# Title: Dynamic Coupling between the Lateral Occipital Cortex, Default Mode and Frontoparietal Networks During Bistable Perception

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#### Abstract

The lateral occipital cortex, LOC, a visual area known to be involved in object recognition, was dynamically coupled with each of two distributed patterns of neural activity depending upon the percept ("default" or "alternative") elicited by a bistable figure. The two distributed patterns included core nodes of the default mode and frontoparietal networks and were most highly coupled to each other during the "alternative" percept whereas they were less-coupled during the "default" percept. Surprisingly, the regions associated with the non-engaged percept exhibited the highest connectivity to the LOC. Together, these findings reveal a dynamic organization between the default mode and the frontopariental networks, and the in-coming bottom-up visual stream during perceptual binding of visual images.

- fMRI functional magnetic resonance imaging
- BOLD blood oxygen level dependent
- PPI psychophysiological interactions
- ROI region of interest
- DMN default mode network
- FPN frontoparietal network
- LOC lateral occipital cortex
- mTC middle temporal cortex
- ACC anterior cingulate cortex
- PCC posterior cingulate cortex
- IPL inferior parietal lobule
- MPFC medial prefrontal cortex
- LPFC lateral prefrontal cortex
- PC precuneus
- mOC middle occipital cortex
- IFC inferior frontal cortex
- SPL -superior parietal lobule
- mFG middle frontal gyrus
- SMA supplementary motor area

## Introduction

The mechanism by which the neural correlates of human vision segment and bind features to form unified percepts from a complex visual world is a long standing central question that has also been linked to more general questions related to the neural correlates of awareness and consciousness (Leopold & Logothetis, 1999; Rees, Kreiman & Koch, 2002; Sterzer, Kleinschmidt & Rees, 2009). Image segmentation is a complex process by which stimulus elements are perceptually arranged into a unified whole. A bistable figure presents a unique opportunity to investigate mechanisms involved in segmentation of visual input because one stimulus elicits two mutually exclusive percepts representing alternative organizations of the same visual input. Although neuroimaging studies have previously confirmed the involvement of parietal and frontal brain regions in high level visual processes including bistable perception (Kleinschmidt, B üchel, Zeki & Frackowiak, 1998), there is no established framework to describe the underlying neural mechanisms of image segmentation. We envision that this complex process of alternating visual perceptions will employ large-scale distributed neural systems.

The default mode network, DMN, sometimes referred to as the task-negative network, has been defined by task induced deactivations as well as higher energy consumption during rest, and consists of temporal and midline structures that are known to be more active during rest than during a task (Buckner, Andrews-Hanna & Schacter, 2008; Greicius, Krasnow, Reiss & Menon, 2003; Gusnard, Raichle & Raichle, 2001; Raichle, MacLeod, Snyder, Powers, Gusnard & Shulman, 2001). It has also been associated with internal stimuli or self-reflection as well as memory of past events (Andrews-Hanna, Reidler, Sepulcre, Poulin & Buckner, 2010). The frontoparietal network, FPN, sometimes referred to as the task-positive network, is classically

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defined by task induced activations, and consists of dorsal, frontal, and parietal regions associated with volitional tasks that require attention to external stimuli (Corbetta & Shulman, 2002; Dosenbach, Fair, Miezin, Cohen, Wenger, Dosenbach, Fox, Snyder, Vincent, Raichle & Schlaggar, 2007; Kastner & Ungerleider, 2000). These two networks have also been identified on the basis of spontaneous correlations during resting states characterized by anti-correlations between them (Anderson, Ferguson, Lopez-Larson & Yurgelun-Todd, 2011; Fox, Snyder, Vincent, Corbetta, Van Essen & Raichle, 2005) suggesting an intrinsic oppositional functional organization of neural processes that mediate cognitive tasks. Despite a general consensus regarding the regions comprising these networks, there is a lack of consensus regarding their functions.

