, $p = .09$). Moreover, task effects on the common face response were not correlated with any behavioural task effects over the occipital ROI (RTs: $r = -0.1$, $p > .1$; accuracy: $r = 0.04$, $p > .1$) or over the OT ROI ($ps > .1$).

3.5. Temporal dynamics of task modulation effects

Finally, we examined the temporal dynamics of the task modulation effect. Fig. 6A shows the individual face discrimination response waveform in the time-domain, averaged across two task conditions. As expected, there was a strong periodic signal with a cycle duration matching the 6 Hz face presentation frequency. In order to examine the brain responses specifically related to the processing of face identity change, the responses at the face presentation frequency and its harmonics were selectively filtered out (Fig. 6B) (see Retter and Rossion, 2016). Consistent with previous findings with the current paradigm (Dzhelyova and Rossion, 2014a), we observed a series of deflections indexing individual face discrimination, with a first positive deflection between ~80 and 120 ms after stimulus onset, followed by a negative

deflection between ~150 ms–300 ms and then a second, more prolonged negativity between ~400 and 800 ms, all predominantly located over the right occipito-temporal cortex.

To investigate the time-course of the task modulation effect, we conducted a cluster-based permutation test (see Methods) between the two tasks (Fig. 7). Results indicate that task effects occurred over two time-windows (Movie 1). Between ~180 and 400 ms, differential activation was found over occipito-temporal, central parietal, and prefrontal regions. Then, from ~450 to 600 ms, task effects were presented over occipital and central parietal regions. Interestingly, there was no modulation effect on the very early time-window containing the occipito-temporal positive component of the face discrimination response (~100 ms after stimulus onset).

4. Discussion

We investigated how a face-related task (i.e., searching for a specific face sex) modulated neural responses reflecting rapid (i.e., single-glance) individual face discrimination, measured with FPVS-EEG. Observers completed either an orthogonal Fixation task (detect rare and random colour changes) or a Face task (detect rare and random male faces among sequences of female faces). Critically, while the Face task was face-related, it did not explicitly involve monitoring individual face identity. Participants completed both of these tasks with near ceiling accuracy (> 95%).
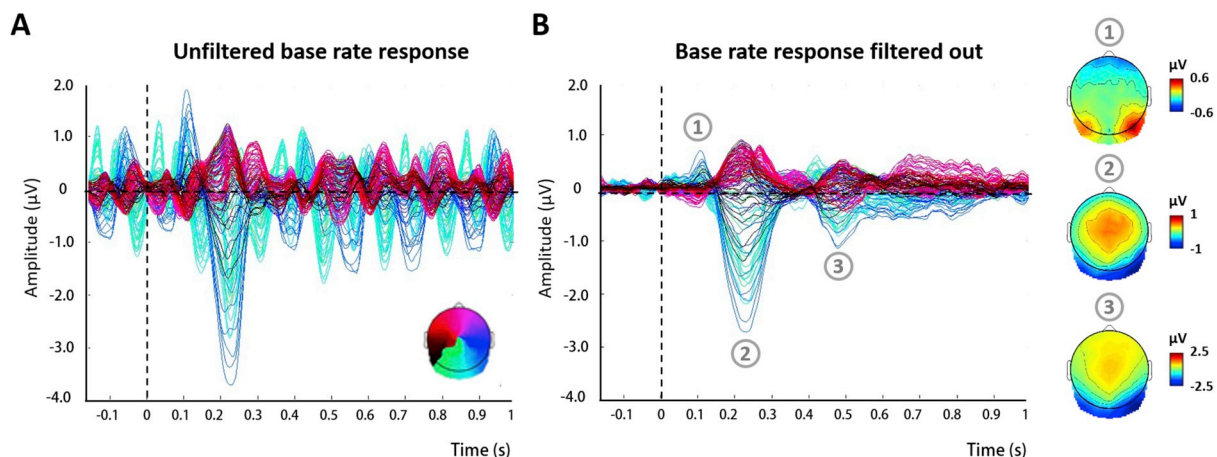
A **B**

