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Investigating holistic face processing within and outside of face-responsive brain regions

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## Investigating holistic face processing within and outside of face-responsive brain regions

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## Abstract

It has been shown that human faces are processed holistically (i.e. as indecomposable wholes, rather than by their component parts) and this holistic face processing is linked to brain activity in face-responsive brain regions. Although several brain regions outside of the face-responsive network are also sensitive to relational processing and perceptual grouping, whether these non-face-responsive regions contribute to holistic processing remains unclear. Here, we investigated holistic face processing in the composite face paradigm both within and outside of face-responsive brain regions. We recorded participants' brain activity using fMRI while they performed a composite face task. Behavioural results indicate that participants tend to judge the same top face halves as different when they are aligned with different bottom face halves but not when they are misaligned, demonstrating a composite face effect. Neuroimaging results revealed significant differences in responses to aligned and misaligned faces in the lateral occipital complex (LOC), and trends in the anterior part of the fusiform face area (FFA2) and transverse occipital sulcus (TOS), suggesting that these regions are sensitive to holistic versus part-based face processing. Furthermore, the retrosplenial cortex (RSC) and the parahippocampal place area (PPA) showed a pattern of neural activity consistent with a holistic representation of face identity, which also correlated with the strength of the behavioural composite face effect. These results suggest that neural activity in brain regions both within and outside of the face-responsive network contributes to the composite-face effect.

*Keywords:* face perception, holistic processing, composite face effect, FFA, LOC, PPA, RSC

## 1. Introduction

Faces are perceived as indecomposable wholes, rather than by their separate component parts (e.g. eyes, nose, mouth), a phenomenon known as holistic processing (Farah et al., 1998; Maurer et al., 2002; Rossion, 2013). Holistic processing of faces has been demonstrated in psychological studies showing that people cannot selectively attend to one part of a face and ignore the rest of it (Maurer et al., 2002; Richler and Gauthier, 2014). For example, if the top-half of one person's face is aligned with the bottom-halves of two different faces (i.e. composite faces), observers often perceive the two identical top-halves as two different identities, as they are unable to ignore the irrelevant bottom-halves of the faces. If the bottom-halves of the faces are spatially misaligned from the top-halves, observers no longer process face holistically and they perceive the two top-halves to be the same. This phenomenon is known as the composite face effect (Hole, 1994; Young et al., 1987).

What neural processes underlie holistic processing of faces? Neuroimaging studies have suggested that holistic face processing occurs in face-responsive regions of the occipitotemporal cortex. Both the occipital face area (OFA) and fusiform face area (FFA) have been shown to respond stronger to intact faces than to scrambled facial parts (Brandman and Yovel, 2016; Zhao et al., 2014), but see (Arcurio et al., 2012), who found higher responses to face parts than to whole faces in the OFA. Some studies have proposed that the FFA may process faces more holistically than the OFA. For instance, two studies found that the FFA responds stronger when face parts are arranged in a normal configuration compared to a scrambled configuration, but did not find these differences in the OFA or object responsive lateral occipital area (Liu et al., 2010; Zhang et al., 2015; but see Engell et al., 2018, who found no difference in FFA activation to normal versus scrambled face configurations). Behavioural studies have shown that inverted faces are processed less holistically than upright faces (Richler et al., 2011b; Rossion and Boremanse, 2008; Tanaka and Farah, 1993; Young et al., 1987), and correspondingly some studies have found that the FFA (but not the OFA) shows higher responses to upright than inverted faces (Goffaux et al., 2013; Pinsk et al., 2009; Yovel and Kanwisher, 2005), but see (Aguirre et al., 1999; Epstein et al., 2006; Grotheer et al., 2014; Haxby et al., 1999). However, other studies

found that neural responses in the FFA are consistent with a mixture of both holistic and part-based representations of faces (Harris and Aguirre, 2010, 2008), and other evidence for a mix of part-based and holistic face neural responses has also been demonstrated from single cell recordings from the middle face patch in macaque monkeys (Freiwald et al., 2009). The FFA is also involved in the perception of changing face identity when participants view composite faces. It has been shown that changes in neural activity in the FFA, and sometimes also the OFA, is consistent with the change in the perception of face identity induced by the composite face effect (Andrews et al., 2010; Goffaux et al., 2013; Schiltz et al., 2010; Schiltz and Rossion, 2006). In combination, these studies suggest that holistic face processing takes place in face-responsive brain regions, in particular the FFA.

Many behavioural studies have demonstrated that holistic processing is not unique to faces. In particular, behavioural studies have demonstrated that objects of expertise can be processed holistically (Bukach et al., 2010; Diamond and Carey, 1986) and when participants are trained to recognise exemplars of novel kinds of objects this training leads to holistic processing of these objects (Chua and Gauthier, 2020; Gauthier and Tarr, 1997; Wong et al., 2009a). Neuroimaging studies have shown that the FFA shows higher responses to expertise objects in experts than in novices (Gauthier et al., 2000a; Xu, 2005), and that the strength of these neural responses in the FFA correlates with behavioural measures of holistic processing of expertise objects (Gauthier and Tarr, 2002; Wong et al., 2009b). Recently, (Ross et al., 2018) showed that there is a correlation between the level of expertise and the amount of neural activity related to holistic processing of expertise objects in the anterior portion of the FFA, known as the FFA2 (Pinsk et al., 2009; Weiner et al., 2016, 2014). These studies suggest that neural activity in the FFA may be involved in holistic processing of both faces and objects of expertise.

These behavioural and neuroimaging studies indicate a strong link between holistic processing, expertise and neural activity in the FFA. However, recent behavioural work suggests that other factors may also contribute to holistic face processing. One study demonstrated that non-expertise objects can be processed as holistically as faces, and that this may be linked to salient Gestalt information in these objects (Zhao et al., 2016). Two recent behavioural studies found that holistic processing of faces and these non-expertise objects is partially overlapping (Curby et al., 2019; Curby and Moerel, 2019). These findings

lead to a new proposal that holistic face processing may involve two components or routes: an expertise component (or top-down route) related to the holistic processing of expertise objects and a perceptual component (or bottom-up route) related to the holistic processing of non-expertise objects with salient Gestalt information (Curby and Moerel, 2019; Zhao et al., 2016; Zhao and Bülthoff, 2017). While the expertise component of holistic face processing has been linked to the FFA, what neural mechanisms underlie the perceptual, Gestalt-related component of holistic face processing remains unknown. Given the behavioural evidence for two different components of holistic face processing, and findings that holistic processing applies to a variety of non-face object categories (e.g. fonts, greebles, music notes, line patterns, Chinese characters and English words, finger prints, chess board arrangements, etc.), see (Curby and Moerel, 2019; Zhao et al., 2016; Zhao and Bülthoff, 2017) for related discussion, we hypothesized that holistic face processing may be supported by broader neural mechanisms beyond face-responsive areas. Candidate mechanisms for a general perceptual route to holistic processing include perceptual grouping and relational processing. While previous studies have identified a set of brain regions related to the perceptual grouping and relational processing of scenes and objects, surprisingly little research has investigated whether they play a role in holistic face processing.

To unravel a broader picture of holistic processing in the brain, in this study, we investigated the neural mechanisms of holistic face processing both within and outside of face-responsive brain regions. In particular, we investigated if holistic face processing involves broader brain networks related to perceptual grouping in scene and object processing. Most previous studies investigated holistic face processing in specifically localized face-responsive brain regions, but they rarely tested whether brain regions responding to scenes, objects or perceptual grouping contribute to holistic processing. Although activity in non-localized regions may be revealed using whole-brain analyses, it is well-known that activity may be masked due to suboptimal alignment of functional brain regions across participants and poor statistical power in these analyses (Saxe et al., 2006; Weiner and Grill-Spector, 2013). In the present study, we recorded brain activity using functional magnetic resonance imaging (fMRI) as participants performed a composite face task (Hole, 1994; Young et al., 1987). As described earlier, when the top-half of one person's

face is aligned with the bottom-halves of two different faces (i.e. composite faces), observers tend to perceive the two identical top-halves as two different identities. Participants viewed pairs of composite-faces and made same/different judgements as to the identity of the top-half of the face.

We localized a variety of regions of interest (ROIs) that are either face-responsive or are sensitive to information that may support holistic processing. For face-responsive ROIs, we localized the FFA and the OFA, which have been shown to be related to holistic processing of faces (Andrews et al., 2010; Goffaux et al., 2013; Harris and Aguirre, 2010; Schiltz et al., 2010; Schiltz and Rossion, 2006). We subdivided the FFA into FFA1 and FFA2 (two components of the FFA) (Weiner et al., 2016, 2014), as some previous work has found evidence of holistic processing only in the FFA2 (Ross et al., 2018). Additionally, we localized a more recently defined, higher-level face-responsive brain region, the anterior temporal face area (ATFA) (Rajimehr et al., 2009; Tsao et al., 2008). If holistic processing is involved in more high-level than early processing of faces (e.g. FFA vs. OFA), the ATFA, an even higher-level face processing region, may also process faces holistically.

For ROIs outside of the face-responsive brain network, we localized several core brain regions related to the processing of scenes, objects, and perceptual grouping. Scene-responsive ROIs included the transverse occipital sulcus (TOS, also known as occipital place area, OPA), parahippocampal place area (PPA) and retrosplenial cortex (RSC). In the same way as the FFA responds more strongly to whole faces than facial parts, both PPA and RSC show higher neural activity for intact scenes than for fractured scenes (Kamps et al., 2016), suggesting that these areas are tuned to whole-scene processing. Although TOS is thought to be sensitive to the local elements of scenes (e.g. surfaces, furniture) (Kamps et al., 2016), it does contribute to the fine-grained perceptual discrimination of very similar scenes (Dilks et al., 2013) and it shows stronger activation to a whole scene (e.g. a furnished room) compared to scene components (e.g. isolated furniture) (Bettencourt and Xu, 2013). Furthermore, both PPA and TOS showed higher responses to holistically processed scene stimuli compared to control stimuli with matched low-level visual features that were not processed holistically (Schindler and Bartels, 2016). If configural/relational processing in general contributes to holistic face processing, these scene-responsive areas may also exhibit neural activity related to holistic processing.

We also localized the object-responsive lateral occipital cortex (LOC) to test whether holistic face processing involves general high-level visual object processing. Finally, we localized a region in the superior parietal lobule (SPL) that is involved in Gestalt grouping and perceptual organization (Grassi et al., 2018, 2016; Zaretskaya et al., 2013) and processing of configural face information (Zachariou et al., 2017). If Gestalt information is important for the perceptual component of holistic processing (Curby and Moerel, 2019; Zhao et al., 2016; Zhao and Bühlhoff, 2017), neural activity in the SPL might contribute to holistic processing of faces during the composite-face task.

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## 2. Materials and methods

### 2.1. Participants

Nineteen participants (13 female, 6 male, 20-39 years old) were included in our fMRI data analyses. Data from three additional participants were excluded prior to the fMRI data analyses, one due to excessive head movement during scanning, two due to poor performance in the behavioural task (less than 65% correct responses on congruent-identity trials, where no illusion is present). All participants provided written informed consent prior to the experiment, and the procedure was approved by the local ethics committee of the University Clinic Tübingen.

