Brain networks underlying bistable perception

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Abstract

Bistable stimuli, such as the Necker Cube, demonstrate that experience can change in the absence of changes in the environment. Such phenomena can be used to assess stimulus-independent aspects of conscious experience. The current study used resting state functional magnetic resonance imaging (rs-fMRI) to index stimulus-independent changes in neural activity to understand the neural architecture that determines dominance durations during bistable perception (using binocular rivalry and Necker cube stimuli). Anterior regions of the Superior Parietal Lobule (SPL) exhibited robust connectivity with regions of primary sensorimotor cortex. The strength of this region's connectivity with the striatum predicted *shorter* dominance durations during binocular rivalry, whereas its connectivity to pre-motor cortex predicted longer dominance durations for the Necker Cube. Posterior regions of the SPL, on the other hand, were coupled to associative cortex in the temporal and frontal lobes. The posterior SPL's connectivity to the temporal lobe predicted longer dominance during binocular rivalry. In conjunction with prior work, these data suggest that the anterior SPL contributes to perceptual rivalry through the inhibition of incongruent bottom up information, whereas the posterior SPL influences rivalry by supporting the current interpretation of a bistable stimulus. Our data suggests that the functional connectivity of the SPL with regions of sensory, motor and associative cortex allows it to regulate the interpretation of the environment that forms the focus of conscious attention at a specific moment in time.

Highlights

- Isolated distinct networks from adjacent regions of parietal cortex with rs-fMRI
- Specific parts of these networks determine dominance durations for bistable stimuli
- Resting state approach avoids confound of non-causal correlations in brain activity
- Parietal cortex integrates low and high level data to interpret the environment

Keywords: bistable perception, resting state fMRI, connectivity, parietal cortex

1 Introduction

A remarkable feature of the human mind is its capacity to process information that is independent of environmental input. We often lose ourselves in our thoughts, decoupling experience from the here and now (Baird et al., 2014). At other times we suddenly realize that we having been looking at the world from the wrong perspective: many famous visual illusions depend upon the resolution of uncertain perceptual input (Sterzer et al., 2009). These examples demonstrate that our conscious experience of our surroundings does not depend solely on the sensory information we receive at any moment in time, an observation that allows insight into the stimulus-independent basis of conscious perception. A popular way to study this dissociation between sensory inputs and conscious experience is to use stimuli that are ambiguous in their interpretation, and for which perception alternates over time. Classic examples include binocular rivalry (Figure 1a), in which incompatible images shown to the two eyes

compete for awareness, and the Necker cube (see Figure 1b), in which a wire-frame cube can be perceived from multiple perspectives. Understanding the neural architecture that mediates these alternations is considered a critical step in uncovering neural correlates of consciousness (Crick and Koch, 1998).

Identifying the neural correlates of bistable perception by recording online activity, however, may confound activity that is causally linked to bistable alternations with activity that is merely correlated with it. The finding that activity in a given brain region (e.g. frontoparietal cortex Kleinschmidt et al., 1998; Lumer and Rees, 1999;

