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Single subject analyses reveal consistent recruitment of frontal operculum in performance monitoring

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ABSTRACT

There are continuing uncertainties regarding whether performance monitoring recruits the anterior insula (aI) and/or the frontal operculum (fO). The proximity and morphological complexity of these two regions make proper identification and isolation of the loci of activation extremely difficult. The use of group averaging methods in human neuroimaging might contribute to this problem. The result has been heterogeneous labeling of this region as aI, fO, or aI/fO, and a discussion of results oriented towards either cognitive or interoceptive functions depending on labeling. In the present article, we adapted the spatial preprocessing of functional magnetic resonance imaging data to account for group averaging artifacts and performed a subject-by-subject analysis in three performance monitoring tasks. Results show that functional activity related to feedback or action monitoring consistently follows local morphology in this region and demonstrate that the activity is located predominantly in the fO rather than in the aI. From these results, we propose that a full understanding of the respective role of aI and fO would benefit from increased spatial resolution and subject-by-subject analysis.

Introduction

Neuroimaging studies have shown that an extensive region located at the junction of the anterior insula (aI) and the frontal operculum (fO) is an integral part of the performance monitoring network. The aI and the fO are distinct cytoarchitectonic areas: whereas aI is an agranular area, fO is a dysgranular area (Foundas et al., 2001; Anwander et al., 2007; Keller et al., 2009, 2011; Amunts et al., 2010; Nieuwenhuys, 2012). Differences in the presence and extent of granular layer IV have been shown to relate to differences in function. For instance, a striking difference is observed between primary sensory (granular) and primary motor (agranular) areas initially described by Brodmann. On a more fine-grained level, adjacent motor regions, for example, show different granularity (primary motor cortex agranular, premotor cortex dysgranular), for which a functional theory has been put forward (Shipp et al., 2013). As such, the difference in granularity in aI and fO would point towards distinct functional contributions of these areas to performance monitoring but which have been difficult to disentangle thus far.

The functional discrimination of these areas is difficult for different reasons: First, the morphological complexity of the region makes the proper identification of the locus of activation extremely challenging, especially using voxel-based neuroimaging methods. More precisely, whereas the circular insular sulcus (cris) delineating the insula is very stable across subjects, the intersection between aI and fO displays morphological heterogeneity (Naidich et al., 2004; Nieuwenhuys, 2012). In addition, because of the local cortical folding, smoothed activation-related voxels may cover both fO and aI subparts. Second, the fact that most studies use conventional linear group averaging methods amplifies this problem. As a result of these anatomical and technical challenges, authors label activity maxima in this region in various manners: they have been described as belonging to aI (Preuschoff et al., 2008; Christopoulos et al., 2009; d'Acremont et al., 2009; Tobler et al., 2009; Rutledge et al., 2010; Ullsperger et al., 2010; Wessel et al., 2011; Amiez et al., 2012b; Harsay et al., 2012; Klein et al., 2013; Becker et al., 2014; Koban and Pourtois, 2014; Rothkirch et al., 2014), to fO (Higo et al., 2011; Nelissen et al., 2013), or to both (aI/fO) (Menon et al., 2001; Dosenbach et al., 2006, 2007; Fair et al., 2007; Seeley et al., 2007; Sridharan et al., 2008; Amiez et al., 2012a; Vaden

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et al., 2013). Consequently, this imprecise labeling often leads to discussions of results orientated in the context of an aI-related interoceptive/emotional perspective (e.g. Klein et al., 2007; Brass and Haggard, 2010; Ullsperger et al., 2010; Koban and Pourtois, 2014) or a cognitive perspective focussed on the fO (e.g. language) (e.g. Friederici et al., 2006; Higo et al., 2011). The specific aim of the present study was to assess whether these two regions could be dissociated with the spatial resolution of fMRI, and whether events related to performance monitoring recruit fO and/or aI.

We took advantage of three studies originally designed to assess the function of the mid-cingulate cortex (MCC) in performance monitoring (Amiez et al., 2013; Wutte et al., unpublished data) and we resorted to subject-by-subject analysis to assess precise structure-to-function relationships. Such analysis consists of performing linear registration in MNI space of individual subject data and assess local relationship between sulcal morphology and functional activity in each hemisphere of each subject. This analysis has the advantage of keeping intact the within-subject relationships between sulci and gyri and that the MNI coordinates could be compared with other neuroimaging studies (and may be used for future meta-analyses). This analysis has already demonstrated its value for the understanding of the anatomo-functional organization of the primary hand motor cortex (Yousry et al., 1997), the dorsal premotor cortex (Amiez et al., 2006; Amiez and Petrides, 2009), the inferior frontal junction (Derrfuss et al., 2012), the mid-cingulate cortex (Amiez et al., 2013; Amiez and Petrides, 2014; Procyk et al., 2016), the angular gyrus (Segal and Petrides, 2013), the postcentral cortex (Zlatkina et al., 2015), and the dorsolateral prefrontal cortex (Amiez and Petrides, 2007) (for comments on this method, see Tomaiuolo and Giordano, 2015). Note that such precise analysis may contribute to the improvement of future group-averaging methods based on non-linear/diffeomorphic brain registration targeted in this aI/fO region, and therefore to allow a better spatial and statistical detection of activity increases (Auzias et al., 2011; Pizzagalli et al., 2013).