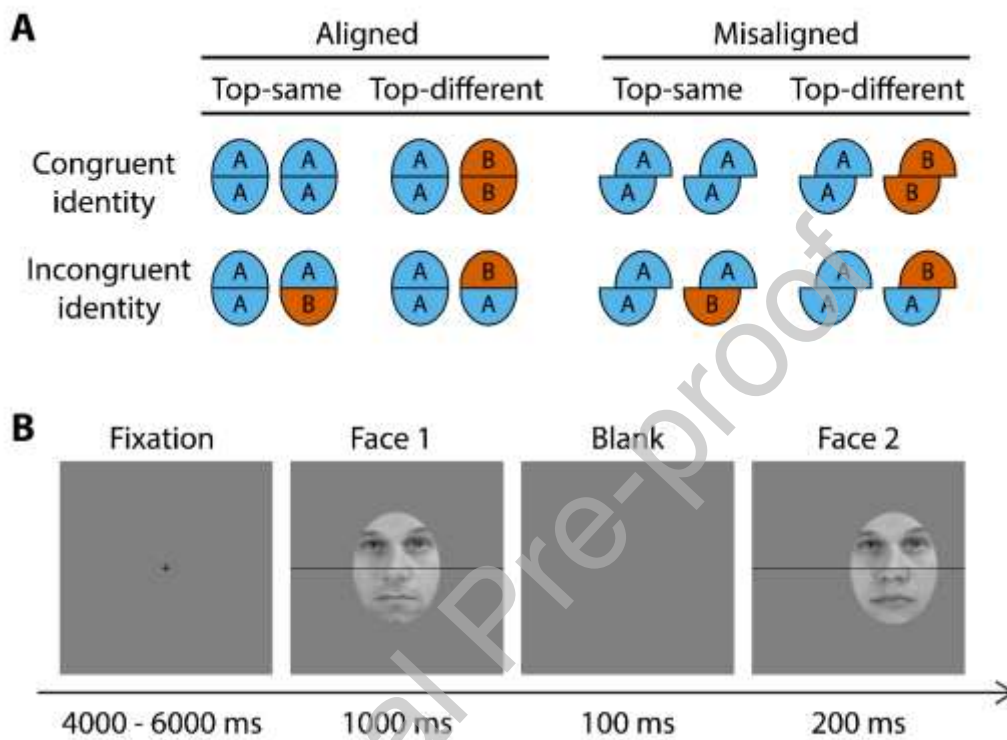
We conducted power analyses using G\*Power3 (Faul et al., 2007) to assess the power of our sample size. For the behaviour measurement of the composite-effect using the complete design, a meta-analysis found an average effect size of  $\eta_p^2 = 0.32$  (Richler and Gauthier, 2014), and a power analysis indicated that a sample size of 15 would be required to detect this effect size at the 0.05 alpha level with 80% power. A previous study investigating the neural mechanisms of holistic processing using the part-whole paradigm found an effect size of  $\eta_p^2 = 0.53$  for a triple-interaction between congruent, face orientation (upright/inverted) and target similarity (same/different) (Goffaux et al., 2013). A power analysis indicated that a sample size of 5 would be required to detect this effect size at the 0.05 alpha level with 80% power.

### 2.2. Stimuli

#### 2.2.1. Main experiment stimuli

The experimental stimuli were created using images of 3D face models from the face database of the Max Planck Institute for Biological Cybernetics (Blanz and Vetter, 1999; Troje and Bühlhoff, 1996). We selected the faces of 12 Caucasian individuals (6 females) and paired each face once with another face of the same sex to make 12 face pairs. Each face was separated into a top and bottom half, and the halves of the pairs were recombined to create composite faces, as illustrated by the 8 conditions in **Fig. 1A**. A horizontal black line (0.03° of visual angle) was shown between the top and bottom halves of each face to clearly separate the two face halves. During the experiment, face stimuli were displayed with a

height of  $3.9^\circ$  and width of  $3.0^\circ$  of visual angle. For misaligned stimuli, the bottom half of the face was shifted  $1.0^\circ$  of visual angle to the left. Faces were grayscale, and were shown in front of a gray background. Stimuli used for the practice trials were created via the same method, using additional faces taken from the database.



**Figure 1.** Experimental conditions and trial outline. (A) Experimental conditions. The conditions consisted of a  $2 \times 2 \times 2$  factorial design, with factors *alignment*, whether the top and bottom halves of the faces were aligned or misaligned, *top-same or top-different*, whether the top halves of the faces were the same or different from each other and *congruency*, whether the bottom half of face 2 was congruent with respect to the top half of face 2 or not (e.g. *congruent-identity* trials are when the bottom-half is the same if the top-half is the same and the bottom-half is different if the top-half is different). (B) Trial outline. Participants fixated for either 4 or 6 s, then viewed a first face, followed by a blank screen and then a second face. Participants then responded during the next fixation whether the top-halves of the two faces were the same or different.

### 2.2.2. Localizer stimuli

The localizer stimuli were grayscale images of faces, objects, scenes and phase-scrambled scenes (9 exemplars per category). Phase-scrambled scenes were Fourier-scrambled versions of the scene images.

## 2.3. Experimental design

Participants lay supine in the scanner and viewed the stimuli on a screen positioned behind their head, via a mirror attached to the head coil. The screen was positioned 82 cm from the participant, and spanned  $28^\circ \times 16^\circ$  of visual angle in horizontal and vertical directions respectively. Stimuli were presented via a projector with resolution 1920x1080. The experiment was programmed with Matlab 2013b using the Psychophysics Toolbox extensions (Brainard, 1997; Kleiner et al., 2007) on a Windows PC.

### 2.3.1. Main experiment procedure

Participants performed a composite face task while their brain activity was recorded using fMRI. On each trial participants viewed two faces and made a judgement whether the top-halves of the faces were the same or different. The experimental design consisted of 8 conditions of a  $2 \times 2 \times 2$  factorial design (see **Fig. 1A**). The factors were *alignment* (whether the bottom halves of the faces were aligned or misaligned with the top halves), *congruency*, (whether the bottom half of the second face was congruent with respect to the top half of the second face or not) and *top-same/top-different* (whether the top halves of the two faces were the same or different from each other). Each participant completed 3 runs, where each run contained 64 trials (8 repetitions per condition). Conditions were presented in a carryover counterbalanced design, such that each condition was preceded by every other condition once per run (Brooks, 2012). This was to avoid biases from carryover blood-oxygen-level dependent (BOLD) activation from a previous condition (Aguirre, 2007).

The trial procedure is illustrated in **Fig. 1B**. Participants viewed a central fixation cross for 4 s or 6 s (50% of trials each, order randomized). The first face was shown centrally on the screen for 1 s, followed by a blank screen (presented for 100 ms), then the second face was shown,  $1.2^\circ$  of visual angle offset to the right of the centre of the screen, for 200 ms. Participants responded using a button press whether they judged the top halves of the two faces to be the same or different. They were instructed to ignore the bottom halves of

the faces and to respond as quickly and accurately as possible. The fingers participants used to respond same/different were counterbalanced across participants.

Participants performed practice trials prior to the experiment to familiarise them with the task. Each participant performed 8 practice trials outside of the MRI scanner and 8 practice trials inside the MRI scanner.

### *2.3.2. Localizer experiment procedure*

Participants completed 2 runs of the localizer experiment, which was used to define face-, scene- and object-responsive ROIs. In each run, participants viewed blocks containing faces, scenes, objects and phase-scrambled scenes. Faces and objects were shown in front of the phase-scrambled scenes to keep the visual field size of the stimuli constant in all blocks (scene images were equal in size to the phase-scrambled scenes). Blocks were presented in a carryover counterbalanced sequence (Brooks, 2012). In each block 8 images were shown, where each image was shown for 1.8 s, followed by a 0.2 s blank, grey screen. Participants performed a one-back task on the images (repetitions once every 9 s on average) to keep their attention to the stimuli.

## **2.4. Imaging parameters**

Images were acquired using a 3T Siemens Prisma scanner with a 64-channel head coil (Siemens, Erlangen, Germany). Functional T2\* echoplanar images (EPI) were acquired using a sequence with the following parameters; multiband acceleration factor 2, TR 1.39 s, TE 30 ms, flip angle 68°, FOV 192x192 mm. Volumes consisted of 42 slices, with an isotropic voxel size of 3x3x3 mm. The first 8 volumes of each run were discarded to allow for equilibration of the T1 signal. For each participant a high-resolution T1-weighted anatomical scan was acquired with the following parameters; TR 2 s, TE 3.06 ms, FOV 232x256 mm, 192 slices, isotropic voxel size of 1x1x1 mm.

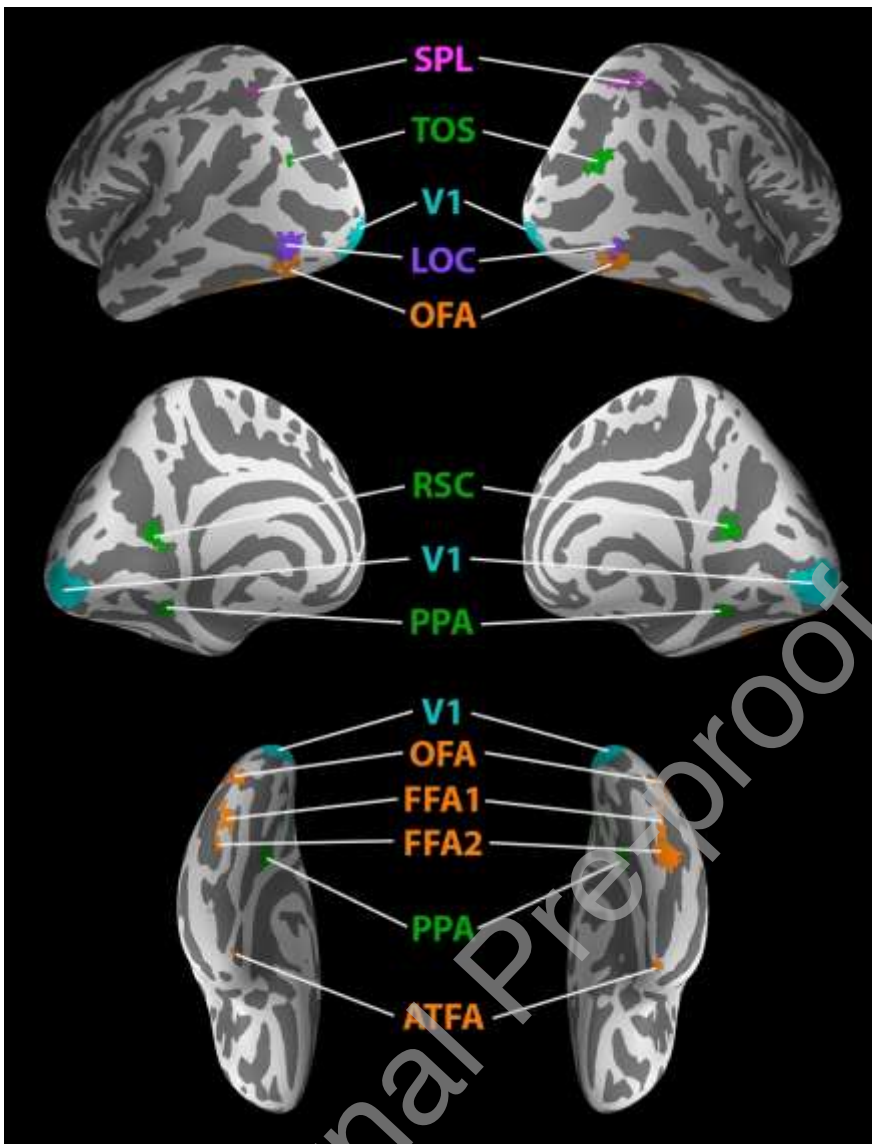
## **2.5. fMRI data preprocessing**

fMRI data was preprocessed with SPM12 (<http://www.fil.ion.ucl.ac.uk/spm/>). Functional images were slice-time corrected, realigned and coregistered to the anatomical image. The images were then normalized to MNI (Montreal Neurological Institute) space and spatially smoothed with a 6 mm full-width at half-maximum Gaussian kernel.

## 2.6. Definition of regions of interest

**Figure 2** illustrates the average locations of our regions of interest (ROIs) and **Table 1** shows the mean MNI coordinates and volumes of each ROI. We defined face-, scene- and object-responsive ROIs using data from the localizer runs. Firstly, the contrast faces > objects and scenes was used to define the OFA, FFA1, FFA2 and ATFA (Gauthier et al., 2000b; Kanwisher et al., 1997; Rajimehr et al., 2009; Tsao et al., 2008). We defined the FFA1 and FFA2 based on functional selectivity and previously described anatomical landmarks (Weiner et al., 2016, 2014). Secondly, the contrast scenes > faces and objects was used to define the TOS, RSC and PPA (Epstein and Kanwisher, 1998; Grill-Spector, 2003; Maguire, 2001). Thirdly, the contrast objects > phase-scrambled scenes was used to define the LOC (Malach et al., 1995). We defined each ROI individually in each participant, by selecting all active voxels falling within spheres (radius 6 mm) centred on the peak of activity in each hemisphere. A threshold of  $p < 0.001$  uncorrected was used to define active voxels. This threshold allowed ROIs to be consistently defined across participants.

