NeuroImage 78 (2013) 426–438

Contents lists available at SciVerse ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Long-range functional interactions of anterior insula and medial frontal cortex are differently modulated by visuospatial and inductive reasoning tasks

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ARTICLE INFO

Article history:
Accepted 14 April 2013
Available online 25 April 2013

Keywords:
Cognitive abilities
Fluid reasoning
Long-range functional interactions
Functional magnetic resonance imaging (fMRI)
Task-dependent state

ABSTRACT

The brain is organized into functionally specific networks as characterized by intrinsic functional relationships within discrete sets of brain regions. However, it is poorly understood whether such functional networks are dynamically organized according to specific task-states. The anterior insular cortex (aIC)–dorsal anterior cingulate cortex (dACC)/medial frontal cortex (mFC) network has been proposed to play a central role in human cognitive abilities. The present functional magnetic resonance imaging (fMRI) study aimed at testing whether functional interactions of the aIC–dACC/mFC network in terms of temporally correlated patterns of neural activity across brain regions are dynamically modulated by transitory, ongoing task demands. For this purpose, functional interactions of the aIC–dACC/mFC network are compared during two distinguishable fluid reasoning tasks, Visualization and Induction. The results show an increased functional coupling of bilateral aIC with visual cortices in the occipital lobe during the Visualization task, whereas coupling of mFC with right anterior frontal cortex was enhanced during the Induction task. These task-specific modulations of functional interactions likely reflect ability related neural processing. Furthermore, functional connectivity strength between right aIC and right dACC/mFC reliably predicts general task performance. The findings suggest that the analysis of long-range functional interactions may provide complementary information about brain–behavior relationships. On the basis of our results, it is proposed that the aIC–dACC/mFC network contributes to the integration of task-common and task-specific information based on its within-network as well as its between-network dynamic functional interactions.

Introduction

The brain is organized in functional networks composed of multiple interacting brain regions. Functional connectivity analysis has been used to investigate intrinsic functional relationships (e.g., brain long-range communication) within discrete sets of brain regions (Bullmore and Sporns, 2009; Fox and Raichle, 2007; Van Dijk et al., 2010). Besides clarifying the intrinsic functional network structure of the brain, functional connectivity analysis also proved complementary to more conventional analysis of task-related neural responses. For instance, functional interactions between regions independent of stimulus-evoked neural responses (e.g., "background" or "baseline" connectivity) may be modulated by task demands, predict variability in task-performance and, hence, provide additional information about the brain–behavior relationship (Al-Aidroos et al., 2011; Baldassarre et al., 2012; Fox et al., 2007; Norman-Haignere et al., 2012; Wang et al., 2012).

A crucial, but still unresolved issue is how distinct networks flexibly interact (Bressler and Menon, 2010). Effective behavior is supported both by the functional integrity of segregated systems and by the dynamic integration of various systems at multiple spatio-temporal scales (de Pasquale et al., 2012; Sadaghiani et al., 2010; Tononi, 2004; Varela et al., 2001). Thus, a relevant question might be if neural networks are dynamically organized according to specific task-states in terms of functional connectivity patterns. It has been suggested that the functional network structure of the brain is dynamic. For instance, intrinsic functional networks are non-stationary and spontaneously interact at behaviorally relevant timescales (de Pasquale et al., 2012). Furthermore, learning may modify the covariance structure of spontaneous activity among distinct task-relevant networks (Lewis et al., 2009). However, these

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1053-8119/$ – see front matter
http://dx.doi.org/10.1016/j.neuroimage.2013.04.058

studies regarded connectivity patterns measured during a task-free state or rather persistent modulations of functional connectivity patterns not directly related to a particular ongoing task-state. In clear contrast, the present functional magnetic resonance imaging (fMRI) study tests whether long-range functional interactions are dynamically modulated by transitory, ongoing task demands.

One of the main functional neural networks of the human brain is the anterior insular cortex (aIC)–dorsal anterior cingulate cortex (dACC)/medial frontal cortex (mFC) network (Cauda et al., 2012; Deen et al., 2011; Dosenbach et al., 2007; Seeley et al., 2007; Taylor et al., 2009; see for reviews Dosenbach et al., 2008; Menon and Uddin, 2010; Nelson et al., 2010). With respect to its function, based on the finding that aIC and dACC/mFC are among the most commonly activated brain regions in neuroimaging research by a wide variety of tasks (Dosenbach et al., 2006; Duncan and Owen, 2000), it has been suggested that they may be involved in general cognitive processes shared across most goal-directed behaviors (Brass et al., 2005; Menon and Uddin, 2010; Wager and Smith, 2003). These functions could include sustained set-maintenance activity that spans across trials in task epochs (Dosenbach et al., 2006, 2007), cognitive control (Cole and Schneider, 2007), identification of stimuli with either internal or external personal salience (Seeley et al., 2007; see also Craig, 2009), or switching between distinct brain networks in order to engage task-relevant processes (Sridharan et al., 2008). The aIC–dACC/mFC network, especially the right hemisphere (RH) aIC, also showed interactions with other large-scale networks that dynamically configured across development (Uddin et al., 2011). Finally, aIC and dACC/mFC also have been proposed as part of a multi-demand (MD) network explaining performance efficiency in a large variety of cognitive activities that, hence, may cause widely diverse cognitive tests to positively correlate, a phenomenon represented by the general factor *g* in cognitive sciences (Barbey et al., 2012; Colom and Thompson, 2011; Duncan, 2010; Glascher et al., 2010).