In this study, functional magnetic resonance imaging (fMRI) and functional connectivity methods were employed to identify neural substrates and dynamics engaged during each of the mutually exclusive percepts elicited by a common bistable figure, the Schröder Staircase (Schröder, 1858). Subjects viewed alternating 15-second blocks of rest and stimulus, and were instructed on each stimulus block which percept to maintain, i.e. "default" or "alternative". All subjects were well practiced and demonstrated competence with the task prior to scanning. This paradigm differs from previous studies of bistable perception (Kleinschmidt, Büchel, Zeki & Frackowiak, 1998; Tong, Nakayama, Vaughan & Kanwisher, 1998) by providing a targeted percept with instructions to maintain a percept for each 15-second block. This paradigm was chosen to provide a structured focus on each percept, which permitted an experimental approach to investigate the underlying neural circuitry associated with each percept.

In the "default" condition the figure was readily perceived as a familiar staircase, whereas in the "alternative" condition, the figure was perceived as an inverted staircase. Although prior

investigations of bistable perception have considered the role that attention plays in forming each of the percepts (Meng & Tong, 2004; Slotnick & Yantis, 2005), the attention network and its relation to the default mode network have not been previously implicated in this process. As is typical with bistable figures, the two percepts differed with respect to the volitional effort and attention required for their realization suggesting a putative role for both the attentional control and the default mode networks. In this study we test the hypothesis that mutually exclusive visual image segmentations, as in the case of two bistable percepts, are associated with neural processes that engage both the default mode and the frontoparietal attention networks. Further, we compare the coupling between the networks and the bottom-up visual stream during the two perceptual states to investigate the intrinsic dynamic organization associated with these percepts.

#### **Materials and Methods**

**Subjects:** A total of 12 healthy volunteers participated in the functional imaging study (8 males and 4 females; ages 18-27 years of age; mean = 22.8 years of age), as approved by the institutional review board of Columbia University Medical Center. All subjects were informed about possible risks of MRI and provided consent according to the established guidelines.

**Stimulus:** The stimulus was a black and white line drawing of a common bistable figure (**Supplementary Figure 1**) referred to as the Schröder Staircase. The two percepts were mutually exclusive, and eye position monitoring has previously provided no evidence for percept-associated variations (Hirsch, Egner, Khalil, Lai & Patel, 2004).

**Functional Imaging Procedures:** The functional study was run as a block design in which the stimulus was presented for 12 fifteen second epochs, each of which was preceded by a fifteen second baseline epoch that featured a black screen with a crosshair (+). Prior to scanning, the "default" and the "alternative" percepts were determined for each subject based on the

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percept that the subject reported as seen first and most automatically. For all subjects the "default" percept was the ascending staircase most resembling a familiar staircase, and the "alternative" percept was the "up-side down" staircase that appeared to be suspended in midair. The subject was instructed to hold the "default" percept for the first fifteen-second stimulus epoch, and then, following a rest epoch, instructed to hold the "alternative" percept for the following fifteen-second stimulus epoch, and to continue this alternation for the duration of the 6.0 minute run. The target percepts were cued by the written words "alternative" or "default" above the image, and the subjects indicated on a keypad the actual engaged percept and whenever a perceptual switch (voluntary or otherwise) occurred. Subjects practiced outside the scanner until they could perform this perceptual task. Button press indications of the engaged percept confirmed that on average the "default" percept was sustained for a total of  $92.36 \pm 6.48$ seconds whereas the "alternative" percept was sustained for a total of 75.7  $\pm$ 6.16 seconds, and are consistent with known difficulty and attentional differences between the two percepts. The average total time that the "default" percept occurred spontaneously during the target "alternative" condition was  $20.34 \pm 6.29$  seconds whereas the average total time that the "alternative" percept occurred spontaneously during the target "default" condition was  $12.01 \pm$ 4.92 seconds, and also consistent with the "default" percept as the more natural and less effortful of the two.

**Image Acquisition and Analysis:** Functional images were acquired on a 1.5T GE MRI scanner located in the Columbia University fMRI Research Center, New York, NY. Whole brain Ecoplanar functional images (EPI) were collected with an 8 channel GE head coil in 25 contiguous axial slices obtained parallel to the AC/PC line (TR=3000 ms, TE=35 ms, flip angle=84 degrees, FoV=19.2 x 19.2cm<sup>2</sup>, array size=128 x 128, spatial resolution of

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acquisition=1.5 x 1.5 x 4.5 mm, voxel size after spatial normalization = 2 x 2 x2 mm). One hundred and twenty whole brain images were acquired during each of two identical 6-minute runs. High-resolution 3-D anatomical scans were also acquired with a T1-weighted SPGR sequence (TR=19 ms, TE=5 ms, flip angle=20 degrees) FoV=220 x 200mm, a slice thickness of 1.5 mm, in-plane resolution of 0.86 x 0.86 mm, and 124 slices per image.