We additionally defined SPL and V1, based on anatomical location and higher activity during stimulus presentation (including all conditions) compared to the fixation interval between trials. This contrast is orthogonal to the activity differences between the conditions in this study (Friston et al., 2006). We used a  $p < 0.05$  familywise error rate (FWE) corrected threshold to define voxels more active during the stimulus than fixation. A more stringent threshold was used for this contrast as all participants showed strong activation in this contrast. SPL was defined by selecting all active voxels falling within spheres (radius 6 mm) centred on the peak of activity in superior parietal cortex of each hemisphere. The entire V1 was defined first for each participant using anatomical labels generated by Freesurfer (Hinds et al., 2009) (<https://surfer.nmr.mgh.harvard.edu/>). To define our final V1 ROI, we selected all posterior V1 voxels that were more active when participants viewed the pairs of face stimuli as compared to when they fixated and viewed a grey screen. Participants could move their eyes when viewing the faces, therefore this V1 ROI reflects the V1 voxels activated for each individual participant when viewing the face stimuli.



**Figure 2.** Locations of ROIs. ROIs include face-responsive OFA (occipital face area), FFA1 (fusiform face area 1), FFA2 (fusiform face area 2) and ATFA (anterior temporal face area) shown in orange, scene-responsive TOS (transverse occipital sulcus), RSC (retrosplenial cortex) and PPA (parahippocampal place area) shown in green, object-responsive LOC (lateral occipital complex) shown in purple, parietal SPL (superior parietal lobule) shown in magenta and V1 shown in cyan. ROIs were defined individually in volume-space for each participant, for visualisation purposes here we show group average ROIs projected onto the inflated cortical surface. We defined group ROIs using a relatively low threshold as some information was lost during projection to the cortical surface. Thus, to create this figure, voxels were included in each group average ROI if they were part of the ROI in at least 25% of participants.

**Table 1. ROI locations and volumes**

Average x, y and z coordinates (in MNI space) and volume of each ROI ( $\pm$  standard deviations). The volume indicates the number of active voxels that were included in each ROI. N indicates the number of participants each ROI was identified in.

ROI	hem	x	y	z	Volume (mm <sup>3</sup> )	N
OFA	left	-39 $\pm$ 4.6	-81 $\pm$ 4.3	-10 $\pm$ 4.0	197 $\pm$ 42.4	19
	right	42 $\pm$ 4.1	-79 $\pm$ 4.3	-10 $\pm$ 4.0	208 $\pm$ 34.3	19
FFA1	left	-40 $\pm$ 4.1	-62 $\pm$ 8.8	-17 $\pm$ 4.0	202 $\pm$ 35.6	18
	right	42 $\pm$ 5.1	-63 $\pm$ 6.6	-16 $\pm$ 4.1	204 $\pm$ 44.8	18
FFA2	left	-41 $\pm$ 4.0	-43 $\pm$ 10.2	-21 $\pm$ 5.3	157 $\pm$ 61.4	16
	right	42 $\pm$ 3.4	-44 $\pm$ 5.5	-19 $\pm$ 3.6	205 $\pm$ 36.5	17
ATFA	left	-35 $\pm$ 5.3	-8 $\pm$ 5.2	-34 $\pm$ 6.0	86 $\pm$ 67.4	14
	right	34 $\pm$ 3.6	-5 $\pm$ 4.9	-38 $\pm$ 4.8	134 $\pm$ 60.7	16
TOS	left	-32 $\pm$ 5.7	-85 $\pm$ 4.9	22 $\pm$ 7.0	203 $\pm$ 35.5	19
	right	37 $\pm$ 4.1	-80 $\pm$ 2.9	21 $\pm$ 7.4	213 $\pm$ 22.1	19
RSC	left	-17 $\pm$ 3.2	-59 $\pm$ 3.3	14 $\pm$ 3.6	184 $\pm$ 48.3	18
	right	19 $\pm$ 3.0	-57 $\pm$ 4.8	17 $\pm$ 4.9	198 $\pm$ 54.1	18
PPA	left	-26 $\pm$ 2.8	-44 $\pm$ 3.9	-10 $\pm$ 3.4	197 $\pm$ 52.9	19
	right	29 $\pm$ 2.6	-45 $\pm$ 5.5	-10 $\pm$ 3.3	212 $\pm$ 19.4	19
LOC	left	-43 $\pm$ 4.1	-79 $\pm$ 4.3	-4 $\pm$ 4.6	222 $\pm$ 13.6	19
	right	43 $\pm$ 3.8	-80 $\pm$ 5.1	-4 $\pm$ 6.0	214 $\pm$ 25.6	19
SPL	left	-26 $\pm$ 4.7	-60 $\pm$ 6.8	50 $\pm$ 6.1	206 $\pm$ 49.2	19
	right	28 $\pm$ 4.9	-56 $\pm$ 6.7	50 $\pm$ 5.9	213 $\pm$ 49.8	19
V1	left	-13 $\pm$ 3.2	-98 $\pm$ 2.7	-7 $\pm$ 4.0	911 $\pm$ 380.6	19
	right	13 $\pm$ 3.2	-96 $\pm$ 1.6	-4 $\pm$ 4.1	911 $\pm$ 211.5	19

## 2.7. Statistical Analyses

### 2.7.1. Behavioural analyses

Participants were instructed to respond to indicate whether they judged the top-halves of the face pairs to be the same or different. Their behavioural performance was measured with accuracy (% correct) and reaction times. For each behavioural measure we first performed a 2 (alignment) x 2 (congruency) x 2 (top-same/top-different) repeated measures ANOVA. We then performed separated 2 (alignment) x 2 (congruency) ANOVAs for the top-same and top-different conditions to investigate whether they both showed patterns of behavioural responses consistent with holistic processing. We separately analysed the top-same and top-different conditions for the following reasons. Firstly, while behavioural studies usually combine the top-same and top-different conditions with a measure of accuracy or  $d'$  prime (in signal detection theory), neural responses to these two conditions cannot be combined in the same way as there is no neural equivalent of hit rates and false-alarm rates. Secondly, how the two conditions contribute to a reliable measure of holistic processing remains in debate (e.g. Richler and Gauthier, 2014; Rossion, 2013). Separate analysis of these two conditions in both behaviour and neural responses may help clarify their roles in measuring holistic processing. Finally, previous studies have suggested that holistic processing is stronger for top-same than top-different conditions (Goffaux, 2012; Goffaux et al., 2013).

According to previous behavioural studies (e.g. Richler et al., 2011a; Zhao et al., 2016), holistic face processing should lead to an interaction effect between congruency and alignment and an effect of congruency. Specifically, the difference between the congruent-identity and incongruent-identity conditions should be larger for the aligned conditions compared to the misaligned conditions. The rationale is the following. For accuracy, a lower performance is expected in aligned incongruent-identity conditions compared to aligned congruent-identity conditions, due to participants being unable to ignore the irrelevant bottom face half information. This difference should be reduced in the misaligned conditions, which disrupt holistic face processing and enable participants to ignore the bottom face half information. For reaction times, a longer reaction time is expected for aligned incongruent-identity conditions compared to aligned congruent-identity conditions, because participants take the irrelevant bottom face half into consideration and therefore



this interferes with their decision for the top half of the face. Again, this difference should be reduced in the misaligned conditions that disrupt holistic processing. Therefore, we first looked at the interaction between alignment and congruency and, in any cases where we found a significant interaction, we performed follow-up *t*-tests to examine whether the pattern of behavioural performance matched the above predictions.

### 2.7.2. fMRI analyses

We modelled a GLM for each participant containing regressors for our 8 conditions, plus 6 realignment regressors from the motion correction, using SPM12. The 8 condition regressors modelled the activity to each trial of the condition, excluding any trials where the participant did not make a task response (i.e. did not press a button to indicate a same/different judgment of the faces, on average 1.8% of trials). Responses to each condition are reported in % signal change with respect to the baseline of the GLM in each ROI. Similarly to the behavioural analysis mentioned above, we performed a 2 (alignment) x 2 (congruency) x 2 (top-same/top-different) repeated measures ANOVA to investigate whether top-same and top different conditions elicit different patterns of response in our ROIs. We then performed two further analyses to investigate specific aspects of composite-face effect.

Firstly, we investigated the effect of alignment. Although behavioural studies often use the interaction between congruency and alignment (i.e. the composite face effect) to measure holistic processing, brain regions involved in holistic face processing may also exhibit in different neural responses to aligned and misaligned faces. This is because, regardless of the congruency manipulation in the composite task, aligned faces are considered to be processed holistically (which is why participants are unable to ignore the to-be-ignored parts in the incongruent aligned condition), whereas misaligned faces are considered to be processed less holistically (Rossion, 2013; Young et al., 1987)<sup>1</sup>. Therefore, we considered that brain regions involved in holistic processing of faces would show differences in activity between aligned and misaligned conditions. We performed 2 (alignment) x 2 (top-same/top-different) repeated measures ANOVAs using only congruent-identity conditions, as the incongruent-identity conditions contain additional change in face

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<sup>1</sup> We thank Dr. Isabel Gauthier for pointing this out in our data analysis.

identity (induced by the composite-face illusion) that differs between aligned and misaligned conditions.

Secondly, we investigated whether any brain regions show a pattern of neural responses consistent with the pattern observed in behaviour. While the aforementioned alignment effect is indicative of holistic face processing, it does not reveal a full picture of neural processes underlying the composite face effect, as the characteristic behaviour is driven by differences in the perception of face identity. We hypothesized that any brain regions that represented face identity in a holistic manner, would show a pattern of repetition-effect responses consistent with the behavioural composite effect (i.e. a larger difference in neural responses between congruent- and incongruent-identity conditions for the aligned than for the misaligned conditions). We predicted we would be likely to find a repetition suppression effect, as this was found in previous studies investigating the neural responses to composite faces (Schiltz et al., 2010; Schiltz and Rossion, 2006), however, we also considered it possible that we could find a repetition enhancement effect, as several studies have found repetition-effects in this direction (Segaert et al., 2013). We performed 2 (alignment) x 2 (congruency) repeated measures ANOVAs to test for neural composite effects. Similarly to our behavioural analysis, we conducted follow-up *t*-tests for any regions showing a significant congruency by alignment interaction. We performed this analysis separately for top-same and top-different conditions, which allowed us to investigate whether the neural and behavioural patterns of responses correspond with each other and whether the composite face effect is more prominent for top-same than top-different conditions (Goffaux, 2012; Goffaux et al., 2013).

We performed all fMRI analyses in our ten ROIs as well as in whole-brain analyses. For ROI analyses, we corrected for multiple comparisons using a Bonferroni-correction to adjust for the number of ROIs tested. For whole-brain analyses, we used a False Discovery Rate (FDR) correction to adjust for multiple comparisons.

### *2.7.3. Analyses linking behaviour and neural activity*

We performed follow-up analyses comparing any effects identified related to participants' behaviour in the composite paradigm in neural and behavioural responses. We performed Pearson's correlation analyses between significant top-same or top-different behavioural composite-effects and corresponding significant top-same or top-different

neural composite-effects in our ROIs. We performed these analyses only in cases where there was a corresponding behavioural and neural top-same or top-different composite-effect, as our aim was to assess whether there was a link between the strength of each participant's behavioural and neural composite-effects. We corrected for multiple comparisons using a Bonferroni-correction to adjust for the number of ROIs tested.

## **2.8. Data and code availability statement**

Data cannot be shared as participants were informed that their data would be stored confidentially, in accordance with the rules of the local ethics committee. Code is available on request.

