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Reversal of cortical information flow during visual imagery as compared to visual perception

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ABSTRACT

The role of bottom-up and top-down connections during visual perception and the formation of mental images was examined by analyzing high-density EEG recordings of brain activity using two state-of-the-art methods for assessing the directionality of cortical signal flow: state-space Granger causality and dynamic causal modeling. We quantified the directionality of signal flow in an occipito-parieto-frontal cortical network during perception of movie clips versus mental replay of the movies and free visual imagery. Both Granger causality and dynamic causal modeling analyses revealed an increased top-down signal flow in parieto-occipital cortices during mental imagery as compared to visual perception. These results are the first direct demonstration of a reversal of the predominant direction of cortical signal flow during mental imagery as compared to perception.

Introduction

Visual mental imagery and perception share similar cortical representations (Cichy et al., 2012; Kosslyn, 2005; Pylyshyn, 2003). It has been proposed that, while brain forward connections convey information from the outside world, backward connections might have a dominant role during the forming of mental images in the absence of external bottom-up inputs (Ganis and Schendan, 2008; Ishai et al., 2000; Kalkstein et al., 2011; Kosslyn, 2005). Despite the relevance of top-down and bottom-up dynamics for the understanding of the generative mechanisms of visual mental representations (Corbetta and Shulman, 2002; Friston, 2002; Kosslyn, 2005), a direct quantitative comparison of the directionality of neural signal flow during visual perception and imagery is still missing.

In the present study, we exploited the temporal resolution of high-density electroencephalography (hdEEG) and two state-of-the-art causal modeling methods to measure cortical directed connectivity during visual perception and visual mental imagery. We hypothesized that during visual perception, bottom-up connectivity from early visual areas to higher order cortices would be predominant; whereas during visual mental imagery, higher order areas would lead the recruitment of early visual cortices in a top-down manner. This idea is consistent with current notions of visual imagery and perception and with indirect experimental evidence (Ganis and Schendan, 2008; Ishai et al., 2000; Kalkstein et al., 2011; Kosslyn, 2005; Mechelli et al., 2004).

We quantified directed connectivity from hdEEG recordings by means of two complementary approaches: Granger causality (GC) and dynamic causal modeling (DCM) (Friston et al., 2013). GC measures how the past signal of one region improves the prediction of the present signal of another region. We inferred cortical GC in the context of a state-space multivariable autoregressive (MVAR) model developed by our team (Cheung et al., 2010). DCM for cross-spectral densities (CSD) uses a nonlinear generative neural model (Friston et al., 2012) to estimate phase-delays and power spectrum contents and infer directionality of connectivity between modeled cortical areas. Both methods have been used in the neuroimaging literature to estimate cortical activity directionality. In the absence of a gold standard (Friston et al., 2013), and because of the different assumptions of GC and DCM, we opted to use both methods to increase confidence in the results.

We recorded brain activity while subjects engaged in both visual perception and imagery under two complementary paradigms: a short movie paradigm, designed to have the highest similarity between the content of visual imagery and that of perception, and a daydreaming paradigm, intended to optimize the spontaneous flow of visual processing during mental imagery. Our experimental design includes two ways of generating visual perception or imagery: 1) the replay of an extrinsically generated percept, and 2) an intrinsically generated series of

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mental images followed by an independently generated percept. We deliberately chose this strategy to confirm the generality of our results, irrespective of how the perceptual content was generated.

We directly compared long-range directed connectivity during imagery and perception in a cortical network comprised of an early visual area, the inferior occipital gyrus (IOG), and two higher order cortices, the superior parietal lobule (SPL), and the dorsolateral prefrontal cortex (PFC, Brodmann area 46) (Fig. 1). Each of these cortical regions, or nodes of the network, is known to be activated during both perception and imagery tasks (Ganis and Schendan, 2008; Gardini et al., 2009; Harrington et al., 2007; Ishai et al., 2000).

Methods

Participants

Twenty healthy right-handed volunteers (10 females and 10 males, mean age of 27.3 years, range from 22 to 38 years) took part in this study. Written informed consent was obtained from each subject following medical screening. Imagery skills were screened using the 32 items of the Vividness of Visual Imagery Questionnaire 2 (VVIQ2, (Cui et al., 2007; Marks, 1995)), for both eyes closed and eyes open imagery. Only subjects with a minimum averaged score of 3 on a 5 point scale (average 3.8, range from 2.9 to 4.9) participated to the study. The subjects were requested to have a good night of sleep and not to consume caffeine the morning before the experiment. All procedures were approved by the University of Wisconsin Institutional Review Board.

Experimental design

Participants arrived at the laboratory between 9 a.m. and 12 p.m. for set-up, then started the experiment. The experimental paradigm combined resting state, perception of movies and visual imagery conditions (Fig. 2). The order of the eyes closed and eyes open baseline and imagery conditions throughout both experimental paradigms was counterbalanced among subjects.

