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Celia Foster ConceptualizationSoftwareInvestigationFormal analysisWriting - Original DraftWriting - Review & Editing
Isabelle Bühlhoff ConceptualizationWriting - Review & EditingSupervision ,
Andreas Bartels ConceptualizationWriting - Review & EditingSupervision ,
Mintao Zhao ConceptualizationWriting - Review & EditingSupervision

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

Celia Foster^{ab1}, Isabelle Bühlhoff^a, Andreas Bartels^{acde} & Mintao Zhao^{af}

Author affiliations:

^aMax Planck Institute for Biological Cybernetics, Tübingen, Germany

^bInternational Max Planck Research School for Cognitive and Systems Neuroscience, University of Tübingen, Tübingen, Germany

^cCentre for Integrative Neuroscience, Tübingen, Germany

^dDepartment of Psychology, University of Tübingen, Tübingen, Germany

^eBernstein Center for Computational Neuroscience, Tübingen, Germany

^fSchool of Psychology, University of East Anglia, Norwich, UK

¹Present address: Biopsychology and Cognitive Neuroscience, Faculty of Psychology and Sports Science, Bielefeld University, Germany

Corresponding authors:

Celia Foster

Biopsychology and Cognitive Neuroscience, Faculty of Psychology and Sports Science,
Bielefeld University, Germany

celia.foster@uni-bielefeld.de

Mintao Zhao

School of Psychology,

University of East Anglia, Norwich, NR4 7TJ, UK

mintao.zhao@uea.ac.uk

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 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 face is combined with the bottom-half 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 per

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 $d = 0.32$ (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 $d = 0.53$ 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° and width of 3.0° of visual angle. For misaligned stimuli, the bottom half of the face was shifted 1.0° 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.

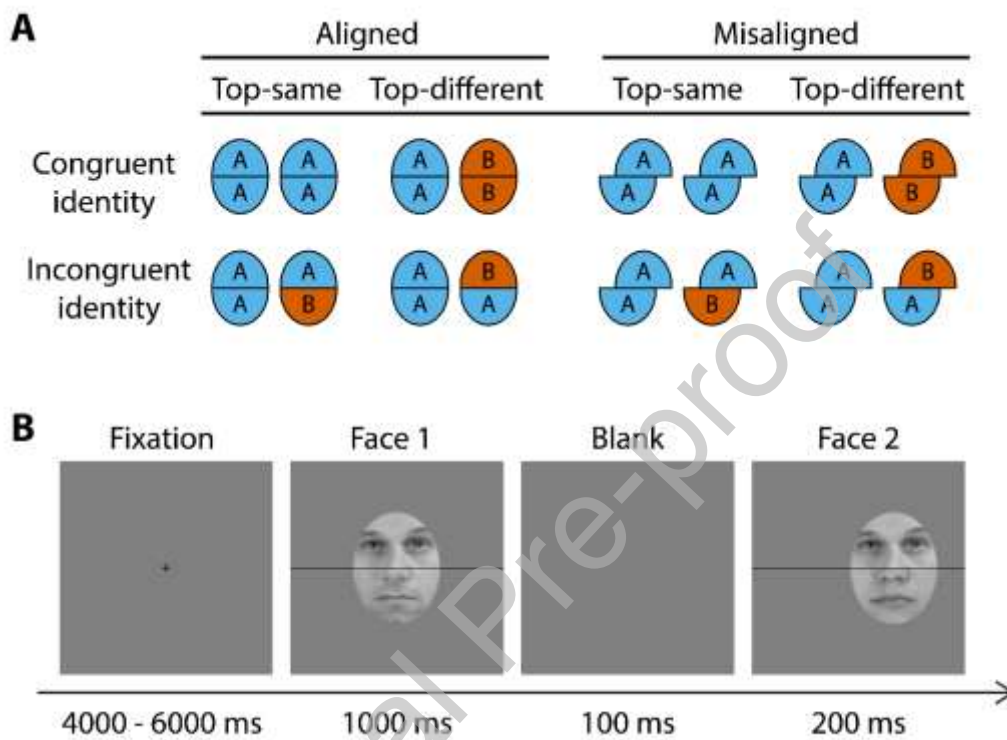


Figure 1. Experimental conditions and trial outline. (A) Experimental conditions. The conditions consisted of a $2 \times 2 \times 2$ factorial design, with factors *alignment*, whether the top and bottom halves of the faces were aligned or misaligned, *top-same or top-different*, whether the top halves 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° 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.