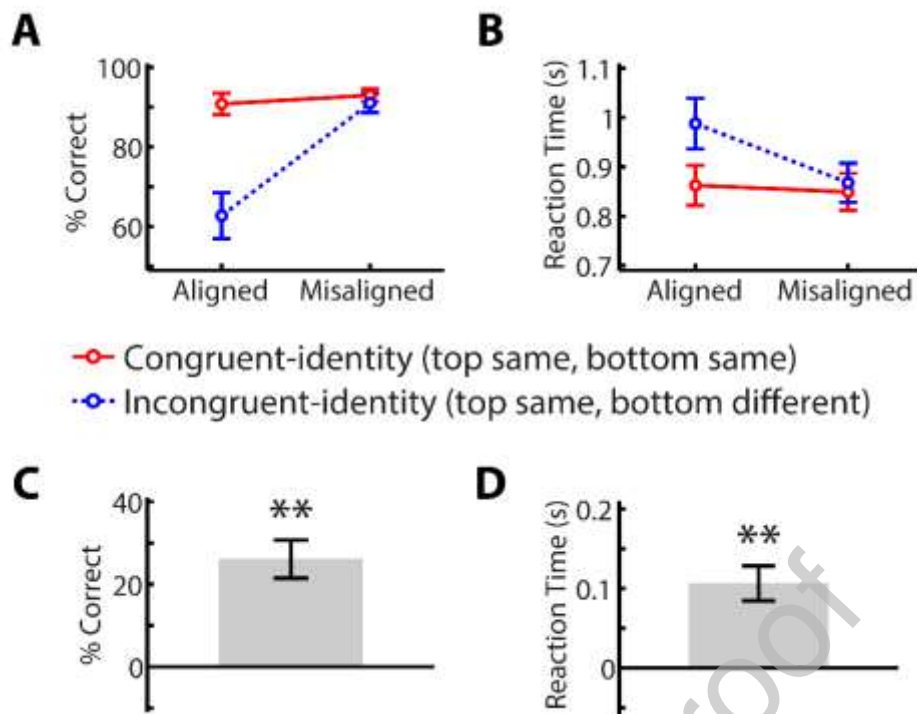
### 3. Results

#### 3.1. Behavioural results

We measured participants' behavioural performance in the composite-face task during scanning using accuracy (% correct) and reaction times. For both behavioural measures 2 x 2 x 2 repeated-measures ANOVAs showed a significant interaction between alignment, congruency and top-same/top-different conditions (accuracy:  $F_{1,18} = 24.24$ ,  $p = 1.1 \times 10^{-4}$ ,  $\eta_p^2 = 0.57$ ; reaction times:  $F_{1,18} = 8.92$ ,  $p = 0.0079$ ,  $\eta_p^2 = 0.33$ ). Note that the same results were observed when participants' performance was measured using  $d'$  prime (see supplemental results). We then conducted further behavioural analyses separately for top-same and top-different conditions.

##### 3.1.1. Accuracy and reaction times for top-same conditions

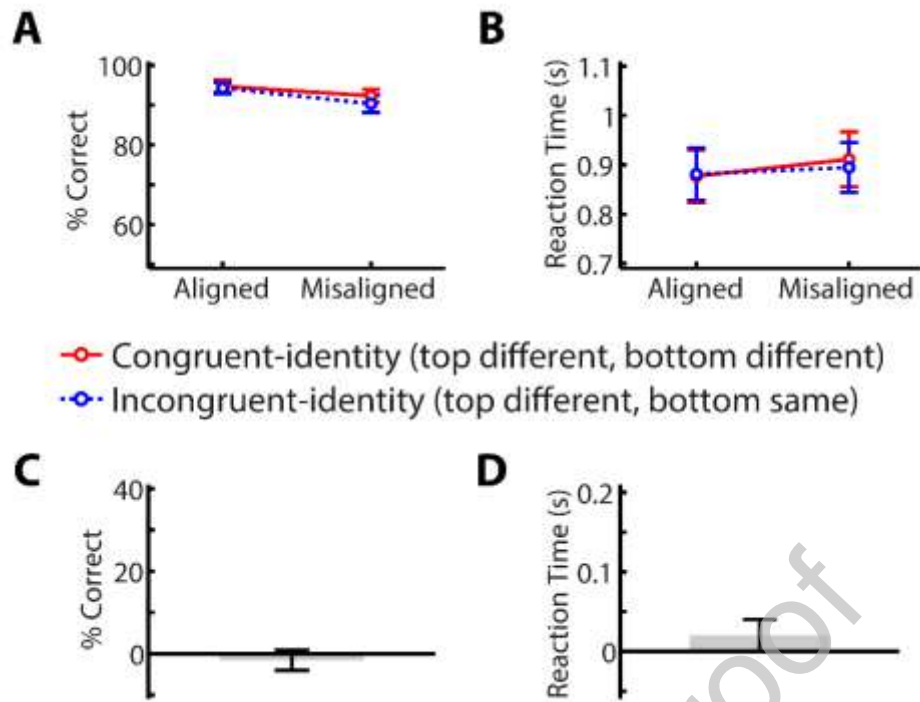
For both accuracy (% correct) and reaction times for the top-same conditions (**Figure 3**), 2 (alignment) x 2 (congruency) repeated-measures ANOVAs revealed a significant effect of congruency (accuracy:  $F_{1,18} = 23.67$ ,  $p = 1.2 \times 10^{-4}$ ,  $\eta_p^2 = 0.57$ ; reaction times:  $F_{1,18} = 15.08$ ,  $p = 0.0011$ ,  $\eta_p^2 = 0.46$ ) and a significant interaction between congruency and alignment (accuracy:  $F_{1,18} = 32.12$ ,  $p = 2.2 \times 10^{-5}$ ,  $\eta_p^2 = 0.64$ ; reaction times:  $F_{1,18} = 23.44$ ,  $p = 1.3 \times 10^{-4}$ ,  $\eta_p^2 = 0.57$ ). Furthermore, paired-sample  $t$ -tests showed that the congruency effect was significant for the aligned conditions (accuracy:  $M = 28.07\%$ ,  $SE = 5.04\%$ ;  $t_{18} = 5.57$ ,  $p = 2.7 \times 10^{-5}$ , Cohen's  $d_z = 1.28$ ; reaction times:  $M = 0.13$  s,  $SE = 0.023$  s;  $t_{18} = 5.51$ ,  $p = 3.1 \times 10^{-5}$ , Cohen's  $d_z = 1.26$ ) but not for the misaligned conditions (accuracy:  $M = 1.97\%$ ,  $SE = 2.07\%$ ;  $t_{18} = 0.95$ ,  $p = 0.35$ , Cohen's  $d_z = 0.22$ ; reaction times:  $M = 0.019$  s,  $SE = 0.020$  s;  $t_{18} = 0.92$ ,  $p = 0.37$ , Cohen's  $d_z = 0.21$ ). These results show characteristic evidence of holistic processing elicited by the top-same conditions in our composite-task.



**Figure 3.** Behavioural performance in the top-same conditions of the composite-face task. (A) shows accuracy (% correct) as a function of congruency and alignment and (B) shows reaction times as a function of congruency and alignment. (C) and (D) show the interaction effect between congruency and alignment (difference between aligned congruent-identity and incongruent-identity conditions, minus the difference between misaligned congruent-identity and incongruent-identity conditions) as measured with accuracy (C) and reaction times (D). Error bars indicate  $\pm 1$  SEM. \*\* indicates  $p < 0.001$ .

### 3.1.2. Accuracy and reaction times for top-different conditions

Accuracy (% correct) and reaction times for the top-different conditions showed a different pattern of responses (**Figure 4**). 2 (alignment) x 2 (congruency) repeated-measures ANOVAs showed neither a significant effect of congruency (accuracy:  $F_{1,18} = 1.35$ ,  $p = 0.26$ ,  $\eta_p^2 = 0.070$ ; reaction times:  $F_{1,18} = 0.25$ ,  $p = 0.63$ ,  $\eta_p^2 = 0.014$ ) nor a significant interaction between congruency and alignment (accuracy:  $F_{1,18} = 0.39$ ,  $p = 0.54$ ,  $\eta_p^2 = 0.021$ ; reaction times:  $F_{1,18} = 1.03$ ,  $p = 0.32$ ,  $\eta_p^2 = 0.054$ ). Thus, the composite face effect seems to be primarily driven by the top-same conditions rather than the top-different conditions.



**Figure 4.** Behavioural performance in the top-different conditions of the composite-face task. (A) shows accuracy (% correct) as a function of congruency and alignment and (B) shows reaction times as a function of congruency and alignment. (C) and (D) show the interaction effect between congruency and alignment (difference between aligned congruent-identity and incongruent-identity conditions, minus the difference between misaligned congruent-identity and incongruent-identity conditions) as measured with accuracy (C) and reaction times (D). Error bars indicate  $\pm 1$  SEM.

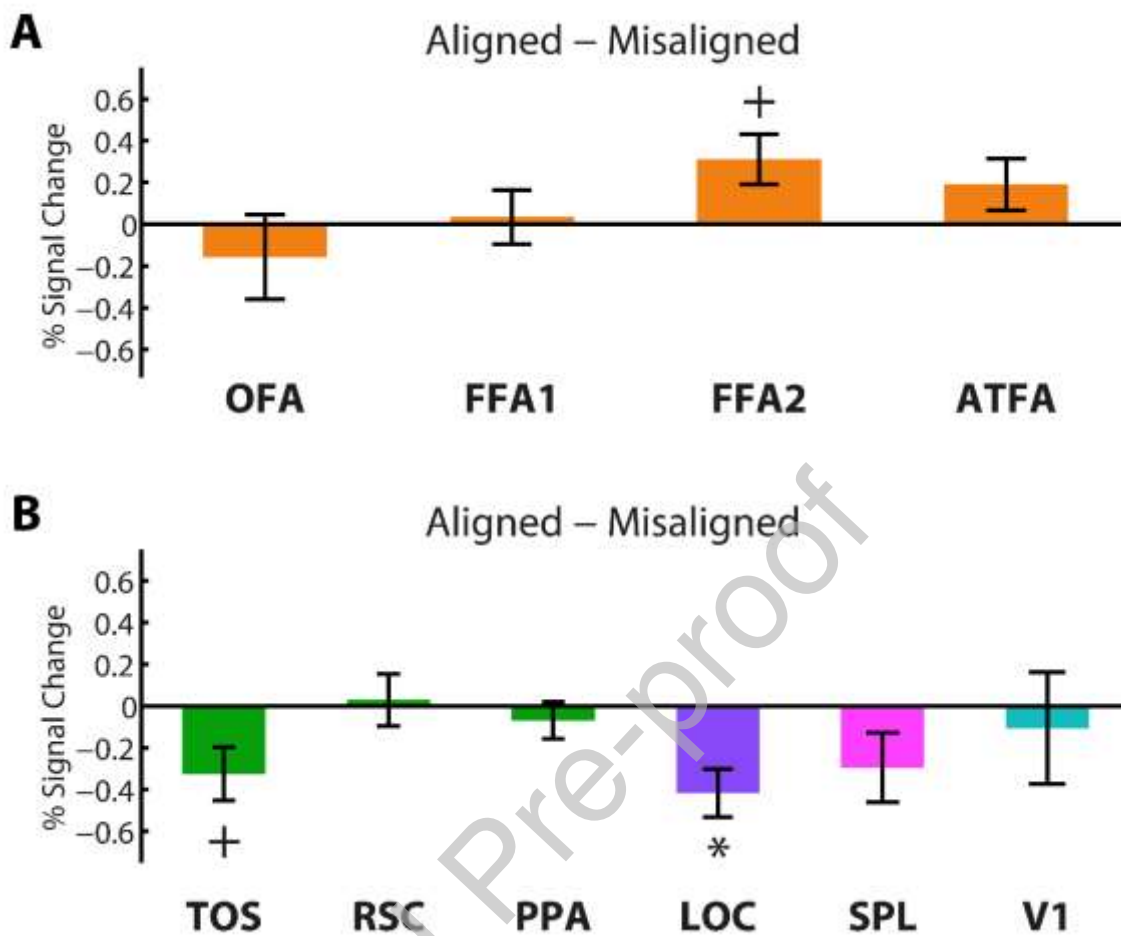
### 3.2. fMRI results

We first performed 2 (alignment) X 2 (congruency) X 2 (top-same/top-different) repeated measures ANOVAs in each ROI. The RSC showed a triple interaction ( $F_{1,17} = 8.66$ ,  $p = 0.0091$ ,  $\eta_p^2 = 0.34$ ) which did not survive Bonferroni-correction for  $N = 10$  ROIs. None of the other ROIs tested showed a significant triple interaction (OFA:  $F_{1,18} = 0.55$ ,  $p = 0.47$ ,  $\eta_p^2 = 0.030$ ; FFA1:  $F_{1,17} = 0.46$ ,  $p = 0.51$ ,  $\eta_p^2 = 0.027$ ; FFA2:  $F_{1,16} = 0.25$ ,  $p = 0.62$ ,  $\eta_p^2 = 0.015$ ; ATFA:  $F_{1,16} = 2.31$ ,  $p = 0.15$ ,  $\eta_p^2 = 0.13$ ; TOS:  $F_{1,18} = 0.85$ ,  $p = 0.37$ ,  $\eta_p^2 = 0.045$ ; PPA:  $F_{1,18} = 2.63$ ,  $p = 0.12$ ,  $\eta_p^2 = 0.13$ ; LOC:  $F_{1,18} = 0.86$ ,  $p = 0.37$ ,  $\eta_p^2 = 0.046$ ; SPL:  $F_{1,18} = 0.41$ ,  $p = 0.53$ ,  $\eta_p^2 = 0.022$ ; V1:  $F_{1,18} = 0.12$ ,  $p = 0.73$ ,  $\eta_p^2 = 0.0065$ ). These results suggest that our manipulation of congruency and alignment may similarly affect the neural responses to the top-same and top-different conditions (cf. Goffaux, 2012; Goffaux et al., 2013).

