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Mechanisms of hemispheric lateralization: Asymmetric interhemispheric recruitment in the face perception network

Stefan Frässle [a,b,*], Frieder Michel Paulus [c], Sören Krach [c], Stefan Robert Schweinberger [d], Klaas Enno Stephan [e,f], Andreas Jansen [a]

[a] Laboratory for Multimodal Neuroimaging (LMN), Department of Psychiatry, University of Marburg, D-35039 Marburg, Germany
[b] Department of Child- and Adolescent Psychiatry, University of Marburg, D-35039 Marburg, Germany
[c] Department of Psychiatry and Psychotherapy, Social Neuroscience Lab|SNL, University of Lübeck, D-23538 Lübeck, Germany
[d] Department of General Psychology and Cognitive Neuroscience, Institute of Psychology, University of Jena, D-07743 Jena, Germany
[e] Translational Neuromodeling Unit (TNU), Institute of Biomedical Engineering, University of Zurich & ETH Zurich, CH-8032 Zurich, Switzerland
[f] Wellcome Trust Centre for Neuroimaging, University College London, London WC1N 3BG, United Kingdom

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ABSTRACT

Perceiving human faces constitutes a fundamental ability of the human mind, integrating a wealth of information essential for social interactions in everyday life. Neuroimaging studies have unveiled a distributed neural network consisting of multiple brain regions in both hemispheres. Whereas the individual regions in the face perception network and the right-hemispheric dominance for face processing have been subject to intensive research, the functional integration among these regions and hemispheres has received considerably less attention. Using dynamic causal modeling (DCM) for fMRI, we analyzed the effective connectivity between the core regions in the face perception network of healthy humans to unveil the mechanisms underlying both intra- and interhemispheric integration. Our results suggest that the right-hemispheric lateralization of the network is due to an asymmetric face-specific interhemispheric recruitment at an early processing stage — that is, at the level of the occipital face area (OFA) but not the fusiform face area (FFA). As a structural correlate, we found that OFA gray matter volume was correlated with this asymmetric interhemispheric recruitment. Furthermore, exploratory analyses revealed that interhemispheric connection asymmetries were correlated with the strength of pupil constriction in response to faces, a measure with potential sensitivity to holistic (as opposed to feature-based) processing of faces. Overall, our findings thus provide a mechanistic description for lateralized processes in the core face perception network, point to a decisive role of interhemispheric integration at an early stage of face processing among bilateral OFA, and tentatively indicate a relation to individual variability in processing strategies for faces. These findings provide a promising avenue for systematic investigations of the potential role of interhemispheric integration in future studies.

Introduction

Perceiving human faces engages various brain regions, most prominently the occipital face area (OFA; Puce et al., 1996), the fusiform face area (FFA; Kanwisher et al., 1997) and the posterior superior temporal lobe (pSTS; Haxby et al., 1999). OFA, FFA and pSTS serve different functions (Hoffman and Haxby, 2000) and have jointly been referred to as the core of the face perception network (Haxby et al., 2000). Although these regions are typically activated in both hemispheres, the right lateralization of the face perception network is well established (De Renzi, 1986; Kanwisher et al., 1997; Puce et al., 1996; Wada and Yamamoto, 2001). Hence, the individual components of the network and their right-hemispheric dominance have been investigated thoroughly; however, the functional integration among these regions has received considerably less attention. We are currently lacking a deeper (mechanistic) understanding of the interplay between the face-sensitive regions and how hemispheric lateralization in the face perception network arises. Nevertheless, such a mechanistic understanding of the network dynamics is crucial for unraveling how the human brain processes faces, and might provide new insights into the pathophysiology of diseases where face perception is impaired (e.g., prosopagnosia, autism).

Only lately have pioneering studies begun to address the effective connectivity (i.e., directed interactions) among face-sensitive regions (Cohen Kadosh et al., 2011; Dima et al., 2011; Ewbank et al., 2013; Fairhall and Ishai, 2007; Ishai, 2008; Li et al., 2010). These studies, however, have only examined intrahemispheric connections, while neglecting the interhemispheric connections of the network. Critically, such an

* Corresponding author at: University of Marburg, Laboratory for Multimodal Neuroimaging (LMN), Department of Psychiatry, Rudolf-Bultmann-Straße 8, 35039 Marburg, Germany.
E-mail address: fraessle@med.uni-marburg.de (S. Frässle).

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approach might be too restricted, as recent imaging studies have suggested a non-negligible role of face-sensitive regions in the left hemisphere during face perception (Bi et al., 2014; Meng et al., 2012). These studies speak to a fundamental functional dissociation between the homotopic regions which complement each other. Specifically, it has been suggested that right FFA is involved in face/non-face judgments whereas left FFA processes 'low-level' face resemblance (Meng et al., 2012). This is consistent with a more general dissociation between right and left hemispheres in terms of holistic and feature-based processing, respectively (Bradshaw and Nettleton, 1981), which might also play an important role for the hemispheric lateralization of the face perception network (Hillger and Koenig, 1991; Leehey et al., 1978; Rossion et al., 2000; Yin, 1970).