Sterzer and Kleinschmidt, 2007; Weilnhammer et al., 2013) correlates with perception does not reveal whether that region drives the alternations, or reflects a consequence of processes occurring elsewhere. Carefully controlling for the character of perceptual transitions has been shown to dramatically reduce the number of brain regions that are viable candidates for determining alternations (Knapen et al., 2011). Consequently, it is still a matter of debate whether different forms of bistable stimuli depend on bottom-up or top down influences, and which specific neural systems support these aspects of conscious experience.
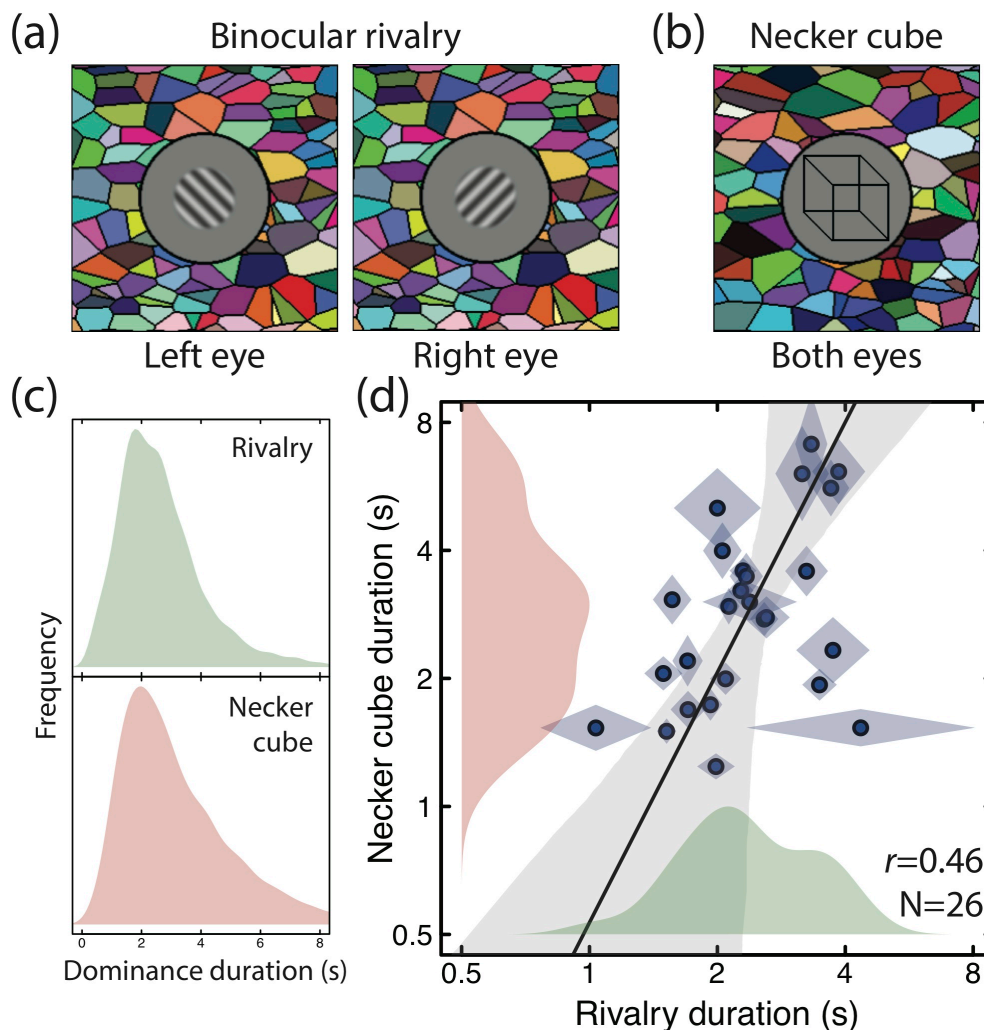

Figure 1: Example stimuli and summary of psychophysical results. (a) Binocular rivalry stimuli shown to the left and right eyes. The central gratings conflict and cause rivalry alternations, the surrounding Voronoi texture was used to encourage good binocular fusion. (b) Necker cube stimulus, shown binocularly. The wireframe cube can be interpreted from two different perspectives, which alternate over time. (c) Histograms of dominance durations for rivalry (green) and the Necker cube (red) across 26 participants. The individual epoch durations were normalized to the geometric (log) mean for their respective participant, then pooled across participants, and rescaled by the group mean. Both distributions show the positive skew typically observed for such stimuli. (d) Scatterplot showing the correlation (r=0.46) between rivalry and Necker cube dominance durations for 26 participants. The blue diamonds indicate ±1SD of each mean, and the red and green density plots show the distributions for each measure. The black line is the best fitting Deming regression line that minimised the absolute (geometric) distance between each point and the line, and the grey shaded region indicates bootstrapped 95% confidence limits of the regression.