As outlined earlier (Section 2.7.2), we performed two further tests to specifically examine the effect of alignment (which investigates the neural processes supporting holistic processing of faces) and the interaction between alignment and congruency (which helps reveal holistic responses to face identity, which underly the composite face effect). To compare the neural responses to aligned and misaligned faces, we included only the congruent-identity conditions (i.e. where top and bottom halves of the face pairs are both the same or both different) to ensure that there is no change in the perception of face identity between the aligned and misaligned conditions. To test whether any brain regions exhibit a neural composite face effect (i.e. interaction between alignment and congruency) consistent with participants' behavioural responses, we performed separate 2 (alignment) X 2 (congruency) repeated measures ANOVAs for top-same and top-different conditions.

#### 3.2.1. Neural responses to face alignment within and outside of face-responsive ROIs

For face-responsive ROIs (**Fig. 5A**), 2 (alignment) x 2 (top-same/top-different) repeated measures ANOVAs revealed an effect of alignment in the FFA2 ( $F_{1,16} = 6.72$ ,  $p = 0.020$ ,  $\eta_p^2 = 0.30$ ), which was driven by higher responses to aligned than misaligned faces ( $M = 0.31\%$ ,  $SE = 0.12\%$ ), but did not survive Bonferroni-correction for  $N = 10$  ROIs. We found no difference in the responses to aligned and misaligned faces in any of the other face-responsive ROIs (OFA:  $F_{1,18} = 0.60$ ,  $p = 0.45$ ,  $\eta_p^2 = 0.032$ ; FFA1:  $F_{1,17} = 0.071$ ,  $p = 0.79$ ,  $\eta_p^2 = 0.0042$ ; ATFA:  $F_{1,16} = 2.33$ ,  $p = 0.15$ ,  $\eta_p^2 = 0.13$ ).



**Figure 5.** Differences in neural responses to aligned and misaligned faces for the congruent-identity conditions (i.e. where top and bottom halves of the face pairs were both the same or both different). We used the contrast aligned minus misaligned faces to investigate differences in neural activity in face-responsive ROIs (A) and in all other ROIs tested (B). Error bars indicate  $\pm 1$  SEM. \* indicates  $p < 0.05$  Bonferroni-corrected for  $N = 10$  ROIs, + indicates  $p < 0.05$  uncorrected.

For other ROIs (scene-responsive, object-responsive, parietal and early-visual ROIs, **Fig. 5B**), we found a significant effect of alignment in the LOC ( $F_{1,18} = 12.85$ ,  $p = 0.0021$ ,  $\eta_p^2 = 0.42$ ) and an effect of alignment in the TOS ( $F_{1,18} = 6.43$ ,  $p = 0.021$ ,  $\eta_p^2 = 0.26$ ), but the effect in TOS did not survive Bonferroni-correction for  $N = 10$  ROIs. Note that both LOC and TOS showed higher responses to misaligned faces than to aligned faces (LOC:  $M = -0.42\%$ ,  $SE =$



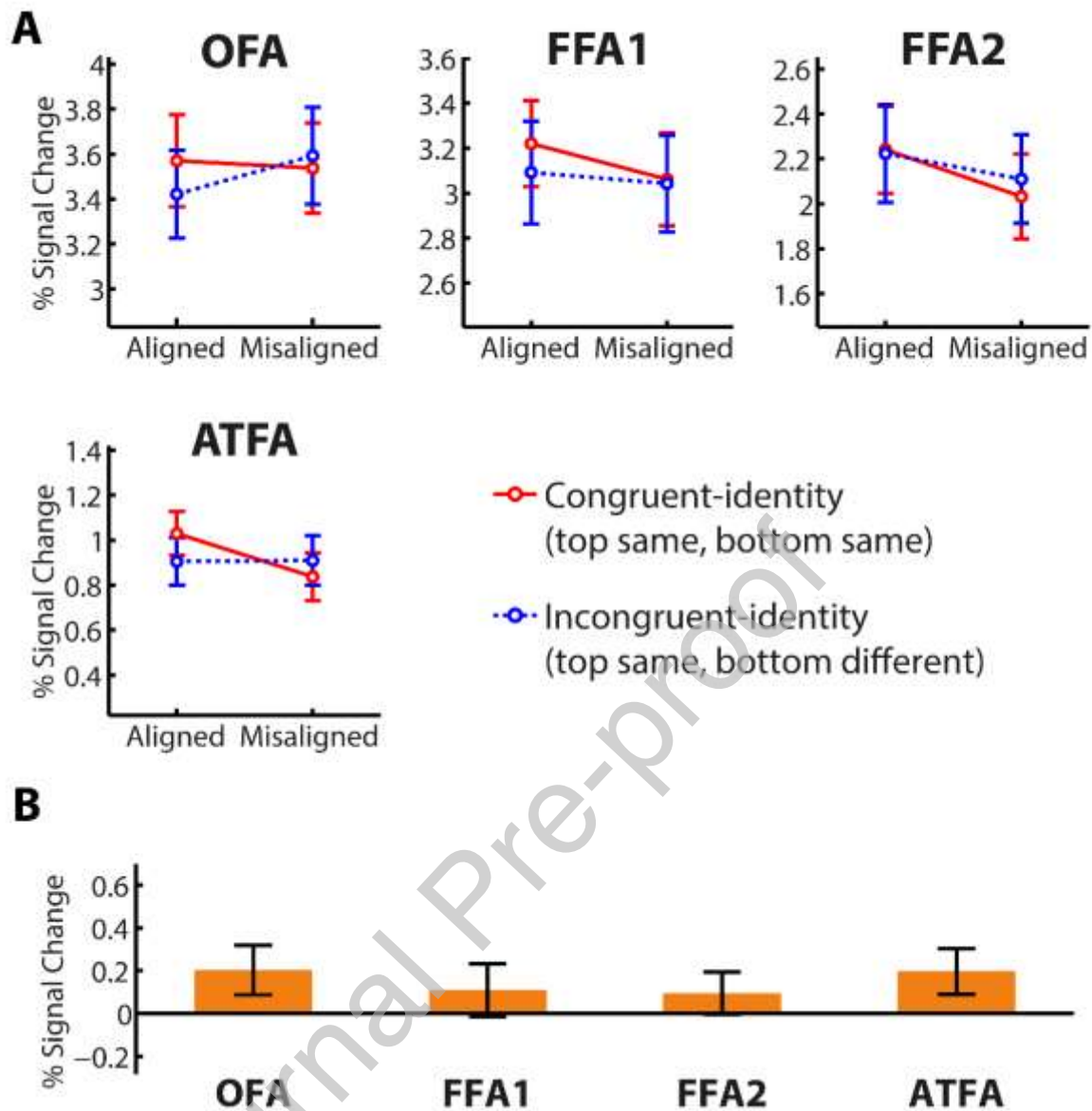
0.12 %; TOS:  $M = -0.32 \%$ ,  $SE = 0.13 \%$ ). None of the other ROIs tested showed significant differences in responses between aligned and misaligned faces (RSC:  $F_{1,17} = 0.055$ ,  $p = 0.82$ ,  $\eta_p^2 = 0.0032$ ; PPA:  $F_{1,18} = 0.59$ ,  $p = 0.45$ ,  $\eta_p^2 = 0.032$ ; SPL:  $F_{1,18} = 3.14$ ,  $p = 0.093$ ,  $\eta_p^2 = 0.15$ ; V1:  $F_{1,18} = 0.16$ ,  $p = 0.70$ ,  $\eta_p^2 = 0.0086$ ).

To confirm that there were significant differences in the alignment effect across ROIs, we performed a 2 (alignment) x 2 (top-same/top-different) x 10 (ROI) repeated measures ANOVA. This analysis showed there was a significant interaction between alignment and ROI ( $F_{9,117} = 34.7$ ,  $p = 4.5 \times 10^{-29}$ ,  $\eta_p^2 = 0.73$ ) indicating that the alignment effect varied significantly across ROIs. Furthermore, we investigated if there were any differences in the effect of alignment across hemisphere in the LOC, FFA2 or TOS by separating each ROI by hemisphere and performing 2 (alignment) x 2 (top-same/top-different) x 2 (hemisphere) repeated measures ANOVAs in each ROI. We did not identify any significant interactions between alignment and hemisphere (LOC:  $F_{1,18} = 1.88$ ,  $p = 0.19$ ,  $\eta_p^2 = 0.095$ ; FFA2:  $F_{1,15} = 2.47$ ,  $p = 0.14$ ,  $\eta_p^2 = 0.14$ ; TOS:  $F_{1,18} = 0.034$ ,  $p = 0.86$ ,  $\eta_p^2 = 0.0019$ ).

We additionally performed a whole-brain analysis to investigate if any other brain regions showed differences in activity between the aligned and misaligned congruent-identity conditions. We did not identify any regions in this whole-brain analysis.

### 3.2.2. Neural composite face effect (congruency x alignment interaction) for top-same conditions

For the face-responsive ROIs (**Fig. 6**), 2 (congruency) x 2 (alignment) repeated measures ANOVAs showed neither significant interactions between congruency and alignment (OFA:  $F_{1,18} = 3.07$ ,  $p = 0.097$ ,  $\eta_p^2 = 0.15$ ; FFA1:  $F_{1,17} = 0.79$ ,  $p = 0.39$ ,  $\eta_p^2 = 0.044$ ; FFA2:  $F_{1,16} = 0.91$ ,  $p = 0.35$ ,  $\eta_p^2 = 0.054$ ; ATFA:  $F_{1,16} = 3.35$ ,  $p = 0.086$ ,  $\eta_p^2 = 0.17$ ) nor significant effects of congruency (OFA:  $F_{1,18} = 0.35$ ,  $p = 0.56$ ,  $\eta_p^2 = 0.019$ ; FFA1:  $F_{1,17} = 2.54$ ,  $p = 0.13$ ,  $\eta_p^2 = 0.13$ ; FFA2:  $F_{1,16} = 0.23$ ,  $p = 0.63$ ,  $\eta_p^2 = 0.015$ ; ATFA:  $F_{1,16} = 0.40$ ,  $p = 0.53$ ,  $\eta_p^2 = 0.025$ ). Thus, no face-responsive ROIs exhibited a neural composite face effect, despite participants showing a robust behavioural composite face effect.



**Figure 6.** Neural responses to the top-same conditions in the face-responsive ROIs. (A) % signal change as a function of congruency and alignment. (B) Interaction between congruency and alignment with the contrast:  $(aligned\ congruent-identity - aligned\ incongruent-identity) - (misaligned\ congruent-identity - misaligned\ incongruent-identity)$ . Error bars indicate  $\pm 1\ SEM$ .

