



Defining face perception areas in the human brain: A large-scale factorial fMRI face localizer analysis

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ABSTRACT

A number of human brain areas showing a larger response to faces than to objects from different categories, or to scrambled faces, have been identified in neuroimaging studies. Depending on the statistical criteria used, the set of areas can be overextended or minimized, both at the local (size of areas) and global (number of areas) levels. Here we analyzed a whole-brain factorial functional localizer obtained in a large sample of right-handed participants (40). Faces (F), objects (O; cars) and their phase-scrambled counterparts (SF, SO) were presented in a block design during a one-back task that was well matched for difficulty across conditions. A conjunction contrast at the group level $\{(F-SF) \text{ and } (F-O)\}$ identified six clusters: in the pulvinar, inferior occipital gyrus (so-called OFA), middle fusiform gyrus (so-called FFA), posterior superior temporal sulcus, amygdala, and anterior infero-temporal cortex, which were all strongly right lateralized. While the FFA showed the largest difference between faces and cars, it also showed the least face-selective response, responding more to cars than scrambled cars. Moreover, the FFA's larger response to scrambled faces than scrambled cars suggests that its face-sensitivity is partly due to low-level visual cues. In contrast, the pattern of activation in the OFA points to a higher degree of face-selectivity. A BOLD latency mapping analysis suggests that face-sensitivity emerges first in the right FFA, as compared to all other areas. Individual brain analyses support these observations, but also highlight the large amount of interindividual variability in terms of number, height, extent and localization of the areas responding preferentially to faces in the human ventral occipito-temporal cortex. This observation emphasizes the need to rely on different statistical thresholds across the whole brain and across individuals to define these areas, but also raises some concerns regarding any objective labeling of these areas to make them correspond across individual brains. This large-scale analysis helps understanding the set of face-sensitive areas in the human brain, and encourages in-depth single participant analyses in which the whole set of areas is considered in each individual brain.

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1. Introduction

The perception and recognition of faces are the objects of intense research in Cognitive Neuroscience. In particular, the localization of this complex function in the human brain is highly investigated. Investigation of the neural basis of face recognition started in the middle of the 19th century, with the reports of patients presenting difficulties at face recognition following brain damage (Quaglino & Borelli, 1867; Wigan, 1844). This neurological syndrome, prosopagnosia (Bodamer, 1947), has for long been the only source of information about the neural basis of face recognition. Correlation between, on the one hand, the behavioral difficul-

ties at recognizing faces and, on the other hand, the localization of lesion causing prosopagnosia, offered the first opportunity to identify cortical areas and white matter tracts considered to be important for face recognition. Patients with prosopagnosia present with either bilateral or unilateral right hemisphere damage, in different areas of the ventral occipital and temporal cortices, in particular the lingual, fusiform and parahippocampal gyri, as well as the anterior temporal pole (Barton, 2008a; Bouvier & Engel, 2006; Damasio & Van Hoesen, 1982; Fox, Iaria, & Barton, 2009; Hecaen & Angelergues, 1962; Meadows, 1974; Sergent & Signoret, 1992; Sorger, Goebel, Schiltz, & Rossion, 2007). Hence, neuropsychological investigations of patients with prosopagnosia revealed early on the dominance of the right hemisphere in face recognition (Hecaen & Angelergues, 1962), and pointed to a critical role of multiple occipito-temporal cortical areas for this function (Sergent & Signoret, 1992). However, for a number of reasons (e.g., large size and variability of the lesions, potential effects of these lesions on the function of other areas), the precise definition of the (sub)cortical areas

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involved in normal face recognition in humans, their function, and whether these areas are uniquely devoted to the processing of faces remained largely unclear before the advent of functional neuroimaging studies of the healthy brain.

Starting with the seminal work of Justine Sergent and colleagues (1992) using positron emission tomography (PET), a wealth of neuroimaging studies have since been carried out, mainly with functional magnetic resonance imaging (fMRI), allowing a definition of the brain areas particularly responsive to face stimulation in the human healthy brain. Even though there were already a number of published neuroimaging studies of face perception at that time, both with PET and fMRI (e.g., Haxby et al., 1994; Puce, Allison, Gore, & McCarthy, 1995 respectively), a landmark paper in this field is the fMRI study reported by Kanwisher, McDermott, and Chun (1997). That study introduced the (face) localizer approach in neuroimaging, comparing the presentation of (blocks of) faces vs. nonface objects while keeping task constant. The authors focused on a single cluster of voxels in the middle section of the right ventral occipito-temporal cortex (fusiform gyrus) that responded the most, and the most consistently across participants, to pictures of faces as compared to other objects. Both the approach and the cluster identified in most individual brains, the so-called “fusiform face area” (FFA) (Kanwisher et al., 1997), have enjoyed a special status in the field of face processing over the past 15 years (e.g., see the reviews of Berman et al. (2010) and Kanwisher and Yovel (2006)). Currently, in many neuroimaging studies of face perception, researchers conduct an independent experiment to localize an FFA in each individual brain. Once an FFA is defined, its response properties can then be tested in another experiment by manipulating face stimuli and tasks of interest.