In a previous fMRI study, we have shown that distinct, but psychometrically unidimensional fluid reasoning tasks were characterized by common neural activation patterns comprising the aIC–dACC/mFC network, though unique activation patterns were also detected (Ebisch et al., 2012). Moreover, task-common aIC activation significantly distinguished between individuals with high and low fluid intelligence abilities. Fluid intelligence (Gf) involves thinking logically, understanding relationships between stimuli, and solving problems in novel situations (Cattell, 1963, 1971), is central for the general factor *g* (Carroll, 1993; Cattell, 1963; Deary et al., 2010; Jensen, 1980, 1998; Spearman, 1927), and is supported by the aIC–dACC/mFC network (Kroger et al., 2002; Roca et al., 2010). It remains unclear, however, if such distinct cognitive tasks also can be characterized by differential background functional interactions between distant brain regions and whether these could provide information complementary to task-evoked activation patterns. Specifically, we wondered whether functional interactions of the aIC–dACC/mFC network commonly modulated by distinct tasks could involve other networks based on specific, ongoing cognitive demands required by these tasks.

Using the same fMRI dataset (see Ebisch et al., 2012), here we compare functional interactions of the aIC–dACC/mFC network during two distinct fluid reasoning tasks, Visualization and Induction. Induction is defined by the ability to inspect a class of stimuli and then to infer/induce/deduce a common characteristic underlying these materials, whereas Visualization involves manipulating or transforming images of spatial patterns into other visual arrangements. In accordance with Carroll's three strata theory of human cognitive abilities (Carroll, 1993), an extensive psychometric calibration study demonstrated that the Induction and Visualization tasks represent distinct "narrow" abilities characterized by some specific variance, but they also show significant common variance than can be explained by the general Gf factor. Furthermore, tasks were carefully matched for difficulty, perceptional input and type of task.

FMRI functional coupling can be quantified by measuring the temporal correlation between low-frequency BOLD signals in distant brain regions (Fox and Raichle, 2007; Van Dijk et al., 2010). This method allows whole-brain analyses not constrained to a pre-definite set of brain regions, as instead required by effective connectivity approaches such as dynamic causal modeling (Friston, 2011), and to test for task-specific functional interactions of task-common brain regions, rather than task-specific brain regions required by psychophysical interaction analysis (O'Reilly et al., 2012). Seed regions of interest (ROIs) in aIC and dACC/mFC were based on the coordinates of a core working memory (WM) network identified by a recent meta-analysis of 189 neuroimaging studies, likely representing cognitive processes that are fundamental, though not specific to WM, and largely overlapping with the aIC–dACC/mFC network (Rottschy et al., 2012). Although the WM core network may include multiple functional networks, the present study focuses on aIC and dACC/mFC as the putative core of a functionally distinguishable network (e.g., Cauda et al., 2012; Menon and Uddin, 2010; Taylor et al., 2009) with distinctive anatomical features, the von Economo neurons that possibly underlie fast control signals to other networks (Allman et al., 2011; Menon and Uddin, 2010; Sridharan et al., 2008; von Economo and Koskinas, 1925). In line with the association between WM and the aIC–dACC/mFC network, WM has been suggested as a crucial and common ability underlying most goal-directed behavior and Gf (Colom et al., 2004, 2007; Engle et al., 1999; Gray et al., 2003; Halford et al., 2007; Jaeggi et al., 2008; Martinez et al., 2011; Saggino et al., 2006).

Based on its central role in goal-directed behavior and cognitive control, we hypothesized that the aIC–dACC/mFC network will show sustained interaction with other brain regions dynamically related to specific, ongoing task-demands. These brain regions could include those involved in the particular tasks as evidenced by specifically enhanced task-evoked activation for either the Induction or the Visualization task (see Ebisch et al., 2012). Background functional interactions also could provide information complementary to task-evoked activation patterns about the neural correlates of cognitive abilities, reflecting distinct physiological processes (Bressler and Menon, 2010; Northoff et al., 2010). Alternatively, they may reflect the intrinsic functional network structure of the brain independently of task-state (Fox and Raichle, 2007). Finally, a significant relationship is expected between task-performance and task-specific or task-common functional connectivity patterns (Cole et al., 2012).

Material and methods

Participants

Twenty-two female university students (age range: 20–24) were selected for participation in the present study according to the procedures described in Ebisch et al. (2012) as both studies concern the same participants. All participants were healthy, right-handed (Edinburgh Handedness Inventory score > 0.85) and had normal or corrected-to-normal vision capabilities. Written informed consent was obtained from all participants after full explanation of the study's procedure, in line with the Declaration of Helsinki. The experimental protocol was approved by the local institutional ethics committee. Participants were paid 25 € for their participation in the fMRI experiment.

Calibration study of the Gf test

The administered fluid intelligence test (FIT) was created by R.R. and A.S. (Romanelli and Saggino, under review). The FIT comprised an item bank of 220 items. Following Carroll's framework (1993), four subtests were included in the original FIT: induction, quantitative reasoning, visualization, and spatial relationships. Two subtests were chosen for the present study as measuring the abilities with the highest and most specific loadings on the Gf construct (Carroll,