Image pre-processing and statistical analysis was completed using SPM8 software (Wellcome Department of Cognitive Neurology, University College London, UK). Functional T2\*-images were slice-timing corrected and spatially realigned to the first volume of the first run. Finally, images were smoothed with a Gaussian kernel of 8.0 x 8.0 x 8.0 mm full-width halfmaximum, and a 128 s temporal high-pass filter was applied.

**GLM analysis**: Statistical analysis of the BOLD signal was modeled using a single factor, percept, with two levels, "alternative" and "default". The analysis aimed to detect activity associated with each perspective. Perceptual durations (according to button presses) for the "default" and "alternative" percepts were convolved with the canonical hemodynamic response function (HRF). Additional nuisance regressors, i.e. six motion parameters, mean white-matter, and mean CSF signal were included to remove unnecessary noise from the data. Contrasts of resulting beta estimates ("Default">"Alternative" and "Alternative">"Default") for each run separately were averaged across both runs, and were passed to 2<sup>nd</sup> level random effects analyses (one-sample t-tests). Beta estimates from each condition were also passed to a 2<sup>nd</sup> level random effects analysis (paired t-test) in order to determine conjoined activation and deactivation common to both percepts in run 1, used for independent ROI analyses (see below).

**PsychoPhysiological Interaction (PPI) analysis**: The PPI analysis measures the extent to which regions are differentially correlated between conditions (Friston, Buechel, Fink, Morris,

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Rolls & Dolan, 1997), and is strictly correlative and not indicative of directional causation. While there are various approaches regarding the removal of task-associated variance in PPI analysis (McLaren, Ries, Xu & Johnson, 2012; O'Reilly, Woolrich, Behrens, Smith & Johansen-Berg, 2012), we have adopted the long-standing standard approach as described in the current version of SPM8 (www.fil.ion.ucl.ac.uk/spm/doc/manual.pdf). Lateral occipital cortex (LOC), the primary seed-of-interest, was defined by averaging the time series of right and left LOC thus merging them into one single bilateral seed. Bilateral LOC was defined by the conjunction of "alternative" and "default" activity, at peak MNI coordinates for right [40-70-8] and left [-38, -78-6], thresholded at p < 0.0001, uncorrected corresponding to the lateral occipital cortex, which has been shown to be active in object recognition (Grill-Spector, Kourtzi & Kanwisher, 2001; Malach, Reppas, Benson, Kwong, Jiang, Kennedy, Ledden, Brady, Rosen & Tootell, 1995). Similarly composite DMN and FPN seeds were defined using the conjunction of both "default" and "alternative" conditions from Run 1. Positive contrast of the conjunction was used to identify the FPN seed and negative contrast was used to identify the DMN seed. All ROIs in a given network were then joined using Marsbar Toolbox (http://marsbar.sourceforge.net/) to form a single composite network seed thresholded at p < 0.0001 (Uddin, Kelly, Biswal, Xavier Castellanos & Milham, 2009). The BOLD time courses were extracted from two 6 mm spheres each centered at the above coordinate locations, respectively, and then regressed on a voxel-wise basis against the product of this time course and the vector of the psychological variable of interest, (1\*Default + -1\*Alternative), with the physiological and the aforementioned psychological variable (a regressor convolved with the HRF representing the contrast "default> alternative") serving as regressors of no interest. Resulting beta maps were subsequently passed to 2nd level random effects analysis (one sample t-test). Results for left and right seeds were

similar; hence reported results are based on the combined bilateral seed. GLM models that were used to extract seed region activity and to estimate PPI results included additional nuisance regressors, i.e. six motion parameters, mean white-matter, and mean CSF signal. For display purposes, statistical maps were thresholded at p<0.05 uncorrected. To control for multiple comparisons throughout the brain, cluster-extent thresholding was applied using an uncorrected cutoff p-value of 0.005 and cluster size threshold of 150 contiguous voxels resulting in an effective p<0.05 corrected (denoted by an asterisk in Table 1). This cluster threshold was determined by 2000 Monte Carlo simulations of whole-brain fMRI data with respective parameters of the presented study (Gaussian kernel = 8x8x8mm, voxel size = 2x2x2mm, mask = whole brain fMRI data) using AlphaSim in AFNI (v2009).