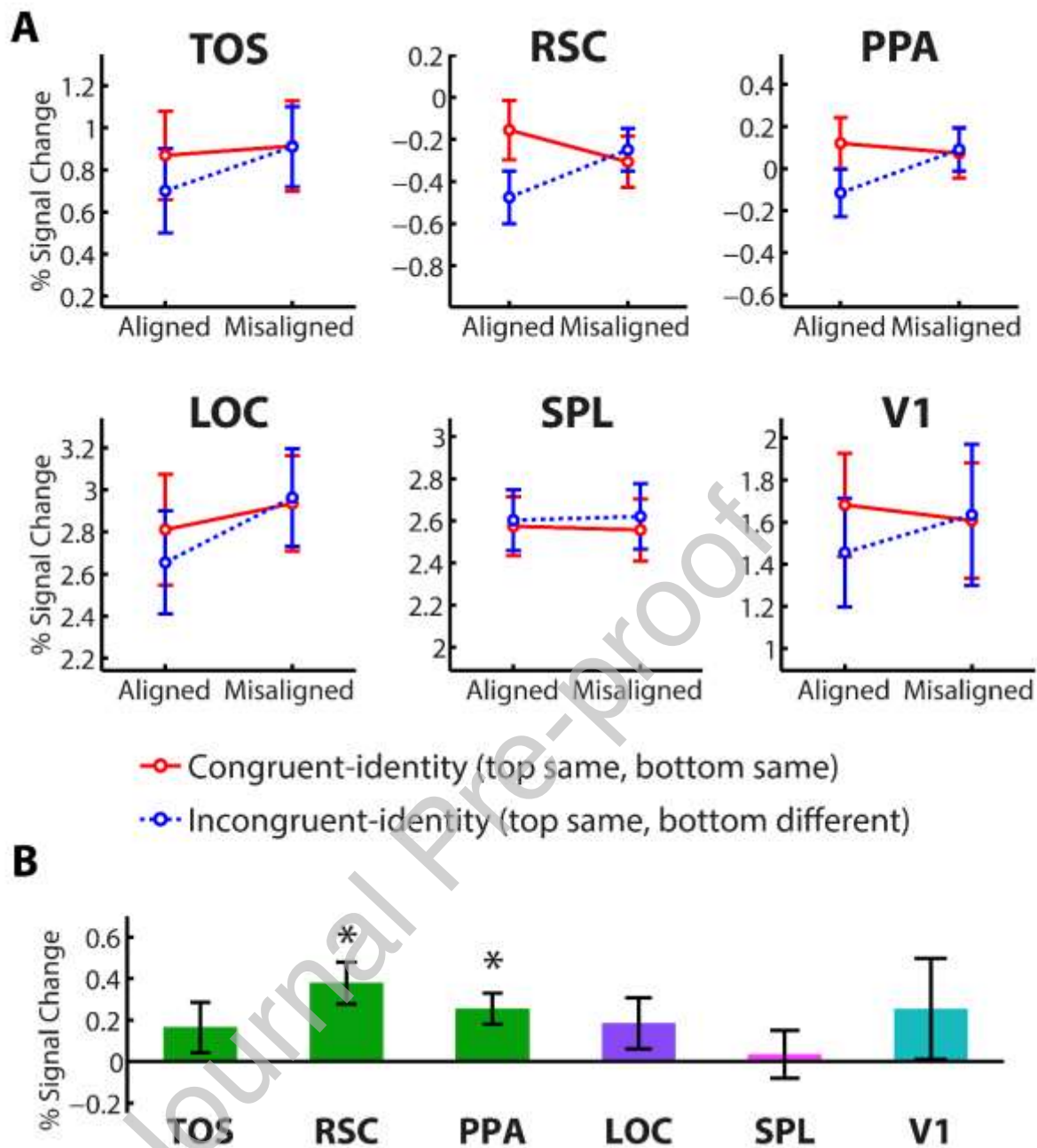
For other ROIs, including scene-responsive, object-responsive, parietal and early-visual ROIs (**Fig. 7**), we found a significant interaction between congruency and alignment in the scene-responsive RSC ( $F_{1,17} = 14.07$ ,  $p = 0.0016$ ,  $\eta_p^2 = 0.45$ ) and PPA ( $F_{1,18} = 11.58$ ,  $p = 0.0032$ ,  $\eta_p^2 = 0.39$ ), both surviving Bonferroni-correction for  $N = 10$  ROIs. Follow-up paired  $t$ -tests showed a significant effect of congruency for the aligned conditions in both RSC ( $M = 0.32\%$ ,  $SE = 0.082\%$ ;  $t_{17} = 3.91$ ,  $p = 0.0011$ , Cohen's  $d_z = 0.92$ ) and PPA ( $M = 0.24\%$ ,  $SE = 0.061\%$ ;  $t_{18} = 3.87$ ,  $p = 0.0011$ , Cohen's  $d_z = 0.89$ ), but not for the misaligned conditions in RSC ( $M = -0.058\%$ ,  $SE = 0.090\%$ ;  $t_{17} = -0.64$ ,  $p = 0.53$ , Cohen's  $d_z = -0.15$ ) and PPA ( $M = -0.018\%$ ,  $SE = 0.067\%$ ;  $t_{18} = -0.27$ ,  $p = 0.79$ , Cohen's  $d_z = -0.063$ ). These results confirm that the interaction observed in RSC and PPA was due to a larger congruency effect for aligned conditions than for misaligned conditions, consistent with the behavioural composite face effect induced by holistic processing. We did not find a significant interaction between congruency and alignment in the scene-responsive TOS ( $F_{1,18} = 1.85$ ,  $p = 0.19$ ,  $\eta_p^2 = 0.093$ ). We did not find a significant effect of congruency in any of these scene-responsive ROIs (RSC:  $F_{1,17} = 3.55$ ,  $p = 0.077$ ,  $\eta_p^2 = 0.17$ ; PPA:  $F_{1,18} = 4.33$ ,  $p = 0.052$ ,  $\eta_p^2 = 0.19$ ; TOS:  $F_{1,18} = 3.98$ ,  $p = 0.061$ ,  $\eta_p^2 = 0.18$ ).

None of the other ROIs we tested showed a significant interaction between congruency and alignment (LOC:  $F_{1,18} = 2.23$ ,  $p = 0.15$ ,  $\eta_p^2 = 0.11$ ; SPL:  $F_{1,18} = 0.095$ ,  $p = 0.76$ ,  $\eta_p^2 = 0.0052$ ; V1:  $F_{1,18} = 1.09$ ,  $p = 0.31$ ,  $\eta_p^2 = 0.057$ ) or a significant effect of congruency (LOC:  $F_{1,18} = 1.91$ ,  $p = 0.18$ ,  $\eta_p^2 = 0.096$ ; SPL:  $F_{1,18} = 1.42$ ,  $p = 0.25$ ,  $\eta_p^2 = 0.073$ ; V1:  $F_{1,18} = 0.52$ ,  $p = 0.48$ ,  $\eta_p^2 = 0.028$ ). We additionally performed a whole-brain analysis to look if any other regions showed an interaction between congruency and alignment or effect of congruency, but we did not identify any regions in this analysis.

To confirm that there were significant differences in the congruency by alignment interaction across ROIs, we performed a 2 (congruency) x 2 (alignment) x 10 (ROI) repeated measures ANOVA. This analysis showed there was a significant triple interaction between congruency, alignment and ROI ( $F_{9,117} = 35.1$ ,  $p = 2.9 \times 10^{-29}$ ,  $\eta_p^2 = 0.73$ ) indicating that the congruency by alignment interaction varied significantly across ROIs. Furthermore, we also investigated if there were any differences in the congruency by alignment interaction across hemisphere in the RSC or PPA by separating both ROIs by hemisphere, and then performing 2 (congruency) x 2 (alignment) x 2 (hemisphere) repeated measures ANOVAs in each ROI.

We did not identify any significant triple interaction between congruency, alignment and hemisphere in either ROI (RSC:  $F_{1,17} = 3.89$ ,  $p = 0.065$ ,  $\eta_p^2 = 0.19$ ; PPA:  $F_{1,18} = 0.023$ ,  $p = 0.88$ ,  $\eta_p^2 = 0.0013$ ).

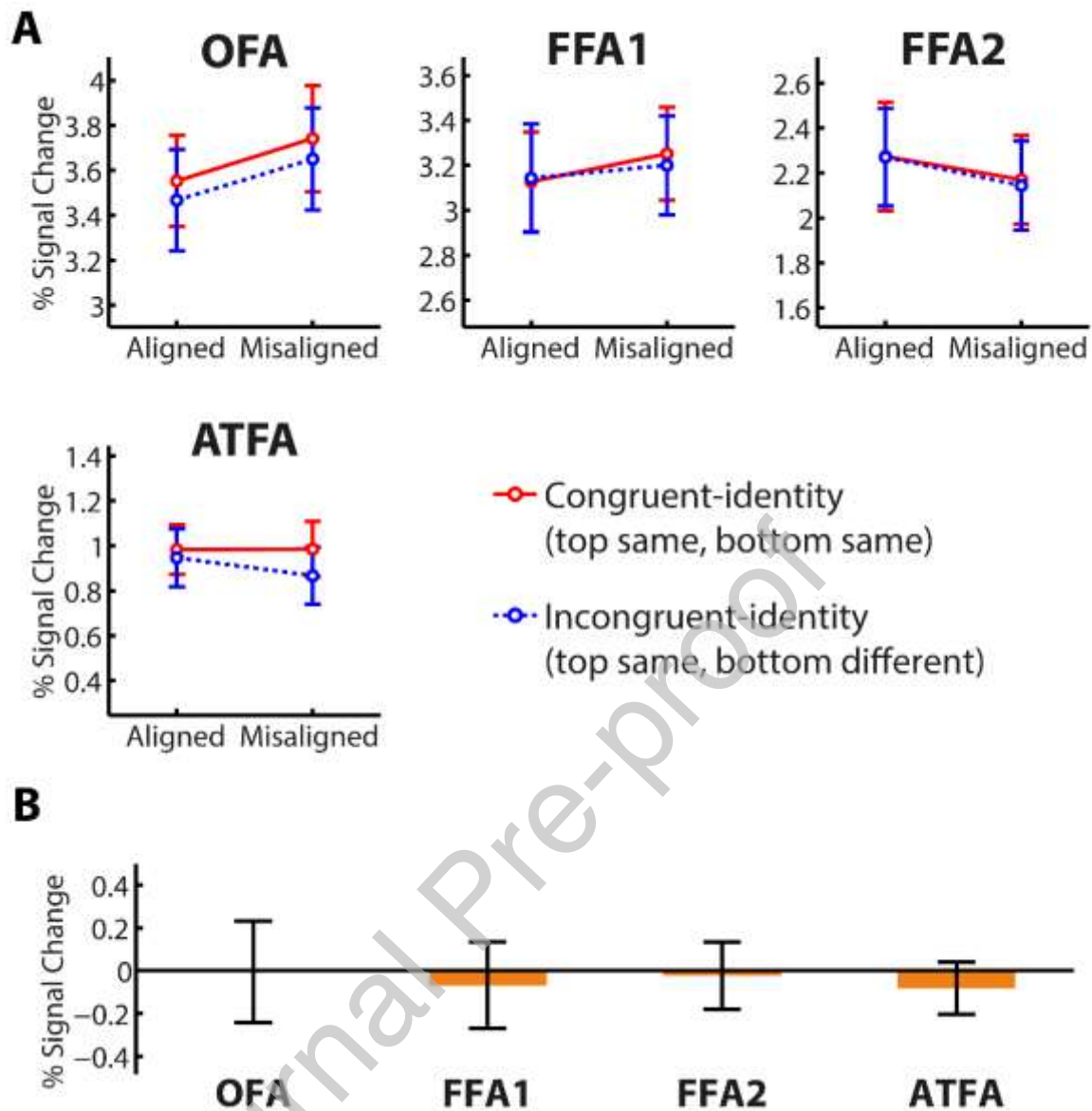
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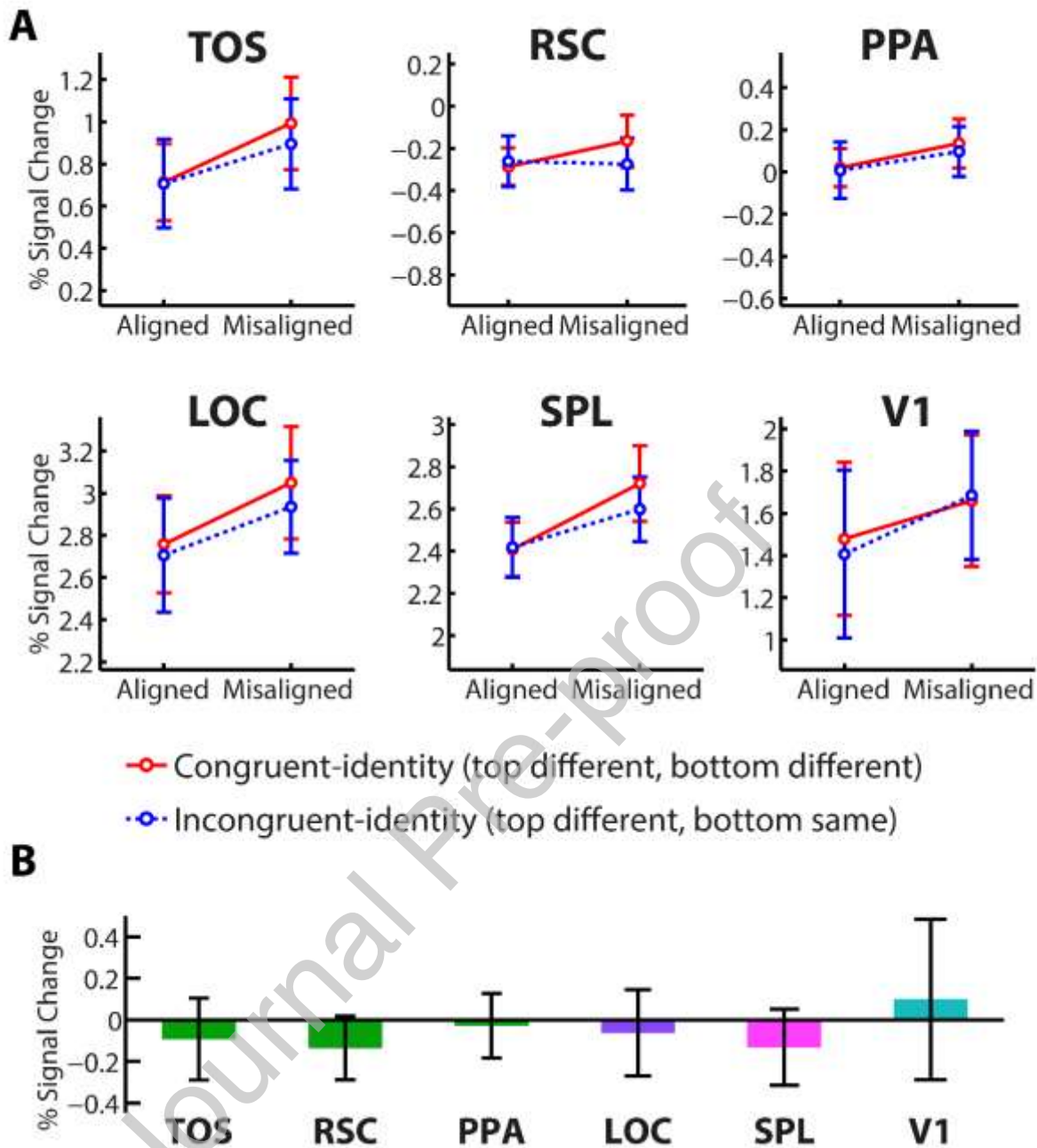
**Figure 7.** Neural responses to the top-same conditions in the scene-responsive, object-responsive, perceptual grouping and early visual ROIs. (A) % signal change as a function of congruency and alignment. (B) Interaction between congruency and alignment with the contrast: (*aligned congruent-identity* – *aligned incongruent-identity*) – (*misaligned congruent-identity* – *misaligned incongruent-identity*). Error bars indicate  $\pm 1$  SEM. \* indicates  $p < 0.05$ , Bonferroni-corrected for  $N = 10$  ROIs.