Fig. 6. Temporal dynamics of the individual face discrimination response. **A.** Mean responses averaged across the two task conditions shown over all 128 channels. The waveforms display a clear periodic signal with the cycle duration matching the face presentation frequency (i.e. 6 Hz). The coloured scalp map on the lower right corner indicates positions of different scalp channels corresponding to each line on the waveform plots. **B.** The same EEG data is shown with signals at 6 Hz and harmonics (12 Hz, 18 Hz, 24 Hz, and 30 Hz) filtered out. Two-D scalp topographies for the positive and negative deflections are shown near their waveform, peaking at 100 ms, 230 ms, and 480 ms after stimulus onset, respectively.
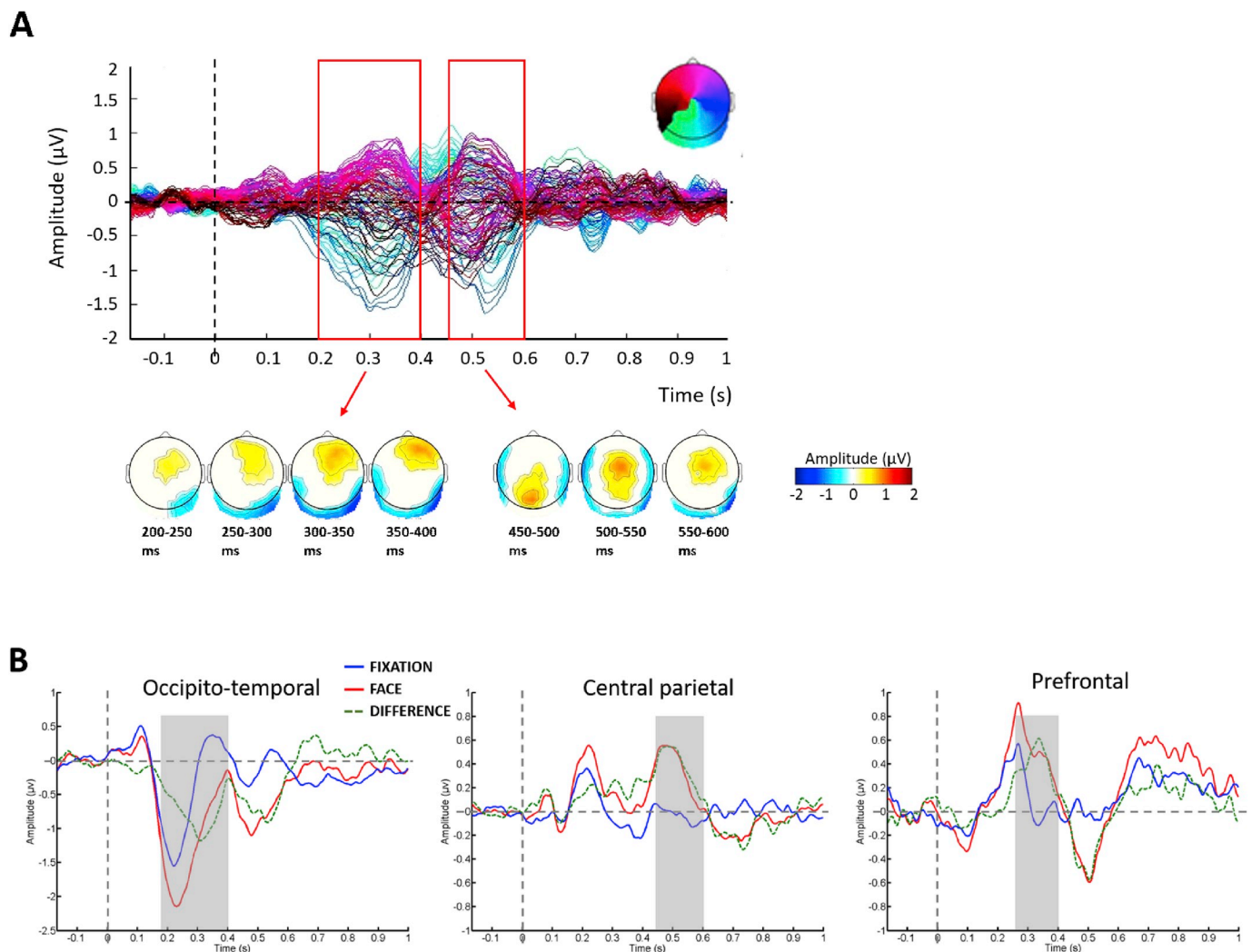
Fig. 7. Cluster-based permutation test on amplitude differences between tasks in the time-domain. **A.** Time-course of the Face – Fixation difference waveform, shown over all 128 channels. Windows containing significant amplitude differences are outlined in red box. Below each window, corresponding 2D scalp topographies of differences averaged within 50 ms steps are displayed. Only significant channel clusters are shaded according to the colour legend on the right. The coloured scalp map on the upper right corner indicates positions of different scalp channels corresponding to each line on the waveform plots. **B.** Average waveforms of the individual face discrimination response in each task and their difference (Face – Fixation), shown within three ROIs. Shaded windows indicate significant amplitude difference between two tasks. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