**Independent ROI analysis**: To test whether the DMN and FPN were significantly more active and functionally connected with visual cortex during one percept vs. the other, we conducted an independent ROI analysis using the Marsbar Toolbox

(http://marsbar.sourceforge.net/). For this, the FPN and DMN were defined using conjunction of both "default" and "alternative" conditions from Run 1 of each subject. These beta estimates were input to a 2<sup>nd</sup> level random effects analysis (2-sample t-test) in which positive and negative conjunction contrasts, thresholded at p<0.0001, uncorrected, defined the independent FPN and DMN ROIs (Uddin, Kelly, Biswal, Xavier Castellanos & Milham, 2009). Contrast values (or beta estimates from PPI analyses) of "Default-Alternative" from Run 2 of each subject were then averaged over all voxels within the above ROIs, and submitted to two separate 2nd level random effects analysis (one-sample t-tests, one for each ROI).

**Effective Connectivity Analysis**: Effective connectivity analysis was carried out using dynamic causal modeling, DCM (Friston, Harrison & Penny, 2003), as implemented in SPM8

(Wellcome Department of Cognitive Neurology, University College London, UK). Predictions based on the observed data consist of the combination of driving inputs, intrinsic connection activity, and bilinear modulation, which reflects the effects of experimental variables. In this case, the default and alternative percept conditions served as both the driving input (on individual regions) and modulatory input (on connections between regions). These effects are modeled by the equation,  $dz_1/dt=(A+u_mB)z_2+Cu_i$  in which  $dz_1/dt$  is the state vector per unit time for the target region,  $z_2$  corresponds to time series data from the source region,  $u_i$  indicates the direct input to the model, and  $u_m$  indicates input from the modulatory variable onto intrinsic pathways specified by the model. Activity in the target region is therefore determined by an additive effect of the intrinsic connectivity with the source region (Az<sub>2</sub>), the bilinear variable ( $u_mBz_2$ , corresponding to the modulatory experimental manipulation), and the effect of direct input into the model (Cu<sub>i</sub>).

Given our specific hypotheses, a fully specified model was estimated (i.e. intrinsic bilateral connections between the LOC, DMN, and FPN, with both conditions modulating all regions and connections). In each subject, the contrast (Default>Alternative) was calculated for each connectivity parameter and submitted to a one-sample t-test over all the subjects. Unless otherwise indicated, there were 11 degrees of freedom for all reported t-values.

## Results

## **Functional Magnetic Resonance Imaging**

Patterns of whole brain fMRI activity based on the Blood Oxygen Level Dependent (BOLD) response observed during the "default > alternative" contrast (**Figure 1a**) and "alternative > default" contrast (**Figure 1b**) corresponded to known activity patterns previously associated with the DMN (Anderson, Ferguson, Lopez-Larson & Yurgelun-Todd, 2011;

Buckner, Andrews-Hanna & Schacter, 2008; Greicius, Krasnow, Reiss & Menon, 2003; Raichle et al., 2001) and FPN (Anderson, Ferguson, Lopez-Larson & Yurgelun-Todd, 2011; Corbetta & Shulman, 2002; Dosenbach et al., 2007; Kastner & Ungerleider, 2000), respectively. In particular, the "default" perspective activity (as defined by the contrast "default > alternative"; **Table 1a)** included the middle temporal cortex (mTC), anterior cingulate cortex (ACC), posterior cingulate cortex (PCC), inferior parietal lobule (IPL), medial prefrontal cortex (MPFC), lateral prefrontal cortex (LPFC), and precuneus (PC), which have been previously associated with the DMN (Buckner, Andrews-Hanna & Schacter, 2008; Greicius, Krasnow, Reiss & Menon, 2003; Raichle et al., 2001). In comparison, the "alternative" perspective activity (as defined by the contrast "alternative > default"; **Table 1b**) included the lateral occipital cortex (LOC), middle occipital cortex (mOC), inferior frontal cortex (IFC), inferior parietal lobule (IPL), superior parietal lobule (SPL), middle frontal gyrus (mFG), and supplementary motor area (SMA), which have previously been associated with the FPN (Corbetta & Shulman, 2002; Dosenbach et al., 2007; Kastner & Ungerleider, 2000). An independent ROI analysis confirmed that activation of the DMN, as a whole, was significantly greater during the "default" perspective ("default > alternative", t=2.29, p<0.05), while activation of the FPN, as a whole, was significantly greater during the "alternative" perspective ("alternative > default", t=2.01, p<0.05) (See Materials and Methods).