### 3.2.3. Neural composite face effect (congruency x alignment interaction) for top-different conditions

We did not observe a neural composite face effect for the top-different conditions (**Fig. 8 & 9**). None of our ROIs showed a significant interaction between congruency and alignment (OFA:  $F_{1,18} = 5.11 \times 10^{-4}$ ,  $p = 0.98$ ,  $\eta_p^2 = 2.8 \times 10^{-5}$ ; FFA1:  $F_{1,17} = 0.11$ ,  $p = 0.74$ ,  $\eta_p^2 = 0.0065$ ; FFA2:  $F_{1,16} = 0.022$ ,  $p = 0.88$ ,  $\eta_p^2 = 0.0014$ ; ATFA:  $F_{1,16} = 0.44$ ,  $p = 0.52$ ,  $\eta_p^2 = 0.027$ ; TOS:  $F_{1,18} = 0.22$ ,  $p = 0.65$ ,  $\eta_p^2 = 0.012$ ; RSC:  $F_{1,17} = 0.79$ ,  $p = 0.39$ ,  $\eta_p^2 = 0.044$ ; PPA:  $F_{1,18} = 0.031$ ,  $p = 0.86$ ,  $\eta_p^2 = 0.0017$ ; LOC:  $F_{1,18} = 0.089$ ,  $p = 0.77$ ,  $\eta_p^2 = 0.0049$ ; SPL:  $F_{1,18} = 0.51$ ,  $p = 0.48$ ,  $\eta_p^2 = 0.028$ ; V1:  $F_{1,18} = 0.065$ ,  $p = 0.80$ ,  $\eta_p^2 = 0.0036$ ) or a significant effect of congruency (OFA:  $F_{1,18} = 2.05$ ,  $p = 0.17$ ,  $\eta_p^2 = 0.10$ ; FFA1:  $F_{1,17} = 0.11$ ,  $p = 0.74$ ,  $\eta_p^2 = 0.0064$ ; FFA2:  $F_{1,16} = 0.18$ ,  $p = 0.68$ ,  $\eta_p^2 = 0.011$ ; ATFA:  $F_{1,16} = 4.06$ ,  $p = 0.061$ ,  $\eta_p^2 = 0.20$ ; TOS:  $F_{1,18} = 0.42$ ,  $p = 0.52$ ,  $\eta_p^2 = 0.023$ ; RSC:  $F_{1,17} = 0.44$ ,  $p = 0.52$ ,  $\eta_p^2 = 0.025$ ; PPA:  $F_{1,18} = 0.19$ ,  $p = 0.67$ ,  $\eta_p^2 = 0.010$ ; LOC:  $F_{1,18} = 2.77$ ,  $p = 0.11$ ,  $\eta_p^2 = 0.13$ ; SPL:  $F_{1,18} = 0.60$ ,  $p = 0.45$ ,  $\eta_p^2 = 0.032$ ; V1:  $F_{1,18} = 0.029$ ,  $p = 0.87$ ,  $\eta_p^2 = 0.0016$ ). We additionally performed a whole-brain analysis to investigate if any other regions showed an interaction between congruency and alignment or an effect of congruency for the top-different conditions. No regions were identified in this analysis. These results are consistent with our behavioural results obtained with top-different conditions, suggesting that top-same and top-different conditions may contribute differently to the behavioural measurement of composite face effect (Richler and Gauthier, 2013; Rossion, 2013).



**Figure 8.** Neural responses to the top-different conditions in the face-responsive ROIs. (A) % signal change as a function of congruency and alignment. (B) Interaction between congruency and alignment with the contrast:  $(aligned\ congruent-identity - aligned\ incongruent-identity) - (misaligned\ congruent-identity - misaligned\ incongruent-identity)$ . Error bars indicate  $\pm 1\ SEM$ .



**Figure 9.** Neural responses to the top-different conditions in the scene-responsive, object-responsive, perceptual grouping and early visual ROIs. (A) % signal change as a function of congruency and alignment. (B) Interaction between congruency and alignment with the contrast:  $(aligned\ congruent-identity - aligned\ incongruent-identity) - (misaligned\ congruent-identity - misaligned\ incongruent-identity)$ . Error bars indicate  $\pm 1\ SEM$ .

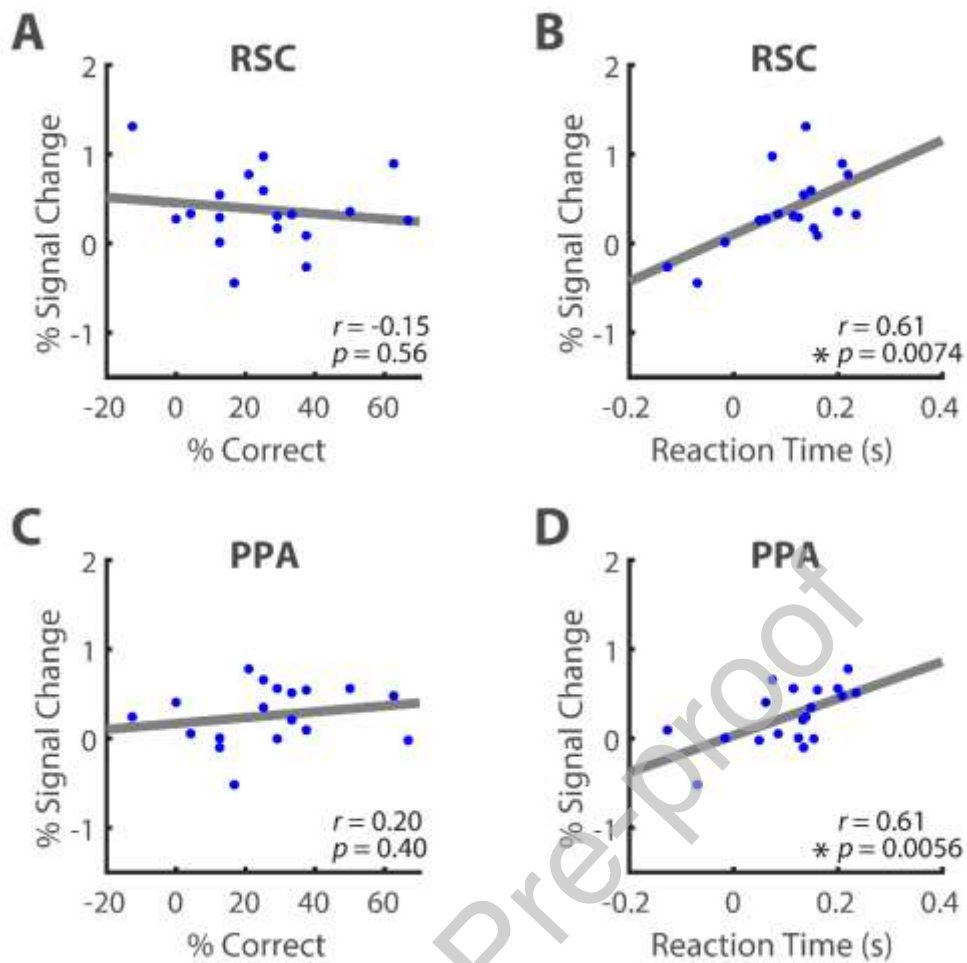


### 3.3. Correlation between the neural and behavioural composite face effect (i.e. congruency x alignment interaction)

We conducted correlation analyses between neural composite face effects observed in the RSC and PPA (**Fig. 7**) and the behavioural composite effect measured with accuracy and reaction times (**Fig. 3**). As illustrated in **Fig. 10**, for the composite face effect measured with response accuracy, there was no significant brain-behaviour correlation in either RSC ( $r = -0.15$ ,  $p = 0.56$ ) or PPA ( $r = 0.20$ ,  $p = 0.40$ ). In contrast, for the composite face effect measured with reaction times, we found significant correlations between the behavioural and neural composite face effect observed in both RSC ( $r = 0.61$ ,  $p = 0.0074$ ) and PPA ( $r = 0.61$ ,  $p = 0.0056$ ), both surviving Bonferroni-correction for  $N = 2$  ROIs.

Our behavioural composite effect measured with reaction times is based on difference scores between reaction times, which might have poor retest reliability when the same subject is tested multiple times (Draheim et al., 2019). To check whether our participants showed a consistent composite face effect in reaction times, we calculated Cronbach's alpha (Cronbach, 1951). We found a Cronbach's alpha of 0.85 for our participants' composite effect in reaction times across the three experimental runs, indicating that our participants showed a consistent strength of composite effect in reaction times across the experiment.