Resting state baseline. At the beginning of the experiment, 5 to 6 min of resting state EEG was recorded during both eyes closed and eyes open conditions. Additional baseline sessions were performed after each paradigm in a subset of 6 subjects. These additional data were not further analyzed in the context of this study. During the resting state, participants were given the instruction to avoid producing vivid visual imagery.

Visual perception — Sims3 paradigm. Participants were shown 6 short movies of about 1 min length. This duration was chosen based on preliminary observations of a good match between the time spent in replaying the movie plot and its actual duration. The movies were obtained from The Sims3, a life-simulation computer game (average duration of 56 s, range from 50 to 63 s, total duration of 5 min and 36 s).

Visual imagery — Sims3 paradigm. Following each presentation of the Sims3 movies, the participants were instructed to mentally replay the movie both with eyes closed and with eyes open, as vividly and in as much detail as they could, focusing on the shapes, colors, texture, and movements previously perceived. The subject signaled the start and the end of the imagery performance orally. The imagery performance fell within the 5 min window of persistence of iconic memory of sensory traces (Ishai and Sagi, 1995). The vividness of the imagery for each segment was rated on a 5 points scale (drawn from the VVIQ2 used for screening the imaginative skills of the participants).

Visual imagery — daydreaming paradigm. Participants were requested to imagine traveling with a magic bike they rode to a destination of their choice, including the depth of the ocean or the sky, without the need to pedal. They were instructed to focus vividly on the details (shapes, colors, textures, and movements) of the scenarios they were imagining. The daydreaming imagery was performed both with eyes closed and with eyes open, for 5–6 min each.

Visual perception — daydreaming paradigm. A silent movie with naturalistic scenes was shown (duration of 5 min and 23 s). This visual perception was performed after the mental imagery daydreaming session described above.

Visual imagery ratings. In both paradigms, the vividness of the imagery was rated on a 5 point scale (VVIQ2). The average subjective rating for the mental replay of short movies (The Sims 3 paradigm) and for the free-guided imagery (daydreaming paradigm) was 3.7 (range from 3 to 4.5) and 4.2 (range from 3 to 5), respectively.

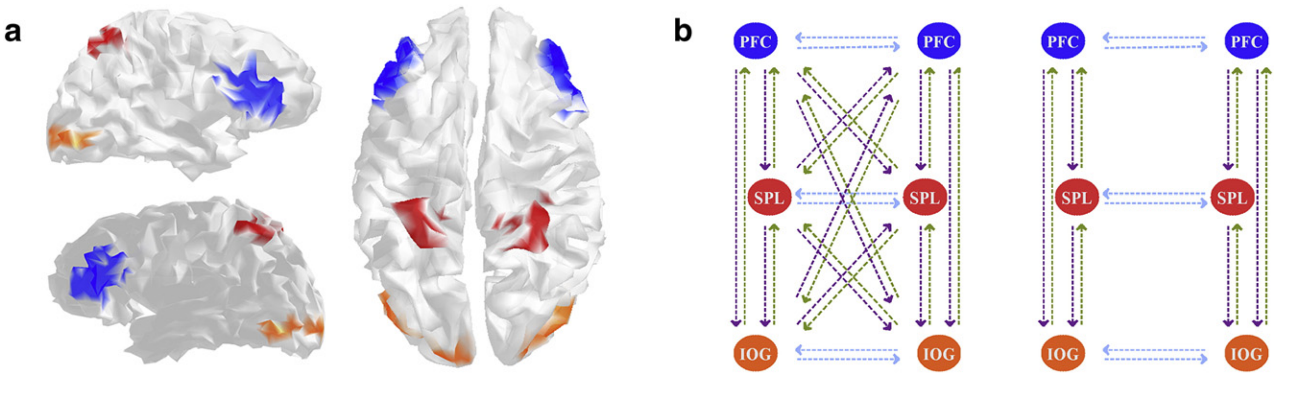

Fig. 1. Panel a. Regions of interest displayed on a cortical surface reconstruction of the average brain from the Montreal Neurological Institute (MNI). Orange, inferior occipital gyrus; red, superior parietal lobule; blue, Brodmann area 46, part of the dorsolateral prefrontal cortex. Left. Lateral views of the brain: right (top) and left (bottom). Right. Brain view from above. Panel b. Network representation of backward (violet), forward (green), and lateral (blue) latent connections included in the MVAR model used to compute GC (left) and the DCM (right). The MVAR models for the GC analyses were based upon the six nodes depicted. However, GC values were computed by pooling over the right and left hemispheres. Consequently, we estimated GC on backward and forward connections grouping the homologous regions in both hemispheres to characterize three functional interactions between the frontal, parietal, and occipital regions. In the DCM, we only allowed condition-specific changes in the backward and forward connections, and then averaged estimates across hemispheres. IOG: inferior occipital gyrus; SPL: superior parietal lobule; PFC: BA46 in the dorsolateral prefrontal cortex.