However, as pointed out early on by Tovee (1998) the FFA certainly needs “a little help from its friends” to carry a complex function such as face perception, in agreement with evidence collected in the above-cited studies on acquired prosopagnosia (see Rossion, 2008). Indeed, it is now widely acknowledged in the neuroimaging community of this field that in each individual human brain there are many clusters, of different sizes and distributed across the whole brain, that respond more to faces than to nonface visual stimuli (e.g., Fox et al., 2009; Haxby, Hoffman, & Gobbini, 2000; Ishai, Schmidt, & Boesiger, 2005; Rajimehr, Young, & Tootell, 2009; Rossion et al., 2003a; Tovee, 1998; Tsao, Moeller, & Freiwald, 2008; Weiner & Grill-Spector, 2010; see also Allison, McCarthy, Nobre, Puce, and Belger (1994), Allison, Puce, Spencer, and McCarthy (1999), and Barbeau et al. (2008) for converging evidence from intracranial recordings in epileptic patients). Specifically, these clusters are localized in the posterior part of the inferior occipital cortex (one of them being termed the “Occipital Face area”, OFA, e.g., Gauthier et al., 2000a; see Pitcher, Walsh, and Duchaine (2011a) for a review), and of the superior temporal sulcus (pSTS, e.g., Puce, Allison, Bentin, Gore, & McCarthy, 1998), the anterior infero-temporal cortex or temporal pole (AIT) as reported mainly in PET studies (e.g., Sergent et al., 1992) but also more recently in fMRI studies (Kriegeskorte, Formisano, Sorger, & Goebel, 2007; Rajimehr et al., 2009) and the amygdala (e.g., Morris et al., 1996). Interestingly, recent fMRI studies carried out in the monkey brain also point to a set of areas responding more to faces than nonface visual stimuli, and distributed in the occipital, temporal and prefrontal cortices (Pinsk et al., 2009; Tsao, Freiwald, Tootell, & Livingstone, 2006; Tsao et al., 2008; see e.g., Desimone, 1991; Gross, Rocha-Miranda, & Bender, 1972; Perrett, Rolls, & Caan, 1982; Rolls, 1992; for earlier evidence coming from single-cell recording studies in non-human primates).

Considering these observations, the community of researchers inside or outside this field may be under the impression that the question of localization of face perception in the human brain is largely solved: there is a set of well identified clusters particularly activated following face presentation, and one should now focus

entirely on defining the respective functions of these localized areas, as well as how they interact anatomically and functionally. However, even if one acknowledges the interest of such a face localizer approach to clarify the neural substrates of human face perception (see the debate by Friston, Rotshtein, Geng, Sterzer, and Henson (2006) and Saxe, Brett, and Kanwisher (2006)), there are a number of important methodological issues that need to be considered and resolved because they can greatly influence the definition of the area(s) involved in face perception, and hence our understanding of the functional neuro-anatomy of this function. More precisely, there are at least four main, and non-independent, methodological issues that arise when defining such a functional face localizer.

First, the *kind of stimuli* that are compared to faces in a functional localizer vary in different studies: objects from multiples categories (chair, table, apple, ball, ...), or (phase-)scrambled faces, or yet exemplars from a single nonface object category (e.g., pictures of different houses). Usually, only one of these three comparisons is performed, and the three kinds of comparisons have been performed in different face localizer studies (e.g., Haxby et al., 1999; Ishai et al., 2005; Kanwisher et al., 1997 respectively). Yet, these different comparisons can lead to highly different definitions (i.e., localization, magnitude and extent) of an FFA and of other areas responding preferentially to faces (see Berman et al., 2010; Wiggett & Downing, 2008).

Second, the *task* that participants have to perform in the face localizer should be considered. Most of the time either passive viewing or a one-back task (detecting immediate repetition of the exact same stimulus in a train of stimuli) is used. Berman and colleagues (2010) recently concluded that the task performed was not a major factor accounting for localization of the human FFA. However, this claim might not be valid for other face-preferential clusters. Moreover, the task cannot be considered as being independent of the kind of stimuli that are compared to faces. Indeed, when using objects from multiple categories to compare to faces, the greater visual homogeneity of the face class implies that a one-back task is much more difficult to perform for faces than objects. For instance, in a typical size group of 15 right-handed participants taken from a previous study of our group (Dricot, Sorger, Schiltz, Goebel, & Rossion, 2008), there was a highly significant difference in accuracy at the one-back task between faces and objects, participants performing much better for objects than faces ($t_{14} = 5.12$, $p < 0.0002$). Such a difference in task difficulty may cause an increase of attention for faces as compared to objects in the face localizer, and therefore an increase of the level of activation and size of the FFA (e.g., Gentile & Jansma, 2010; Wojciulik, Kanwisher, & Driver, 1998) or even possibly in the number of clusters above statistical threshold that would be erroneously defined as reflecting face-selective voxels. This issue has been largely neglected in neuroimaging studies using face localizer paradigms, for which, most of the time, behavioral data is not even reported.

A third issue is whether the whole brain, or only a portion of it (as in the original Kanwisher et al. (1997) study), should be considered. While scanning the whole brain allows identification of preferential response to faces without a priori localization constraints, it requires a relatively long recording time and is thus potentially less sensitive to disclose and characterize such local preferential response to faces (i.e., in the middle fusiform gyrus), also increasing the severity of corrections for multiple statistical tests.

Fourth, the statistical criteria used to define the voxels presenting a larger response to faces than comparison stimuli have a huge impact on the outcome of a face localizer. For instance, contrary to previous neuroimaging studies (e.g., Puce et al., 1995; Sergent et al., 1992), Kanwisher and colleagues (1997) focused on a single cluster only whose response was larger for faces than control

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