Attention reorganizes connectivity across networks in a frequency specific manner

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ABSTRACT

Attention allows our brain to focus its limited resources on a given task. It does so by selective modulation of neural activity and of functional connectivity (FC) across brain-wide networks. While there is extensive literature on activity changes, surprisingly few studies examined brain-wide FC modulations that can be cleanly attributed to attention compared to matched visual processing. In contrast to prior approaches, we used an ultra-long trial design that avoided transients from trial onsets, included slow fluctuations (< 0.1 Hz) that carry important information on FC, and allowed for frequency-segregated analyses. We found that FC derived from long blocks had a nearly two-fold higher gain compared to FC derived from traditional (short) block designs. Second, attention enhanced intrinsic (negative or positive) correlations across networks, such as between the default-mode network (DMN), the dorsal attention network (DAN), and the visual system (VIS). In contrast attention de-correlated the intrinsically correlated visual regions. Third, the de-correlation within VIS was driven primarily by high frequencies, whereas the increase in DAN-VIS predominantly by low frequencies. These results pinpoint two fundamentally distinct effects of attention on connectivity. Information flow increases between distinct large-scale networks, and de-correlation within sensory cortex indicates decreased redundancy.

1. Introduction

Attention is a key mechanism for optimizing adaptive behavior. It sharpens perceptual tuning (Spitzer et al., 1988), lowers perceptual thresholds (Treue and Martínez Trujillo, 1999), and shortens reaction times (Eason et al., 1969). The behavioral advantage is conveyed by a number of neural processes, many of which are not yet fully understood. One aspect involves local changes in neuromodulators, synaptic, neural and circuit properties (Herrero et al., 2008). These are accompanied by up-modulation of neural responses in sensory cortices, generally more so towards higher processing stages, as observed both in neurophysiology (Moran and Desimone, 1985) and fMRI (Kastner et al., 1998). Another aspect concerns changes in inter-regional connectivity. Sensory processing is up-modulated through long-distance projections from the dorsal attention network that is also up-modulated by attention (Corbetta and Shulman, 2002). At the same time, the default-mode network, involved in introspection and mind-

wandering, is down-modulated (Fox et al., 2005; Greicius et al., 2003). Attentional effects are therefore mediated by connectivity changes that orchestrate activity modulation across the whole brain and that are task-dependent (Gonzalez-Castillo et al., 2015; Mattar et al., 2015). Their characterization is crucial for our understanding of brain function in health and disease.

At fast time-scales, this has been done using electrophysiology. Monkey studies demonstrated that attention selectively increases synchronization in high-frequency (gamma) LFP oscillations between visual regions and those of the dorsal attention network, the lateral intraparietal area (LIP) and the frontal eye fields (FEF) (Gregoriou et al., 2009; Saalmann et al., 2007), with corresponding findings in human MEG (Siegel et al., 2008). In turn, these couplings are thought to be modulated by the dorso-frontal attention network through theta-to-beta frequency bands (Fries, 2015; Hanslmayr et al., 2013).

At slower time-scales, interregional interactions have been examined using fMRI. For example, attentional coupling between V2 and

V5/MT was shown to be mediated by parietal activity (Friston and Büchel, 2000), early visual areas enhanced correlations topographically (Haynes et al., 2005), and early and high-level visual regions selectively coupled as function of the attended feature (Al-Aidroos et al., 2012). Other fMRI studies examined relations between visual and parietal regions, and found increases as well as decreases between distinct combinations of visuo-parietal regions (Lauritzen et al., 2009). Interestingly, two studies found a de-correlation among visual regions, one with attention compared to rest (Spadone et al., 2015), the other with visual stimulation compared to rest (Bartels and Zeki, 2005). But since both studies used resting state (with minimal or no visual stimulation) as comparison point, it is unclear whether visual de-correlation can be attributed to attention or to sensory processing. The distinction would be crucial, as such decorrelations may point to reduction of shared noise, and increased information, and have also been observed in noise-correlations of spiking activity within V4 (Cohen and Maunsell, 2009; Mitchell et al., 2009).

Unfortunately, there are not many studies examining whole-brain connectivity changes as a function of attention with matched visual stimulation. Most of these studies are optimized for detection of changes in activity rather than connectivity, and thus used short trials only lasting 10–20 s (Al-Aidroos et al., 2012; Friston and Büchel, 2000; Haynes et al., 2005; Lauritzen et al., 2009). However, while short trials are optimal for activity contrasts, they lead to severe limitations for connectivity measurements. In particular, condition on- and offsets induce large, long-lasting transients affecting time-courses in consequent trials. Their inconsistent nature prevents removal by mean regression. Only much longer trials allow their removal, as well as inspection of faster and slower frequency bands, introduced in resting-state connectivity analyses (Cordes et al., 2001; Salvador et al., 2008; Wu et al., 2008).