## Functional Connectivity with the Lateral Occipital Cortex

The functional roles of the DMN and FPN in bistable image segmentation were explored in relation to the incoming bottom-up visual stream. Psychophysiological interaction (PPI) analysis of functional connectivity between the LOC, which was active during both percepts, and all other brain regions revealed that higher connectivity was observed between the LOC and the network associated with the unconscious percept. For example, during the "default" percept ("default > alternative" contrast), LOC connectivity increased specifically with the FPN regions (**Figure 2a**), whereas connectivity during the "alternative" percept ("alternative > default" contrast) increased specifically with the DMN regions (**Figure 2b**). An independent ROI analysis confirmed that connectivity with the FPN was significantly greater during the "default" perspective ("default > alternative", t=4.80, p<0.05), while connectivity with the DMN was greater during the "alternative" perspective ("alternative" perspective ("alternative" perspective ("alternative") t=5.39, p<0.05) (**See** 

# Materials and Methods).

### **Connectivity Between the FPN and DMN**

In addition to the dynamic connectivity between the LOC and the two networks, the connectivity between the DMN and FPN was also measured using PPI analysis in order to investigate possible cross-network connectivity in association with connectivity with the incoming visual stream. During the "default" contrast, both the DMN (**Supplementary Figure 2a**) and the FPN (**Supplementary Figure 2b**) exhibited higher connectivity within their respective networks. Independent ROI analyses confirmed that connectivity within each network was significantly greater during the "default" perspective ("default > alternative", DMN t=4.45, p<0.05 and FPN t=6.58, p<0.05). During the "alternative" contrast, however, the two networks increased their connectivity to each other, such that the DMN was more connected to the FPN (**Supplementary Figure 3a**) and the FPN was more connected to the DMN (**Supplementary Figure 3b**) as shown by the PPI results. This "cross-network" connectivity that was observed most prominently during the "alternative" perspective was also confirmed by independent ROI analyses ("alternative > default", DMN connectivity with FPN seed, t=3.63, p<0.05 and FPN connectivity with DMN seed t=5.33, p<0.05). In general, the PPI analysis indicates that during

the "default" contrast, the individual networks tended to be more connected within themselves, whereas during the "alternative" percept, the cross network functional connectivity was increased.

## **Effective Connectivity**

The PPI findings were also confirmed by a dynamic causal model (Penny, Stephan, Mechelli & Friston, 2004), where effective connectivity between the LOC, DMN, and FPN, was estimated during both conditions using a fully specified model. In accordance with our model, significant contrasts of connectivity parameters (Alternative > Default) were observed for the connectivity from the DMN to the LOC (t=1.91 and p<0.04), and from the FPN to the DMN (t=1.79 and p<0.05). Thus, these two approaches, PPI and DCM, provide convergent findings indicating that during the alternative percept the connection was increased between the LOC and the DMN, and also between the FPN and DMN.

#### Discussion

Differences in connectivity between cortical regions have previously been reported depending upon volitional (top-down) goals (Chadick & Gazzaley, 2011), as well as interactions between the DMN and the FPN (Fox et al., 2005; Uddin, Kelly, Biswal, Xavier Castellanos & Milham, 2009). Here we extend these findings and show that volitional image segmentation tasks also engage distributed neural patterns consistent with the DMN and the FPN. Further, functional connectivity reveals a mechanism of oppositional coupling and decoupling between the incoming visual stream and these networks that is associated with the bistable percepts.

