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Research report

Granger causal connectivity dissociates navigation networks that subserve allocentric and egocentric path integration

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ABSTRACT

Studies on spatial navigation demonstrate a significant role of the retrosplenial complex (RSC) in the transformation of egocentric and allocentric information into complementary spatial reference frames (SRFs). The tight anatomical connections of the RSC with a wide range of other cortical regions processing spatial information support its vital role within the human navigation network. To better understand how different areas of the navigational network interact, we investigated the dynamic causal interactions of brain regions involved in solving a virtual navigation task. EEG signals were decomposed by independent component analysis (ICA) and subsequently examined for information flow between clusters of independent components (ICs) using direct short-time directed transfer function (sdDTF). The results revealed information flow between the anterior cingulate cortex and the left prefrontal cortex in the theta (4–7 Hz) frequency band and between the prefrontal, motor, parietal, and occipital cortices as well as the RSC in the alpha (8–13 Hz) frequency band. When participants prefered to use distinct reference frames (egocentric vs. allocentric) during navigation was considered, a dominant occipito-parieto–RSC network was identified in allocentric navigators. These results are in line with the assumption that the RSC, parietal, and occipital cortices are involved in transforming egocentric visual-spatial information into an allocentric reference frame. Moreover, the RSC demonstrated the strongest causal flow during changes in orientation, suggesting that this structure directly provides information on heading changes in humans.

1. Introduction

Successful navigation in well-known and unknown environments requires simultaneous processing and integration of spatial information based on allocentric and egocentric spatial reference frames (SRFs) (Klatzky, 1998). Reference frames are a means to represent spatial information based on egocentric or allocentric coordinate systems. An allocentric representational system is centered on aspects of the environment and represents the location of entities in space with respect to allothetic information like cardinal directions. In contrast, an egocentric representational system is centered on aspects of the navigator's physical structure and thus varies with changes in orientation of the navigator. Importantly, successful navigation requires integration of spatial information from both egocentric and allocentric representations to allow goal-directed action in the environment (Gramann, 2013).

The computation, integration, and exchange of spatial information based different SRFs involves a network of brain structures including the medial temporal cortex, the cingulate gyrus, the frontal, parietal, and occipital cortices, as well as the retrosplenial complex (RSC) (Hartley et al., 2003; Maguire et al., 1998; Whitlock et al., 2008). Imaging studies investigating the neural structures underlying egocentric and allocentric spatial navigation have revealed that the parietal cortex subserves the computation of egocentric SRFs by integrating self-motion cues from the kinesthetic, vestibular, and visual systems (Zaehle et al., 2007; Committeri et al., 2004; Cohen and Andersen, 2002). In contrast, the use of an allocentric SRF mainly engages medial temporal brain structures (Doeller et al., 2010; Ekstrom et al., 2003; Howard et al., 2014; Jacobs et al., 2013; Maguire et al., 1998; Wolbers and Büchel, 2005). Moreover, the RSC has been found to play important roles in computing and maintaining allocentric spatial representa-

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tions and in transforming spatial information between egocentric and allocentric reference frames (Byrne et al., 2007; Dhindsa et al., 2014; Vann et al., 2009; Zhang et al., 2012).

Many of these brain areas are simultaneously active during navigation tasks, and coupling of functionally specialized brain regions appears to be necessary for successful navigation (Ekstrom et al., 2014). Recent EEG studies have reported high coherence of the alpha and theta frequency bands in a large-scale cortical network recruited during spatial navigation (Li et al., 2009; Ramos-Loyo and Sanchez-Loyo, 2011). Connectivity across various brain areas with modulations in the theta and alpha frequency ranges may support the synchronization of large-scale cortical interactions (Palva and Palva, 2011; Sauseng et al., 2005) and is one of the essential neuronal mechanisms for higher cognitive functions (Siegel et al., 2012). However, investigations describing the flow of information within these cortical networks with high temporal resolution are scarce, and the architecture of the spatial navigation network is not well understood.

To further our understanding of connectivity in the navigation network, we used high-density EEG and Granger causality analysis to investigate which brain regions are causally connected while participants updated their position and orientation during navigation. Previous studies using path integration paradigms showed that the individual preference to use either an egocentric or an allocentric reference frame is stable for individuals (Gramann et al., 2005), is based on higher cognitive functions (Gramann et al., 2009), depends on core areas of the navigation network (Gramann et al., 2006; Gramann et al., 2010; Seubert et al., 2008), and can be reliably observed in different populations (Gramann et al., 2012; Goeke et al., 2013, 2015). Previous studies also demonstrated navigation-related modulations of distinct frequency bands that were dependent on the reference frame proclivity of participants (Chiu et al., 2012; Gramann et al., 2010; Lin et al., 2015; Plank et al., 2010). To further investigate the information flow in the human navigation network and to understand how information flow differs between egocentric and allocentric navigators, we analyzed granger causal information flow in EEG data recorded during a virtual path integration task.