We additionally performed whole brain analyses to investigate if any other brain regions showed a correlation between neural activity and behaviour related to the composite face effect. No regions were identified in these analyses.



**Figure 10.** Correlation of interaction effect of congruency and alignment measured with neural responses and behavioural measures. (A) and (C) show the correlation between the interaction effect of congruency and alignment measured with response accuracy (% correct) and neural responses in the RSC (A) and PPA (C). (B) and (D) show the correlation between the interaction effect of congruency and alignment measured with reaction times and neural responses in the RSC (B) and PPA (D). \* indicates  $p < 0.05$ , Bonferroni-corrected for  $N = 2$  ROIs.

## 4. Discussion

In this study, we investigated the neural substrates underlying the composite face effect—one of the most convincing demonstrations of holistic face processing—both within and outside of face-responsive brain regions. We found significantly different neural responses to aligned and misaligned faces in the LOC, as well as trends in the FFA2 and TOS. As aligned faces are processed more holistically than misaligned faces, the neural alignment effect suggests that these regions are sensitive to how holistically faces are processed. Furthermore, we found that the RSC and PPA showed a pattern of neural activation consistent with processing face identity in a holistic manner, which is a key factor underlying the characteristic responses of a behavioural composite face effect. The strength of this neural composite face effect in RSC and PPA also correlated with the behavioural composite face effect measured in reaction times. These results indicate that brain regions both within and outside the commonly defined face-responsive network contribute to the composite face effect.

### 4.1. Neural responses to face alignment

Contrasting the neural responses to aligned and misaligned faces provides one way to reveal the neural substrates supporting holistic face processing (Schiltz et al., 2010; Schiltz and Rossion, 2006). Although in the composite task, the behavioural effect of holistic processing is measured as different responses to congruent versus incongruent aligned faces, holistic processing is assumed to occur for both types of aligned faces whereas part-based processing is more prominent for misaligned faces. Therefore, brain regions showing differences in neural activation between aligned and misaligned faces would indicate their relative contribution to holistic and part-based face processing. In the present study, we found a significant alignment effect in the LOC driven by higher activation to misaligned faces compared to aligned faces. This pattern of results shows remarkable similarity to the differences in neural activation between upright and inverted faces. Several studies have found higher activation to inverted compared to upright faces in the LOC (Aguirre et al., 1999; Epstein et al., 2006; Goffaux et al., 2013; Grotheer et al., 2014; Haxby et al., 1999). It has been proposed that this could be due to inverted faces being processed similarly to objects or due to a recruitment of these regions for more demanding face processing

(Aguirre et al., 1999; Haxby et al., 1999). Given that inverted faces are also processed in a more part-based manner (Rossion, 2013; Young et al., 1987) these results suggest that misaligned faces may be processed similarly to inverted faces (see also Schiltz and Rossion, 2006). Together, these results suggest that the LOC contributes primarily to part-based processing of misaligned or inverted faces.

We also found marginal alignment effect trends in the FFA2 and TOS, but these effects did not survive Bonferroni correction for  $N = 10$  ROIs. Although the FFA2 result was not significant after Bonferroni correction, this region has been associated with holistic processing in several previous studies (Andrews et al., 2010; Goffaux et al., 2013; Pinsk et al., 2009; Ross et al., 2018; Schiltz et al., 2010; Schiltz and Rossion, 2006). Our FFA2 results are comparable to those found in previous studies, though our Bonferroni correction might be too stringent to demonstrate a significant difference (note that Bonferroni correction may increase Type II errors, (Nakagawa, 2004)). Under such strict criteria, the FFA2 showed a trend towards higher activation to aligned faces compared to misaligned faces, suggesting that this region may process faces in a holistic manner. A specific involvement of FFA2 in holistic face processing is consistent with previous work showing higher activation to upright vs inverted faces in the FFA2 (Pinsk et al., 2009) and with previous work showing that the FFA2 is involved in holistic processing of expertise objects (Ross et al., 2018). Furthermore, several previous studies that did not separate the two components of the FFA have also linked activity in the FFA to holistic processing of faces (Andrews et al., 2010; Goffaux et al., 2013; Schiltz et al., 2010; Schiltz and Rossion, 2006).

An involvement of the FFA2, but not the FFA1 in holistic face processing may explain why studies investigating the neural responses to face inversion in the FFA have found mixed results. Some studies found higher responses to upright compared to inverted faces in the FFA (Goffaux et al., 2013; Yovel and Kanwisher, 2005), whereas some studies did not find differences in responses (Aguirre et al., 1999; Epstein et al., 2006; Grotheer et al., 2014; Haxby et al., 1999). One study that separated the FFA into two components, found higher activation to upright vs inverted faces in the FFA2 but not the FFA1 (Pinsk et al., 2009). Thus, the discrepant results across these studies might be due to differences in their FFA localization. Furthermore, (Pinsk et al., 2009) did not find differences in activity to upright vs inverted faces in the ATFA, which is consistent with our results in this region. The similarity

between our results in the FFA2 and the effect of face inversion in FFA in previous studies suggests that the FFA, particularly its anterior part FFA2, is involved in processing faces in a holistic manner.

#### **4.2. Neural responses to composite-faces**

Although a neural alignment effect helps reveal the neural substrates underlying the difference between holistic and part-based face processing, the neural alignment effect alone cannot tell us what neural mechanisms support the characteristic behaviour related to processing face identity holistically in the composite face paradigm. To address this question, we hypothesized that brain regions processing face identity holistically would show a similar pattern of neural responses to the pattern observed in behaviour: a larger congruency effect for aligned faces than for misaligned faces. We investigated which brain regions exhibit such a neural composite face effect. Our results identified two ROIs, the RSC and PPA, that showed neural responses consistent with the behavioural composite face effect. The RSC and PPA are known for their crucial role in scene perception, memory, navigation (Epstein, 2008; Epstein and Kanwisher, 1998; Vann et al., 2009) and contextual relationships (Bar, 2004; Bar and Aminoff, 2003). Recent studies have shown that the RSC and PPA also contribute to configural/relational processing of visual scenes. These two regions show stronger responses to whole scenes than parts of scenes (Kamps et al., 2016), and the PPA also shows higher responses when scene stimuli are processed holistically than when they are not (Schindler and Bartels, 2016). Our finding of a neural composite face effect in these ROIs suggests that the behavioural composite face effect may involve neural mechanisms supporting general configural/relational processing of face identity. However, we note that we did not identify a neural alignment effect in the RSC or PPA, suggesting that these regions do not play a general role in holistic processing of faces.

We did not identify a neural composite face effect in the FFA, though previous studies suggest an important role of FFA in holistic face processing (Goffaux et al., 2013; Schiltz et al., 2010; Schiltz and Rossion, 2006), nor any other face-responsive region, including the higher-level ATFA which was not localized in most previous studies. It is possible that these discrepant results in the FFA may be due to differences in the experimental design. In this study, we used a different design of the composite-face paradigm than was used in previous studies (Schiltz et al., 2010; Schiltz and Rossion, 2006).

Thus, it may be that the measurement of holistic processing in the FFA is less sensitive when using this design, for example due to differences in the frequency of top-same and top-different conditions, as this may change participants' expectations (see below).

Furthermore, it is also known that repetition effects can sometimes differ across the duration of an experiment (Müller et al., 2013), thus it is possible that differences in the number of faces used in the stimulus set or differences in the number of trials could lead to differences in the measured repetition effects.

We found higher BOLD responses when two faces were aligned and congruent (i.e. identical faces) compared to when they were aligned and incongruent (i.e. same top-halves, different bottom-halves) and this repetition-effect disappeared when faces were misaligned. Most studies find a repetition-suppression effect when subjects view two identical faces compared to when they view two different faces (Grill-Spector et al., 1999), although repetition-enhancement was also found in many studies (Segaert et al., 2013). We speculate that this repetition-enhancement effect might be due to the role of expectation in fMRI repetition effects. Expectations may modulate how stimulus repetition affects evoked neural activity. For example, the probability of repetitions occurring in an experimental run changes the repetition-effect strength (Larsson and Smith, 2012; Summerfield et al., 2008). In both the FFA and PPA the neural response to faces was reduced when subjects had higher expectation of seeing a face, compared to lower expectation of seeing a face (Egner et al., 2010). In our experiment, there were more trials where participants perceived the top-halves of the faces to be different compared to trials where they perceived them to be the same, due to the composite face illusion. Thus, subjects may expect top-different trials more often than top-same ones, leading them to have a lower BOLD response when they perceive the faces to be different compared to when they perceive them to be the same. It is worth noting that our expected pattern for the neural composite face effect is an interaction between congruency and alignment (larger congruency effect for aligned than for misaligned faces) regardless of whether there is a repetition enhancement or repetition suppression effect.

#### **4.3. Linking composite face effect in neural activity and behaviour**

We found that the strength of the neural composite face effect (i.e. congruency x alignment interaction) in the RSC and PPA is correlated with the behavioural composite face

effect measured with reaction times, but not with accuracy. The correlation between the behavioural composite face effect and the neural composite face effect measured in RSC and PPA suggests that the neural activity in these areas contributes to the strength of the behavioural composite face effect across individuals. The different results between the two behavioural measures might be because reaction times are sometimes more sensitive to the individual differences in the composite face effect (e.g. Richler et al., 2011a) or are more sensitive to measurements of the composite face effect when the stimulus presentation times are long, as in the present study (Rossion, 2013). One may also argue that our observed correlations with reaction times are just due to different neural responses in the RSC and PPA that are sensitive to reaction times or their associated attentional differences. This attention-associated account is unlikely to be the case for two reasons. Firstly, tasks requiring longer reaction times or greater attention (e.g. incongruent-identity conditions) often elicit stronger neural responses rather than the lower neural activations we observe in RSC and PPA (e.g. compared to congruent-identity conditions). Secondly, we found no theoretical basis that such reaction time or attention differences would only modulate neural responses in the RSC and PPA and not also other ROIs. However, we note that we cannot fully exclude differences in trial difficulty contributing to the responses in these regions, in particular as the negative deflection in these regions could be due to a greater deactivation during the more difficult aligned incongruent conditions.

We separately investigated the neural activity and behavioural responses to the top-same and top-different conditions, which allowed us to perform consistent analyses across neural and behavioural responses and to evaluate the relative contribution of these conditions to the composite face effect. The necessity of incongruent-identity top-different conditions for measuring holistic face processing with the composite paradigm is debated (Richler and Gauthier, 2013; Rossion, 2013). It has also been suggested that the composite face effect is mainly found when the target face part being matched is more similar rather than different (Goffaux, 2012; Goffaux et al., 2013). We found different patterns of behavioural responses across these two conditions: the composite face effect was primarily driven by top-same conditions whereas the top-different conditions showed no evidence of a composite face illusion. Consistent with the behavioural responses, the neural composite face effect was observed with the top-same conditions but not with the top-different

conditions. Nonetheless, it is worth noting that we only observed a three-way interaction in one (i.e. the RSC) of 10 ROIs tested. Together, these results suggest a more prominent role of top-same than top-different conditions in measuring the behavioural and neural composite face effect.

#### 4.4. Conclusion

Holistic processing has been measured with different research paradigms, and different underlying cognitive and neural processes have been proposed (e.g. Harris and Aguirre, 2008; Haxby et al., 1999; Maurer et al., 2002; Ross et al., 2018; Schiltz et al., 2010). In the present study, when holistic processing is measured using a face alignment effect, we found that the FFA2 showed a trend toward responses consistent with holistic face processing whereas the LOC showed a pattern of responses consistent with part-based face processing. Furthermore, we found neural activity consistent with holistic processing of face identity, a key component of the composite face effect (i.e. congruency x alignment interaction), in the RSC and PPA, two brain regions sensitive to configural and relational processing of scene elements, and this neural composite face effect linked to behaviour. These results suggest that the composite face effect is supported by neural processes both within and outside of the face-responsive brain network.

#### Credit author statements

**Celia Foster:** Conceptualization; Software; Investigation; Formal analysis; Writing - Original Draft; Writing - Review & Editing

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**Declarations of interest**

None.

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