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Task modulates functional connectivity networks in free viewing behavior

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ABSTRACT

In free visual exploration, eye-movement is immediately followed by dynamic reconfiguration of brain functional connectivity. We studied the task-dependency of this process in a combined visual search-change detection experiment. Participants viewed two (nearly) same displays in succession. First time they had to find and remember multiple targets among distractors, so the ongoing task involved memory encoding. Second time they had to determine if a target had changed in orientation, so the ongoing task involved memory retrieval. From multichannel EEG recorded during 200 ms intervals time-locked to fixation onsets, we estimated the functional connectivity using a weighted phase lag index at the frequencies of theta, alpha, and beta bands, and derived global and local measures of the functional connectivity graphs. We found differences between both memory task conditions for several network measures, such as mean path length, radius, diameter, closeness and eccentricity, mainly in the alpha band. Both the local and the global measures indicated that encoding involved a more segregated mode of operation than retrieval. These differences arose immediately after fixation onset and persisted for the entire duration of the lambda complex, an evoked potential commonly associated with early visual perception. We concluded that encoding and retrieval differentially shape network configurations involved in early visual perception, affecting the way the visual input is processed at each fixation. These findings demonstrate that task requirements dynamically control the functional connectivity networks involved in early visual perception.

1. Introduction

Studies of brain functional connectivity (for a review, see Rubinov and Sporns, 2010) exhibit a vital interest in dynamic network reconfiguration (Medaglia et al., 2015). Reconfiguration during eye-movement, while hitherto unexplored, may be of particular interest. This process seems to occur instantaneously: every saccadic eye-movement is accompanied by phase resetting of ongoing electrical brain activity (Rajkai et al., 2008; Ito et al., 2011). Each reset synchronizes the activity of multiple brain systems involved in visual processing, including oculomotor, sensory, and attentional networks, in order to configure them for new information uptake (Jutras and Buffalo, 2010). The dynamic configuration of these network, however, should be flexible to be effective, and hence will show sensitive dependency on the task. We therefore raised the question: how specific to the task is the functional connectivity that appears immediately after a saccade?

The effects of task on brain networks have intensively been studied in relation to memory. fMRI revealed that early visual areas carry information about the identity of memorized items (Harrison and Tong, 2009; Serences et al., 2009; Emrich et al., 2013). Task goals are reflected in the activity of various parts of the frontal and parietal cortices (Lee et al., 2013; Freedman et al., 2001; Rowe et al., 2008). Via feedback connections from the fronto-parietal to sensory areas, task-specific influences coordinate the construction and maintenance of stimulus representations in the posterior areas (D'Esposito and Postle, 2015; Sadaghiani and Kleinschmidt, 2016; Passingham et al., 2013). In free viewing behavior, perceptual information over sequential eye movements accumulates in visual short-term memory (Irwin, 1991; Melcher and Kowler, 2001; Prime et al., 2011). These findings suggest that memory-related brain networks may shape visual processing during eye movement.

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Visual processing at fixations is manifested in EEG, in the lambda activity. This activity reaches a maximum around 100 ms after fixation onset, reflecting early visual processing at fixation (Dimigen et al., 2009; Gaarder et al., 1964; Kazai and Yagi, 2003; Thickbroom et al., 1991). In the frequency domain, the lambda activity is most prominent in the alpha band (Dimigen et al., 2009; Ossandón et al., 2010; Nikolaev et al., 2016). The lambda activity has the spatiotemporal characteristics of a travelling wave (Zanos et al., 2015; Giannini et al., 2015).

Since early perceptual networks are under top-down task-specific influences (D'Esposito and Postle, 2015; Sadaghiani and Kleinschmidt, 2016), we propose that memory processes modulate the topological characteristics of brain networks in fixation intervals. We investigated whether the type of memory task could influence early perceptual networks at each fixation during free visual exploration of a display.

We analyzed the functional connectivity networks in lambda intervals belonging to two different stages of a combined visual search-change detection task – encoding and retrieval. In this task, two displays are shown in succession, a search and a change detection display. In the search display, observers have to locate targets and store their identities into visual short-term memory; during the change detection display, these targets have to be retrieved from memory and compared with the current ones. Thus, inspection of the first display is dominated by encoding and the second by retrieval. This offers the opportunity to compare fixation-related brain networks for (near)-identical displays under contrasting task requirements.

Analysis of EEG activity in free viewing behavior is complicated by the issue of overlapping EEG responses due to the sequential nature of saccadic eye movements (Dimigen et al., 2011; Dias et al., 2013; Nikolaev et al., 2016). If eye movement characteristics are different between conditions they may systematically affect fixation-related EEG, making its comparison between conditions unreliable. To ensure that the amplitude of lambda activity is comparable between visual search and change detection stages we thoroughly matched eye movement characteristics between these conditions (Nikolaev et al., 2016).