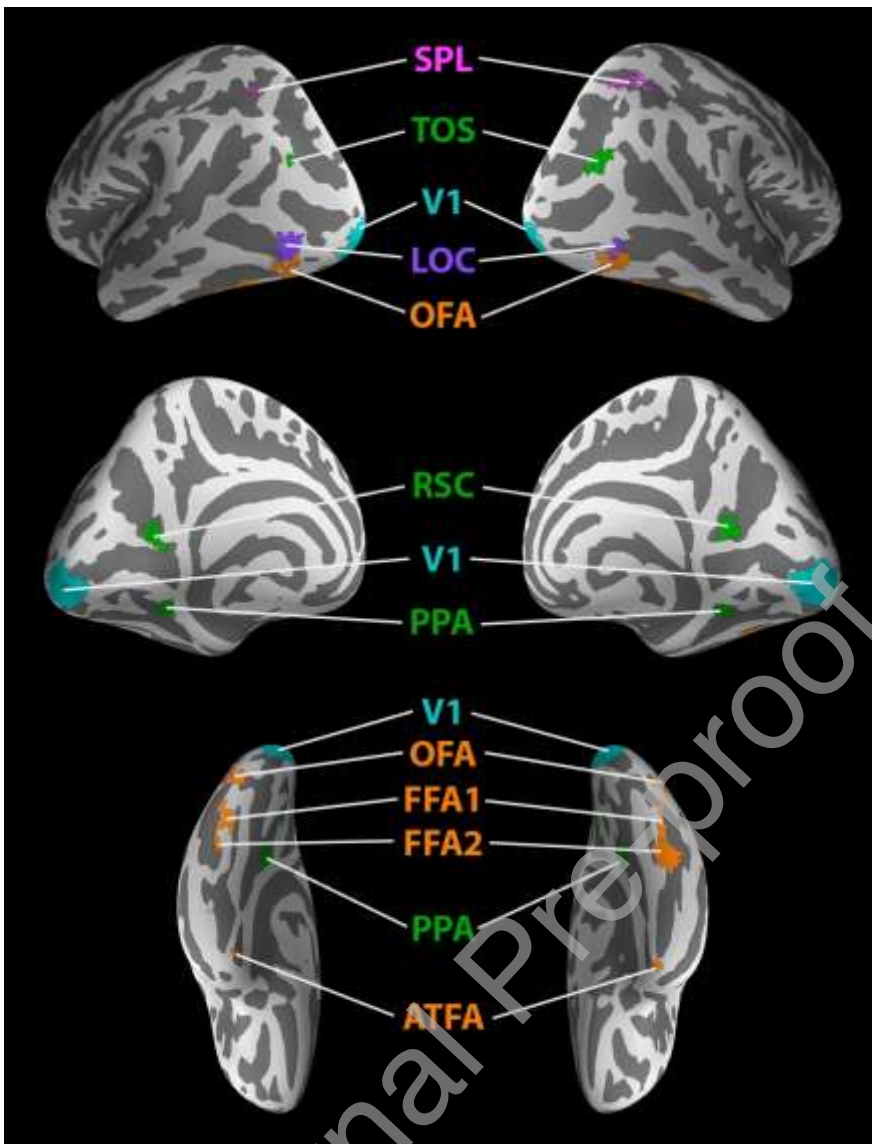


Figure 2. Locations of ROIs. ROIs include face-responsive OFA (occipital face area), FFA1 (fusiform face area 1), FFA2 (fusiform face area 2) and ATFA (anterior temporal face area) shown in orange, scene-responsive TOS (transverse occipital sulcus), RSC (retrosplenial cortex) and PPA (parahippocampal 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.

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 trials (i.e. top-same trials are more frequent than top-different trials).

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

Isabelle Bühlhoff: Conceptualization; Writing - Review & Editing; Supervision

Andreas Bartels: Conceptualization; Writing - Review & Editing; Supervision

Mintao Zhao: Conceptualization; Writing - Review & Editing; Supervision

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Declarations of interest

None.

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