Here, we extend recent effective connectivity analyses and examine functional interactions in the bilateral core of the face perception network. We hypothesized that not only the intra- but also the interhemispheric integration of face-sensitive regions is crucial for face perception and for understanding its hemispheric lateralization. This follows from recent behavioral evidence using divided visual field stimulation (Compton, 2002; Mohr et al., 2002; Schweinberger et al., 2003). Specifically, in matching tasks that required observers to indicate whether a target face matched one of two probe faces, superior performance was generally obtained when matches involved across-hemifield (as opposed to within-hemifield) presentation of faces, requiring interhemispheric interaction (Compton, 2002). Similarly, in other studies on face recognition, interhemispheric cooperation was indicated by enhanced performance when stimuli were simultaneously presented to both visual fields, compared to a single visual field. Importantly, this "bilateral gain" which had initially been demonstrated for words but not pseudowords in lexical decision tasks (Mohr et al., 1994) was most prominent for familiar faces compared to unfamiliar faces in face recognition tasks (Mohr et al., 2002; Schweinberger et al., 2003). Those findings were interpreted as face recognition accessing acquired memory representations, instantiated via cortical cell assemblies that are distributed across the two hemispheres. Finally, recent experiments which involved chimaeric presentation at the fovea of two hemifaces from either the same face (consistent) or from different faces (inconsistent) also showed behavioral evidence for cross-hemispheric processing of facial information. Importantly, these effects were reduced or absent for inverted faces (Yovel et al., 2005). Because face inversion is generally thought to suppress holistic processing, the above effects suggest that interhemispheric integration takes place at a higher level of holistic representations of faces.

Hence, we here aimed at unraveling the potential role of the interhemispheric interactions in the face perception network. To this end, we adapted a recent paradigm (Stephan et al., 2007), presenting stimuli in one hemifield to restrict visual input to the contralateral hemisphere. Subjects fixated a central cross while covertly shifting attention to the stimuli in the periphery. Using dynamic causal modeling (DCM; Friston et al., 2003) for fMRI, we then tested whether interhemispheric integration played an important role for hemispheric lateralization of the face perception network. In this case, one might also expect correlations between functional measures of interhemispheric integration and hemispheric asymmetries in other modalities, particularly asymmetry of cerebral gray matter (Good et al., 2001). Notably, whereas we have concepts for understanding the function of the intrahemispheric connections (e.g., hierarchical forwarding of face-specific information from OFA to FFA; Haxby et al., 2000), the role of the interhemispheric connections for face perception is largely unknown. One possibility is that interhemispheric integration might play a role in the above-mentioned dissociation between holistic and feature-based processing. Using measures of pupil size, which was recently suggested to be sensitive to holistic versus feature-based processing of visual stimuli (Conway et al., 2008; Naber and Nakayama, 2013), we performed an exploratory analysis to test this presently speculative link. In summary, using a multimodal approach which combines DCM with structural MRI and pupillometry, we aimed at developing a mechanistic model for the hemispheric lateralization of the core system for face perception and at shedding light on the potential role of interhemispheric connections in this system.

Materials and methods

Subjects

Twenty healthy subjects (8 male, age range: 21–30 years, mean age: 24.2 ± 2.6 years) participated in the experiment. All were naïve to the purpose of the study, except for one (author SF). Subjects had normal or corrected-to-normal vision, were right-handed and gave written informed consent prior to the experiment. The study conformed to the Declaration of Helsinki and was approved by the local ethics committee of the Medical Faculty of the University of Marburg.

Experimental procedure

Subjects viewed either gray-scale neutral faces or scrambled images in the periphery while holding their gaze on a fixation cross in the center of the screen. Note that presenting the stimuli in the periphery is crucial here, as it allowed us to investigate more refined hypotheses on the interhemispheric integration in the face perception network (cf. Stephan et al., 2005, 2007). Faces were full-frontal photographs taken from the Center for Vital Longevity Face Database (Ebner, 2008). Scrambled images were the randomized Fourier transforms of the face stimuli (i.e., assigning random values to the phase component), thus discarding any shape information while leaving the amplitude spectrum (e.g., mean luminance) unaffected. Stimuli were presented as circular patches (radius: 2.17°) on a gray background (luminance equal to the average brightness of all stimuli) via an MRI-compatible LCD screen (LG SL9000, 60 Hz, 4:3, 1024 × 786 pix) using the Presentation 11.0 software package (Neurobehavioral Systems, Albany, CA, USA, http://www.neurobs.com/). Subjects viewed the stimuli via a mirror mounted on the MR head coil. Faces and scrambled images appeared either in the right ("RVF") or left visual field ("LVF"), thus, the experimental design of the study was a 2-way repeated measures within-subject design (stimulus × hemifield). The center of the circular patches was located 4.02° lateral to the fixation cross. Subjects were instructed to attend to and process the stimuli in the periphery while holding their gaze on the central fixation cross. Proper fixation was controlled for by recording the direction of eye gaze at a rate of 500 Hz using an MRI-compatible infrared-sensitive camera (EyeLink 1000, SR Research, Osgoode, ON, Canada). This ensured that subjects engaged in non-foveal vision and that visual inputs therefore reached the primary visual area (V1) of the contralateral hemisphere only.

A number of control steps ensured the quality of subjects' fixation. First, adequate fixation was monitored on-line during the experiment by the experimenter. Second, post-hoc analyses tested for differences in eye gaze between the different experimental conditions. To this end, the mean gaze eccentricity was calculated for each subject and experimental condition, separately. Individual eccentricity values were then entered into a 2-way repeated measures ANOVA (within-subject factors: stimulus, hemifield) in IBM SPSS Statistics 20 (Armonk, NY: IBM Corp. Released 2011). The ANOVA revealed no significant main effect of stimulus ($F_{(1,19)} = 2.99$, $p = 0.10$) or hemifield ($F_{(1,19)} = 0.08$, $p = 0.78$). Similarly, there was no significant effect for the stimulus × hemifield interaction ($F_{(1,19)} = 0.25$, $p = 0.62$). This, however, does not rule out the occurrence of occasional shifts in gaze or some individuals not maintaining central fixation. Therefore, in a final step, the quality of subjects' fixation was investigated by estimating the percentage of time subjects properly fixated the cross in the center of the screen. In brief, a region centered on the fixation cross with a radius of 1° was defined. The radius was used to guarantee that for fixations within that region, subjects still perceived the stimuli in the periphery (the medial