Recent EEG findings reporting that neural activity precedes the perceptual emergence of the "hidden" percept (Britz, Landis & Michel, 2009), are consistent with our finding that the non-engaged percept is associated with an active process correlated with the incoming visual

stream. Further, previously proposed models for bistable perception suggest that "fatigue" or "satiation" of the neural correlates associated with conscious percept contribute to the emergence of the "suppressed" percept (Toppino & Long, 1987). Our data are also consistent with the notion that active stages of percept construction involve neuronal suppression between levels of visual information processing. For example, our finding that the DMN and the FPN are more internally correlated during the "default" percept, i.e. increased intra-network connectivity, and more cross-correlated during the "alternative", i.e. increased inter-network connectivity, is consistent with previously reported competitive and suppressive interactions between these networks (Kelly, Uddin, Biswal, Castellanos & Milham, 2008; Uddin, Kelly, Biswal, Xavier Castellanos & Milham, 2009).

A framework proposed by (Spreng, Stevens, Chamberlain, Gilmore & Schacter, 2010) can be applied to our findings where a model of interactive top-down neural processes originating from the FPN mediate between the two networks (**Figure 3**). During the "default" percept the distributed BOLD response was consistent with DMN activity (the DMN was less deactivated during the default percept relative to the alternative percept) whereas during the "alternative" percept the distributed BOLD response was consistent with FPN activity indicating that when one network was active (**Figure 3 - yellow**), the other was relatively less active.

The functional connectivity between the bottom-up visual stream, originating from the LOC (**Figure 3 – green**), was highly correlated with the less-engaged network. Variations in concurrent deactivations of irrelevant sensory input have been associated with a suppressive mechanism (Amedi, Malach & Pascual-Leone, 2005; Shmuel, Yacoub, Pfeuffer, Van de Moortele, Adriany, Hu & Ugurbil, 2002; Wade, 2002). Accordingly, our finding of the increased connectivity between the FPN and the deactivated DMN suggests that the FPN may suppress

DMN activity during the "alternative" percept. Additionally, during the "default" percept, the less-engaged FPN was internally connected suggestive of a regulation of this suppressive mechanism. These findings lead to the novel interpretation that increased connectivity between the visual stream and the deactivated network reveals a suppressive mechanism associated with the conscious percept possibly mediated by oppositional long-range networks that interact with the incoming visual information (**Figure 3**).

The discovery that the bottom-up visual stream was "anti-correlated" with the network associated with the on-going conscious percept is surprising. However working with the framework put forth, these new findings can be interpreted as reflecting a balance between suppressive and excitatory interactions between the networks that are associated with the unconscious and conscious percepts and the bottom-up visual stream. Together, these findings are consistent with a model where active image segmentation, as observed in bistable figures, is mediated by top-down mechanisms that influence incoming visual information.

## Conclusion

Bistable percepts provide a unique opportunity to investigate the neural mechanism of image segmentation because a single visual figure gives rise to two mutually exclusive perceptual constructs. In this study, percepts elicited by the Schroder Staircase differentially gave rise to distributed patterns of neural activity consistent with the default mode network, DMN, and a frontoparietal network, FPN, during functional magnetic resonance imaging. In particular, the DMN was observed during the "default" percept, while the FPN was observed during the "alternative" percept. Additionally functional connectivity revealed that the incoming visual stream was more coupled with the DMN during the more effortful, "alternative" percept, and that the DMN and FPN were most interconnected during the "alternative" percept. These findings

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## **Author Contributions**

JH supervised the study. AK and DK performed the experiments. AK analyzed the activation data. SPP analyzed the functional connectivity data. JH and AK drafted the manuscript. XZ assisted with data analysis and provided technical advice.

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## Captions

**Figure 1** – a. BOLD-related fMRI activity associated with the "default" percept as defined by the contrast "default > alternative". The boxed clusters indicate regions previously identified as part of the DMN. b. fMRI activity associated with the "alternative" percept as defined by the contrast "alternative > default". The circled clusters indicate regions previously identified as the FPN. Images are shown on a normalized brain with slice positions in mm from the AC/PC line indicated on the upper left. For display purposes, maps are thresholded at p<0.05, k=10. **Table 1** - **a**. Areas active during the "default" percept as defined by the contrast "default > alternative" and also identified as elements of the DMN. ROI abbreviations, peak voxel MNI coordinates (x,y,z), t-values and cluster sizes are shown for each region. **b**. Areas active during the "alternative" percept as defined by the contrast "alternative > default" and also identified as elements of the FPN. ROI abbreviations, peak voxel MNI coordinates (x,y,z), t-values, and cluster sizes are shown for each region. Asterisks indicate regions that survive cluster correction thresholding at p<0.005 and a cluster size of 150.