Previous work shows systematic co-activation of MCC and aI/fO during performance monitoring (Dosenbach et al., 2006, 2007; Higo et al., 2011; Amiez et al., 2012a, 2012b, 2013), both after relevant feedbacks (Amiez et al., 2012a, 2012b, 2013), and action errors (Klein et al., 2007, Ullsperger and von Cramon, 2004; Wessel et al., 2011). We here focus on this co-activated aI/fO region and perform subject-by-subject analyses in order to assess the relationships between local aI and fO morphology and activation related to performance monitoring.

Classical cytoarchitectonic studies have delineated the opercular cortical region that lies next to the pars opercularis (BA 44) and pars triangularis (BA 45) (see Petrides, 2014 for discussion). For instance, Economo and Koskinas refer to the opercular region adjacent to the pars opercularis as area FCDop and the opercular region adjacent to the pars triangularis as area FDop (von Economo and Koskinas, 1925) and Petrides (2014) as areas 44op and 45op. A recent receptor architectonic study (Amunts et al., 2010) demonstrated the existence of four fO areas: Op8, located adjacent to area 44; Op9, located adjacent and ventral to area 45; Op7, located adjacent to Op8, and Op10, located adjacent to Op9 (Fig. 1). These fO areas display different receptor type distributions than those observed in areas 44 and 45. Taking differences in granularity and receptor organization together, we can hypothesize important functional dissociations between aI, fO areas (Op7, 8, 9, 10), and lateral frontal areas 44/45, as other authors suggested (Nieuwenhuys, 2012; Morel et al., 2013; Neubert et al., 2014). This anatomo-functional organization is also supported by a diffusion-weighted magnetic resonance imaging study showing a segregation of areas 44, 45, and fO on the basis of differential connectivity (Anwander et al., 2007).

The current study aimed therefore to locate the activations observed at the intersection of the circular insular sulcus and frontal operculum with reference to the organization of the cytoarchitectonic areas described above. The results demonstrated that performance monitoring activity is mainly associated to the fO and not (or very weakly to) the aI. We provide precise methodological steps to help further studies in the identification of the locus of activations in the aI/fO region.

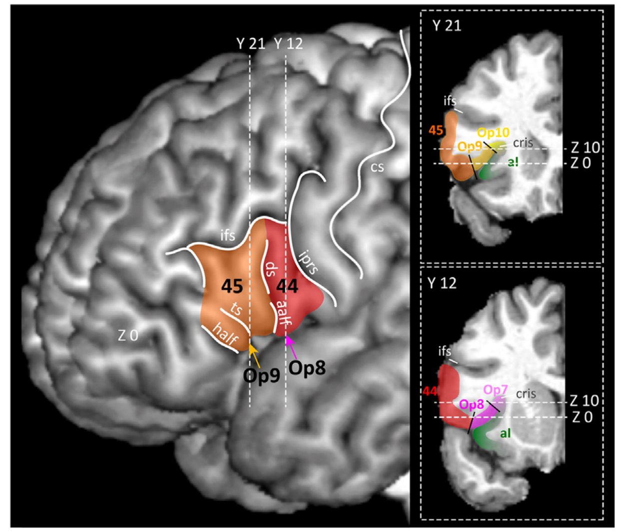

Fig. 1. Anatomical description of the region of interest in a typical subject (S2, study 1), according to Amunts et al. (2010) nomenclature. Areas 44 and 45 are represented on the cortical surface of the left hemisphere of S2 (left panel). Area 44 is delimited rostrally by the anterior ramus of the lateral fissure (aalf) and caudally by the inferior precentral sulcus (iprs). Area 45 is delimited caudally by the ascending anterior ramus of the lateral fissure (aalf) and rostrally by the horizontal anterior ramus of the lateral fissure (half). Dorsally, both areas 44 and 45 are delimited by the inferior frontal sulcus (ifs). On the left panel, the orange and pink arrows indicate the point of the frontal operculum in the depth of which Op9 and Op8 are located, respectively. Op8 is located adjacent to area 44, at the same anteroposterior level, as it can be observed on the coronal section presented in the bottom right panel (see dotted line on the cortical surface at MNI coordinate Y 12). Op7 is located adjacent to Op8, at the intersection between the operculum and the circular insular sulcus (cris). Op9 is located adjacent to area 45, at the same anteroposterior level, as it can be observed on the coronal section presented in the top right panel (see dotted line on the cortical surface at MNI coordinate Y 21). Op10 is located adjacent to Op9, at the intersection between the operculum and the circular insular sulcus (cris). Note that the limit of Op7 and Op10 within the insular wall is not represented because it has not been described by Amunts et al. (2010). Abbreviations: cs, central sulcus; ds, diagonal sulcus.

Materials and methods

The methods related to study 1 have been published previously (Amiez et al., 2013) and will therefore be presented briefly here. The methods in studies 2 and 3 have not been published and will be presented in greater detail.

Studies 1 and 2 relate to feedback monitoring during trial and error learning with, respectively, juice feedback and visual feedback. Study 3 corresponds to a compatibility task challenging action monitoring and error processing referred to as "internal" feedback processing.

These studies were performed in accordance with the Declaration of Helsinki and approved by the local ethics committees. All participants gave written consent to participate in these studies. All of them had normal or corrected-to-normal vision. None of them were taking medication or had any history of neurological disease.

Participants

Studies 1 and 2

Fifteen right-handed healthy volunteers (7 females, mean age = 26.3), participated in the first fMRI study. Twelve of them (6 females) participated in the second study.

Study 3

Thirty-two healthy volunteers participated in this study. Two subjects were excluded from the MR analysis due to neurological findings