We replicated previous results by finding an individual (unfamiliar) face discrimination response in the EEG frequency-domain over occipito-temporal channels, with a right hemisphere dominance, at the group-level and in every single observer tested (e.g., Dzhelyova and Rossion, 2014a, 2014b; Liu-Shuang et al., 2014, 2016; Xu et al., 2017). This further consolidates the FPVS-EEG as a robust neurofunctional technique for probing high-level perceptual processing with high objectivity and sensitivity. More importantly, our data showed that the task significantly modulated the neural response elicited by face identity changes. Attending to face sex increased this response even over bilateral occipito-temporal regions (∼60% amplitude increase over both right and left hemispheres). This observation is consistent with previous studies showing that selective attention can enhance face processing (Baldauf and Desimone, 2014; Boutet et al., 2002; Furey et al., 2006; O'Craven et al., 1999; Palermo and Rhodes, 2002; Wojciulik et al., 1998; Yi et al., 2006), and extends this conclusion to unfamiliar face identity processing. Critically however, the Face task boosted the overall amplitude of the response across the entire scalp, and in fact reduced the relative spatial selectivity of the neural discrimination response. Indeed, by applying a topographical normalization, we found that the Face task elicited relatively stronger

increases of activity over parietal and prefrontal regions than over occipito-temporal regions. This indicates that directed focus on faces boosts neural face discrimination by recruiting additional processes that are not typically and automatically associated with specialized face processing. Hence, while in the orthogonal Fixation task, the neural discrimination response is predominantly driven by specialized face identity processing and reflects individual face discrimination, the response in the explicit Face task appears to contain more of a mixture of processes. On the one hand, activity over occipito-temporal regions very likely represents similar mechanisms as in the Fixation task. On the other hand, activity over parietal and frontal regions may stem from the involvement of more general deviance detection mechanisms.

The above observations imply that an absolute task-related difference in overall response magnitude during face perception can be misleading, since it could be contaminated with more general cognitive processes that might not be directly involved in visual perceptual processing. The impact of such non-specific factors could potentially weight even more in developmental or non-neurotypical observers, thus complicating the interpretation and generalization of results across populations. This also highlights the importance of spatially normalising response patterns and considering the relative contribution of

each region in order to properly assess the impact of attentional modulation.

The time-domain analysis of the individual face discrimination response further informed about the spatio-temporal dynamics of the task-related modulation effect. An early component of the individual face discrimination response (∼100 ms post stimulus-onset) was insensitive to modulatory effects by the Face task. Although this early response may be considered as reflecting individual face discrimination based on lower-level features (i.e., being less resistant to large variations of image size, see Dzhelyova and Rossion, 2014a), it was nevertheless located almost exclusively on a small region of the (right) occipito-temporal cortex (Fig. 6B), indicating a higher-level process than mere luminance processing. Note that the early latency of this deflection may be due to the type of stimulation used here, where the face processing system is continuously (pre)activated during the stimulation. In any event, the lack of modulation of this early component cannot be attributed to a lack of power of the present manipulation, since large modulatory effects were found overall. Rather, it suggests that the initial cortical discrimination of a difference between unfamiliar individual faces is largely task-free.

Beyond this latency, attending to faces affected the entire response waveform starting from ∼200 to 600 ms over lateral and occipito-temporal regions, suggesting that focusing on faces alters face identity processing from an earlier stage than what has been previously reported (Engell and McCarthy, 2010; Lueschow et al., 2004; see Mohamed et al., 2009 for an exception). Amplitude changes over frontal regions occurred during an earlier time-window (∼200–400 ms) compared to parietal regions (∼450–600 ms). Importantly, responses at the face identity change frequency over frontal and parietal regions during the Face task were not correlated with individual face discrimination responses over occipito-temporal channels. Rather, these frontal and parietal responses are likely to be distinctly related to attentional operations (Kastner et al., 1999; Kastner and Ungerleider, 2000), such as response inhibition and task difficulty, respectively. Responses over the prefrontal region could have reflected the efforts to activate the response inhibition system and to interrupt preparations for response execution (Géczy et al., 1999). In the Face task, observers were required to detect random male targets within the sequence of female faces. While any face change could signal potential target, participants had to withhold response when this change was a female identity change. Thus, this Go-NoGo situation could have recruited structures involved with inhibition of motor responses (Bokura et al., 2001; Fallgatter and Strik, 1999). The timing of the prefrontal amplitude increase (between 200 and 400 ms) is consistent with this hypothesis. Responses over parietal regions in particular were correlated with behavioural performance, such that observers who were slower in detecting male target faces also showed the largest activity over parietal channels. By contrast, face discrimination responses over occipito-temporal regions did not correlate with behaviour, consistent with previous reports that neural correlates of face identity processing within this area were independent from perceptual load (Neumann et al., 2011; Neumann and Schweinberger, 2008). Although the significance of the correlational analysis should be taken with caution due to our relatively small sample size (N = 16; Yarkoni, 2009), the current response pattern generally supports our interpretation and is in line with existing literature.