**Figure 2** – Functional connectivity (PPI) between the lateral occipital cortex and regions where connectivity during one percept (as defined by the contrasts) exceeds connectivity in comparison to the other. The same global networks observed in the fMRI analysis (**Fig 1**) were also observed in the PPI analysis, however, **a**. the connectivity pattern from the lateral occipital cortex is highest to FPN regions during the "default" percept contrast, and **b**. the connectivity pattern from the lateral occipital cortex during the "alternative" percept contrast is highest to DMN regions. For both figures a and b, group results are shown on a normalized brain with slice positions in mm from the AC/PC line indicated on the upper left. For display purposes, maps were thresholded at p<0.05, k=10.

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**Figure 3** – A conceptual summary of findings. **a**. During the conscious "default" percept, as revealed by the "default > alternative" contrast, the DMN was more engaged and functional connectivity increased between the LOC and the FPN. There was no evidence for cross network connectivity during this percept. **b**. During the conscious "alternative" percept, as revealed by the "alternative > default" contrast, the FPN was more engaged and functional connectivity increased between the LOC and the DMN. Additionally, functional connectivity between the FPN and DMN was observed in this condition.

**Supplementary Figure 1** – The Schröder Staircase figure gives rise to two mutually exclusive percepts. The dominant, "default", percept resembles a typical staircase, whereas the less perceptually stable, "alternative", percept resembles an upside-down or inverted staircase. **Supplementary Figure 2** – Functional connectivity (PPI) based on **a.** the composite DMN seed or **b.** the composite FPN seed, see **Materials and Methods**. a. During the "default" percept contrast, the DMN seed showed an overall increased connectivity with the DMN regions (squares; t=4.45, p=0.00049). b. Similarly, during the "default" percept contrast the FPN seed showed an overall increased connectivity with the FPN regions (circles; t=6.58, p=0.00002). For all panels, group results are shown on a normalized brain with slice positions in mm from the AC/PC line indicated on the upper left. For display purposes, maps are thresholded at p<0.05, uncorrected, k=10.

**Supplementary Figure 3** - Functional connectivity (PPI) based on **a.** the composite DMN seed or **b.** the composite FPN seed, see **Materials and Methods**. a. During the "alternative" percept contrast, the DMN seed exhibited a greater connectivity with the FPN regions (circles; t=3.63, p=0.002). b. Similarly, during the "alternative" percept contrast the FPN seed exhibited a greater connectivity with the DMN regions (squares; t=5.33, p=0.00012). For all panels, group results

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are shown on a normalized brain with slice positions in mm from the AC/PC line indicated on

the upper left. For display purposes, maps are thresholded at p<0.05, uncorrected, k=10.

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a "Defa	"Default > Alternative" Contrast (DMN)						h "Alternative > Default" Contrast (FPN)						
GLM Region		x	У	z	t-value	Cluster Size	GLM Region		x	У	z	t-value	Cluster Size
Middle Temporal Cortex	*mTC (L)	-58	-36	-4	4.60	1939	Lateral Occipital Cortex	LOC (L)	-46	-58	-8	3.80	642
	mTC (R)	54	-40	-2	4.42	1195		LOC (R)	40	-78	-12	5.83	448
Anterior Cingulate Cortex	ACC	-2	24	-4	5.24	765	Middle Occipital Cortex	mOC (L)	-26	-88	6	3.85	188
Posterior Cingulate Cortex	C PCC	-8	-36	32	3.02	584		mOC (R)	20	-98	10	2.87	358
Inferior Parietal Lobule	*IPL (L)	-44	-64	40	4.38	1510	Inferior Frontal Cortex	IFC	46	8	26	4.43	733
	IPL (R)	54	-64	40	3.31	347		IPL (L)	-46	-34	50	6.68	597
Medial Prefrontal Cortex	*MPFC	4	46	44	4.95	2486	Inferior Parietal Cortex	IPL (R)	20	-52	50	4.85	313
Lateral Prefrontal Cortex	*LPFC	12	38	46	5.90	2488		IPL (R)	48	-38	46	3.74	280
Precuneus	PC	-6	-56	52	3.59	1462 Superior Pariotal Cartey	Superior Pariatal Cartay	SPL (L)	-18	-68	52	3.48	126
							Superior Farietal Cortex	SPL (R)	16	-76	52	3.14	241
							Middle Frontal Gyrus	mFG (L)	-32	-10	50	4.84	382
								mFG (R)	24	-4	52	5.07	281
							Supplementary Motor Area	SMA	-4	6	52	5.20	986