Finally, also real life scenarios frequently require deployment of attention over much longer durations, e.g. during steering tasks, focused work, or communication. Hence, the fast-paced paradigms that are optimal for neuroimaging may not optimally characterize neural processes serving longer-term attention.

For these reasons we examined connectivity across visual, dorsal-attention, and default-mode networks during identical visual stimulation but distinct attentional load. We applied the same paradigm in traditional blocks of 20 s and in ultra-long blocks lasting 2 min. Functional connectivity across and within networks was analyzed as a function of block duration and attentional state, and data of ultra-long blocks were additionally analyzed in a frequency segregated manner.

Our results indicate that massively stronger connectivity modulation can be observed during long periods compared to short trials. They also show that distinct frequency bands mediate the de-correlation among visual regions and the overall enhancement of correlations across the brain's large scale networks.

2. Materials and methods

2.1. Subjects

22 healthy volunteers (9 female, 13 male, 21–37 years) participated in the study. Two subjects were excluded from the analysis due to poor signal quality, leading to a total of 20 subjects entering connectivity analyses. All subjects provided informed consent and the study protocol was approved by the joint ethics committee of the university clinics and the Max Planck Institute. Prior to scanning, each subject participated in a psychophysics session to determine the visual noise level required in the main motion stimulus to achieve consistent performance of around 80% correct across subjects. This was achieved by adjusting the ratio of target to distractor dots in the visual flow stimulus; see below for details.

2.2. Main experimental design and task

We conducted two main experiments, one with short trials of 20 s length, and one with long trials of 120 s length, with otherwise identical parameters and conditions. Both experiments had the same two experimental conditions: one attention condition and one passive viewing condition. The visual stimulus was identical in both conditions. It consisted of a continuous stream of random dot motion that changed its state every second (with a jitter of ± 0.25 s) in a random sequence between 4 possible states: clockwise-outward, clockwise-inward, counterclockwise-outward and counterclockwise-inward. In the attention condition, clockwise-outward was set as target motion that observers needed to detect and indicate by button press. In both conditions, participants were required to fixate a central fixation cross.

Long trial runs lasted 480 s and contained four stimulus blocks (of 120 s each) such that each condition was repeated twice. Short trial runs lasted 320 s and contained 16 blocks (of 20 s each) and each condition was repeated 8 times. The trial sequence was counterbalanced across runs. Results were replicated using equal amounts of data points for comparisons between long- and short-trial experiments (see also Supplemental information).

2.3. Stimulus details

Dot-kinematograms consisted of 300 dots on a grey background of 180 cd/m^2 luminance. Dots were randomly black or white at 100% contrast, and were randomly positioned within a round annulus that extended to the edge of the screen (10 degrees eccentricity). Their rotation speed around the center was 3°/s (either clockwise or counterclockwise), and their contraction/expansion speed was also 3°/s. The size of the dots randomly varied between 0.35 to 0.71°. Dots were rear-projected onto a projection screen and viewed via an angled surface-mirror, with a projector resolution of 1280×1024 pixels at a refresh rate of 75 Hz. All stimuli were generated using the Matlab (Mathworks) extension Psychtoolbox (3.0.8) running on Windows XP (32 bit).

Subjects were instructed to either detect the target-motion in the attention blocks or to fixate only in passive viewing blocks. The central fixation disc displayed a 't' throughout the attention task, or an 'x' during passive viewing.

The performance level was kept around 80% correct for each subject individually as follows. In addition to each of the four presented coherent motion types a varying fraction of the presented dots moved in random directions, constituting noise. Using the QUEST procedure implemented in Psychtoolbox, the fraction of noise dots was altered according to the subject's responses. The noise-fraction was inherited for subsequent passive viewing trials to maintain matched visual stimuli across conditions. The initial noise-level was determined in each subject individually prior to scanning to ensure that only minimal adjustments had to be made during scanning.

2.4. Region of interest (ROI) definition

Regions of interest (ROIs) were defined for the task positive network (TPN) and for the default mode network (DMN). The TPN consisted of following ROIs: retinotopic areas V1-V3, hV4, V5+/MT+, and the dorsal attention network (DAN) including frontal eye-fields (FEFs) and the intraparietal sulcus (IPS). The DMN consisted of the middle frontal cortex (MFC), the posterior cingulate cortex (PCC), and the lateral parietal cortex (LP). All non-retinotopic ROIs (V5/MT+, DAN and DMN ROIs) were defined using the MarsBaR toolbox (Brett 2002) with the contrasts specified below. We used individually varying p-values (0.05 > p > 0.001, uncorrected) for each participant and ROI in order to maintain comparable ROI sizes across participants (Fox et al., 2009; Murray and Wojciulik, 2004).

Directly preceding the main experiment, a separate localizer experiment was conducted in each participant to identify area V5/