In addition to attentional modulation of the individual face discrimination response, we also found (relatively weaker) task-dependent amplitude differences on the common face responses, with stronger responses in the Face task than in the Fixation task. Since these responses represent the overall processing of all face stimuli, this difference was to be expected given that, by design, the Face task required observers to monitor the sex of each single face stimulus in the sequence. Yet, one potential cause of concern is that the heightened attention of the individual faces evidenced by these common response results might have driven stronger awareness of the periodicity of the stimuli, and by extension, the periodicity of the face identity changes.

This is unlikely for several reasons. First, there was no correlation between the attentional modulation of the common face responses and the face discrimination responses. Second, we have recently demonstrated that temporal expectation had little impact on the differential responses elicited in this type of "oddball" FPVS-EEG paradigms (Quek and Rossion, 2017). In other words, there were no significant differences between the responses evoked by periodic "oddball" stimuli and non-periodic "oddball" stimuli. Finally, considering the short presentation durations (166 ms SOA), the periodicity of the repeating face identities at the 6 Hz face presentation frequency would be a more salient and noticeable "beat" compared to the face identity changes embedded every 7th image. If this was the case however, common face responses should have been reduced in the Face task, considering that temporal expectation decreases neural responses to repeated and predicable stimuli (Alink et al., 2010; Kok et al., 2012).

As elaborated in the introduction, the aim of the current FPVS-EEG paradigm was to test human face perception under severe time-constraints, measuring automatic responses. For a typical adult, faces identities are recognised within 1–2 fixations (Hsiao & Cottrell, 2008; Orban de Xivery et al., 2008), and without any explicit decision to do so. The question asked here was whether an orthogonal, non face-related task would be sufficient and adequate to study the neural mechanisms of face identity perception in this context. Previous work within the FPVS-EEG framework have predominantly used an orthogonal fixation cross task similar to the one in the current study. Together with previous data, the current findings indicate that this type of task is sufficient to investigate high-level, specialized face perception mechanisms given that it retains the spatial and functional specificity of these processes. Hence, individual face discrimination responses measured this way occur over occipito-temporal regions with a consistent right hemisphere lateralization and are decreased following stimulus inversion and contrast-reversal (Liu-Shuang et al., 2014), two manipulations known to selectively disrupt individual face recognition (Yin, 1969; Galper, 1970). Additionally, this approach has been shown to be effective in revealing differences between typical and neuropsychological populations (i.e., prosopagnosia, Liu-Shuang et al., 2016) or typical children and children with Autism Spectrum Disorder (ASD; Vettori et al., 2019), thanks in part to the simplicity of the orthogonal fixation task. It could be argued that this simplicity might lead to some observers simultaneously attending to the task-irrelevant face images and face identities, so that faces are not equally unattended across individual participants. However, the same critique also applies to more explicitly face-related tasks, which cannot either guarantee that all observers will focus on the task-relevant stimuli in the same manner. As a result, unless participant behaviour is directly relevant to the theoretical question, the present data suggest that the FPVS-EEG paradigm paired with a simple orthogonal task is a methodology of choice for investigating individual face perception.

5. Conclusions

The present study took the advantage of human brain's synchronisation to periodic visual input to investigate how individual face discrimination was modulated by a face-related task. Results show that the visual system discriminated individual faces automatically and rapidly (within ∼100 ms) in the absence of explicit attention to faces. Although a face-related task substantially increased the individual face discrimination response over occipitio-temporal regions from ∼200 ms onwards, it also reduced response specificity by eliciting disproportionately larger responses over prefrontal and parietal regions that are likely related to attentional operations rather than perceptual face processing.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuropsychologia.2019.04.002.

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