Table 1 - a. Areas active during the "default" percept as defined by the contrast "default > alternative" and also identified as elements of the DMN. ROI abbreviations, peak voxel MNI coordinates (x,y,z), t-values and cluster sizes are shown for each region. b. Areas active during the "alternative" percept as defined by the contrast "alternative > default" and also identified as elements of the FPN. ROI abbreviations, peak voxel MNI coordinates (x,y,z), t-values, and cluster sizes are shown for each region. Asterisks indicate regions that survive cluster correction thresholding at p<0.005 and a cluster size of 150.

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Figure 1 – a. BOLD-related fMRI activity associated with the "default" percept as defined by the contrast "default > alternative". The boxed clusters indicate regions previously identified as part of the DMN. b. fMRI activity associated with the "alternative" percept as defined by the contrast "alternative > default". The circled clusters indicate regions previously identified as the FPN. Images are shown on a normalized brain with slice positions in mm from the AC/PC line indicated on the upper left. For display purposes, maps are thresholded at p<0.05, k=10.

Brain Connectivity Dynamic Coupling between the Lateral Occipital Cortex, Default Mode and Frontoparietal Networks During Bistable Perception (doi: 10.1089/brain.2012.0119) This article has been peer-reviewed and accepted for publication, but has yet to undergo copyediting and proof correction. The final published version may differ from this proof.



Figure 2 – Functional connectivity (PPI) between the lateral occipital cortex and regions where connectivity during one percept (as defined by the contrasts) exceeds connectivity in comparison to the other. The same global networks observed in the fMRI analysis (Fig 1) were also observed in the PPI analysis, however, a. the connectivity pattern from the lateral occipital cortex is highest to FPN regions during the "default" percept contrast, and b. the connectivity pattern from the lateral occipital cortex is highest to DMN regions. For both figures a and b, group results are shown on a normalized brain with slice positions in mm from the AC/PC line indicated on the upper left. For display purposes, maps were thresholded at p<0.05, k=10.



Figure 3 – A conceptual summary of findings. a. During the conscious "default" percept, as revealed by the "default > alternative" contrast, the DMN was more engaged and functional connectivity increased between the LOC and the FPN. There was no evidence for cross network connectivity during this percept. b. During the conscious "alternative" percept, as revealed by the "alternative > default" contrast, the FPN was more engaged and functional connectivity increased between the LOC and the DMN. Additionally, functional connectivity between the FPN and DMN was observed in this condition.



Supplementary Figure 1 – The Schröder Staircase figure gives rise to two mutually exclusive percepts. The dominant, "default", percept resembles a typical staircase, whereas the less perceptually stable, "alternative", percept resembles an upside-down or inverted staircase.



Supplementary Figure 2 – Functional connectivity (PPI) based on a. the composite DMN seed or b. the composite FPN seed, see Materials and Methods. a. During the "default" percept contrast, the DMN seed showed an overall increased connectivity with the DMN regions (squares; t=4.45, p=0.00049). b. Similarly, during the "default" percept contrast the FPN seed showed an overall increased connectivity with the FPN regions (circles; t=6.58, p=0.00002). For all panels, group results are shown on a normalized brain with slice positions in mm from the AC/PC line indicated on the upper left. For display purposes, maps are thresholded at p<0.05, uncorrected, k=10.



Supplementary Figure 3 - Functional connectivity (PPI) based on a. the composite DMN seed or b. the composite FPN seed, see Materials and Methods. a. During the "alternative" percept contrast, the DMN seed exhibited a greater connectivity with the FPN regions (circles; t=3.63, p=0.002). b. Similarly, during the "alternative" percept contrast the FPN seed exhibited a greater connectivity with the DMN regions (squares; t=5.33, p=0.00012). For all panels, group results are shown on a normalized brain with slice positions in mm from the AC/PC line indicated on the upper left. For display purposes, maps are thresholded at p<0.05, uncorrected, k=10.