Measures of functional connectivity may be inflated by volume conduction in scalp EEG. We adopted an index that is independent of volume conduction as our connectivity measure: the weighted phase lag index (WPLI) (Vinck et al., 2011). The WPLI shows high test-retest-reliability for estimation of the graph-theoretical properties of brain networks (Hardmeier et al., 2014). Functional connectivity networks are calculated among sensors (Micheloyannis et al., 2009; Boersma et al., 2011; Demuru et al., 2013; Hardmeier et al., 2014; Li et al., 2016; Yu et al., 2016; Xing et al., 2017) or, alternatively, among sources (Sun et al., 2014; Tewarie et al., 2014; Olde Dubbelink et al., 2014; van Dellen et al., 2014). The latter facilitates interpretation and comparison across individuals. Source localization solutions, however are not unique, especially when the number of sources is large. Neither of these approaches has a solution to the fundamental problem that, since WPLI is independent of amplitude, spurious couplings can be observed in regions remote to their respective sources (Schoffelen and Gross, 2009). In the current study, we are interested in network connectivity statistics rather than in interpreting the connections between specific sources. Interpreting individual sources in the fixation interval is complicated by the observation that lambda activity has traveling wave characteristics (Zanos et al., 2015; Giannini et al., 2015). Moreover, the problems of inflated connectivity estimates may be considered to affect our experimental conditions equally, as long as these do not differ in the EEG amplitude. For these reasons, in this study we analyzed brain networks in sensor space. WPLI values calculated between sensor pairs were used as the basis for assembling functional connectivity networks.

We constructed weighted undirected networks and studied their global properties, such as clustering, path length, and modularity (Moussa et al., 2011) as well as local clustering and local interconnectivity (Ekman et al., 2012). Both global and local measures describe brain activity along the dimensions of integration (connectedness, path length, efficiency) and segregation (average clustering coefficient, modularity); local measures describe to what extent a site is integrated with (centrality) or segregated from (clustering, modularity) the rest of the network. Integration and segregation are dynamic modes of brain activity, which play a fundamental role in information processing (Bressler and Kelso, 2001).

We found that the search condition is associated with a more segregated mode of operation than the change detection condition. Since memory encoding is the predominant ongoing task in the search condition, and memory retrieval in the change detection condition, we conclude that in free viewing behavior the ongoing brain process defined by the task requirements dynamically reconfigures the brain network connectivity structure, in a manner likely to systematically modify the way the visual input at each fixation is processed.

2. Material and methods

We used a dataset of simultaneous EEG-eye movement recordings, of which the eye movement and EEG characteristics were described before (Meghanathan et al., 2015; Nikolaev et al., 2016).

2.1. Participants

Twenty-three participants (7 male/16 female) in the age range of 18–29 years took part in the experiment. The departmental Ethics Committee of KU Leuven had approved the study and all participants had provided written consent. Data from two participants were not analyzed because of excessive eye movements outside the screen. Of the remaining, we used the data from 11 participants that fulfilled the eye movement matching criteria described below.

2.2. Task

Stimulus displays comprising 40 items, of which 3, 4 or 5 were target “T”s ($0.41^\circ \times 0.41^\circ$) placed randomly among the remaining distractors “L”s ($0.31^\circ \times 0.41^\circ$), were presented in black within a rectangular $32.9^\circ \times 23.12^\circ$ region on a grey background of size $39.9^\circ \times 30.5^\circ$. All items were surrounded by black circles (0.83°) to avoid being detected peripherally. Targets and distractors were randomly oriented in one of 20°, 80°, 140°, 200°, 260° or 320°, with all targets oriented differently within a trial.

In each trial, the first stimulus display presented was the *search* display. It remained on the screen for 10s. Participants were asked to locate targets and remember their orientations. After an interval of 1–1.5s, a *change detection* display was presented. In half of the trials, this second display was identical to the first; in the other half the orientation of one of the targets was changed. Participants were asked to indicate if a change had occurred or not, by pressing counterbalanced left or right arrow keys with their dominant hand. The change detection display was presented for 10s or until keypress, whichever was shorter. Afterwards, participants were given feedback by presenting the same display with targets encircled in green if the response was correct and in red if response was incorrect. The changed target was additionally surrounded by a larger circle (Fig. 1).

2.3. Experiment setup

Participants completed 270 trials over 10 blocks separated by short breaks, in an experiment session lasting approximately 1.6 h. Eye movements and EEG were recorded simultaneously. The recording setup involved 3 computers – one for eye movement data collection, one for EEG data collection and another for stimulus presentation. The stimulus display was at a distance of 55 cm from the participant and was presented on a CRT monitor of size 40 cm × 30 cm (1600 × 1200 pixels) and a refresh rate of 75 Hz. A TTL pulse was issued via a parallel port from the stimulus presentation computer to synchronize trial start events between the EEG and eye tracking systems.