2. Results

For allocentric and egocentric participants, the behavioral performance including homing angle and homing position were reported. The analysis of direct information transfer between clusters of ICs revealed event related causality (ERC) in the time-frequency distribution between several cortical regions. Widespread brain regions were involved in path integration, revealing directed ERC between the anterior cingulate cortex (ACC), the RSC, and the lateral prefrontal, motor, parietal, and occipital cortices for all participants. The causal information flows were significantly increased in distinct frequency bands including delta (below 3.5 Hz), theta (4–7 Hz), alpha (8–13 Hz), and beta (14–30 Hz).

2.1. Behavioral performance

The mean homing responses are displayed in Fig. 1 for both allocentric and egocentric indicated as dotted and straight line, respectively. In Fig. 1A, the result of homing response indicating that using an egocentric SRF indicated opposite homing directions as compared to homing responses of allocentric, using an allocentric SRF ($p < .01$). The homing responses for allocentric and egocentric consistently differed in each path configuration supported the hypothesis that both strategy groups used a distinct reference frame for their homing responses for path integration in the virtual navigation environment. The homing performance also shows the significant differences in homing error for allocentric and egocentric participants in Fig. 1B ($p < .01$). In Fig. 1B, egocentric reveals higher accuracy for low eccentric end positions (18.4°, 26.5°, and 33.6), in contract, the allocentric were more accurate for higher eccentricities (above 45°).

2.2. Time-frequency distribution of causal information inflow

Fig. 2 displays the average dynamic causal relationships between selected anterior brain regions during path integration as compared to the baseline condition for egocentric and allocentric participants (please see Supplementary Fig. 1 for connectivity pattern between all clusters). As shown in Fig. 2, significant ERC increases were observed between a cluster with its centroid located in or near the ACC and clusters with their centroids located in or near the left and right prefrontal areas (bootstrapping, false discovery rate (FDR)-adjusted $p < .05$). The ERC flow between these areas was significant for the theta, the alpha, and the beta frequency band (bootstrapping, FDR-adjusted $p < .05$). The sustained bidirectional ERC increase in the theta and alpha band between ACC and left prefrontal cortex (ACC ↔ LPF) was observed for both egocentric and allocentric participants while only egocentric navigators showed ERC increases in the beta band around 20 Hz (ACC → LPF & ACC → RPF). The prefrontal cortex further revealed sustained ERC decreases from the left motor to the left prefrontal cortex (LM → LPF) for allocentric navigators only. Additional sustained ERC increases between the prefrontal cortex and posterior cortex were observed (see Supplementary Fig. 1), from the left parietal to the left prefrontal cortex (LP → LPF).

The time course of ERC demonstrated more pronounced information flow in the theta band between ACC and the left motor cortex (ACC ↔ LM) for egocentric participants during the stimulus turn (see Fig. 2). Reciprocal ERC in the alpha band between right prefrontal and the right motor cortex (RPF ↔ RM) increased during the stimulus turn and the following straight segments. For allocentric navigators, in contrast, alpha ERC from the left prefrontal cortex to the left motor cortex (LPF → LM) was strongest during stimulus turns and part of straight segments before and after the turn (see Fig. 2). Allocentric participants also showed reciprocal alpha ERC between the right prefrontal cortex and the right motor cortex (RPF ↔ RM) mainly during straight segments (see Fig. 2).

Stronger ERC increases were revealed in more posterior brain regions including the motor, the parietal, and the occipital cortex as well as the RSC (see Fig. 3). ERC increases in the alpha band were found between the motor and parietal areas during the complete path most pronounced for egocentric participants. Significant reciprocal alpha ERCs between the left and right motor cortices (LM ↔ RM) was only found for egocentric participants while alpha ERCs between the left and right parietal cortices (LP ↔ RP) were more pronounced in allocentric participants (bootstrapping, FDR-adjusted $p < .05$). Both strategy groups demonstrated stronger intrahemispheric ERC, for example, reciprocal alpha ERC between the parietal and motor cortices within the right and left hemisphere were more pronounced than between the hemispheres. The left parietal cortex showed more pronounced ERC with anterior regions such as the prefrontal and motor cortices, whereas the right parietal cortex showed stronger ERC with posterior regions such as the RSC and occipital cortex (see Supplementary Fig. 1). This difference in the ERC pattern was more pronounced for allocentric participants (bootstrapping, FDR-adjusted $p < .05$).

In or near the RSC, ERC flows from and to the parietal and occipital cortices comprised a wider frequency range, including the delta and alpha bands. Bidirectional ERC between the RSC and parietal cortex (RSC ↔ RP) in the alpha and delta frequency bands was found for both allocentric and egocentric participants, although more pronounced in allocentric navigators (bootstrapping, FDR-