The current work capitalizes on the fact that *stimulus-independent* changes in neural processing occur naturally during wakeful rest. Neuroimaging has revealed that almost all functional networks that support aspects of task related processing have a comparable resting state network (Smith et al., 2009), and the integrity of these networks varies across individuals in a manner that is predictive of complex forms of cognition such as meta cognitive accuracy (Baird et al., 2013), spontaneous thought (Gorgolewski et al., 2014), reading comprehension (Smallwood et al., 2013) and executive control (Reineberg et al., 2015). As the neural activity at rest is uncontaminated by external input, it provides a relatively pure method to explore stimulus-independent neural processes and so a useful tool to understand the functional architecture of bistable perception.

The current study explores the functional connectivity of two regions of the superior parietal lobule (SPL) that have been shown to play a key role in bistable perception in studies using repetitive transcranial magnetic stimulation (rTMS). Application of TMS to the anterior region of the superior parietal lobule (aSPL) in the right hemisphere causes binocular rivalry and bistable motion alternations to speed up (Carmel et al., 2010; Kanai et al., 2011). By contrast, a more posterior region of the same structure (pSPL) slows down the alternations of a bistable structure from motion stimulus when targeted with TMS (Kanai et al., 2010). The apparently opposing functions of these two regions of the SPL is surprising given their physical proximity (see Figure 2). Recent fMRI work has demonstrated that the regions interact with visual areas involved in processing motion to resolve bistable motion percepts, and the strengths of connections are able to predict individual alternation rates accurately (Megumi et al., 2015).

In Experiment One, we examined the functional architecture associated with these regions in a large group of participants with the aim of identifying the large-scale networks that these areas participate in. Building on prior work linking individual differences in perception to neural organisation (Kanai et al., 2011, 2010; Megumi et al., 2015; Song et al., 2013a; 2013b; van Loon et al., 2013; Watanabe et al., 2014), in Experiment Two we probed the functions of these networks by examining whether modulations in the connectivity across individuals contains explanatory information on their rate of perceptual alternations. We did this for two different bistable stimuli, selected for their reliance on either lower-level stimulus features (binocular rivalry between two orthogonal gratings) and higher-level stimulus features (alternations between two interpretations of the Necker cube). By selecting contexts in which bistability occurs at either lower or higher levels of analysis we hoped to be able to reveal neural processes that contribute to top down and bottom up processing in bistable perception. We were especially interested whether the different regions of the SPL had different functional architectures at rest, and whether such differences could explain the heterogeneous relationship between rivalrous experience in this region of cortex.

2 Experimental Procedures

2.1 Resting state scans

The dataset from the Nathan Kline Institute (NKI) / Rockland contained 141 subjects. The resting state fMRI data were acquired with the following parameters: TR 2500 ms, TE 30 ms, 120 volumes, matrix size 72x72, 38 slices, flip angle 80°, 0.3 mm spacing between slices, voxel size 3x3x3 mm and an interleaved slice acquisition order. A high-resolution anatomical image was also acquired for each subject using the MPRAGE sequence (Magnetization Prepared Rapid Acquisition Gradient Echo).

Data from Experiment Two were acquired using an eight-channel phased array head coil (GE) tuned to 127.4 MHz on a GE 3 Tesla Signa Excite HDx MRI scanner at York Neuroimaging Centre, at the University of York. 31 participants were recruited. 1 was excluded due to insufficient brain coverage, 2 for excessive movement and 2 were identified as outliers based on their rivalry or MRI data falling more than ±3SD from the group mean. Blood oxygen level-dependent (BOLD) contrast images with fat saturation were acquired using a gradient single-shot echo planar imaging (EPI) sequence with the following acquisition parameters: repetition time (TR) 2000 ms, echo time (TE) minimum full (~19 ms), 210 volumes, flip angle 90°, matrix 64 x 64, field of view (FOV) 192 mm, slice thickness 3 mm with a 0.5mm gap and 32 slices with an interleaved (bottom -> up) acquisition order.

These functional data were co-registered onto high-resolution structural images. For this reason, a sagittal isotropic 3D fast spoiled gradient-recalled echo (3D FSPGR) structural T1 weighted scan was acquired for each of the participants (TR 7.8 ms, TE minimum full, flip angle 20°, matrix size 256 x 256 x 176, voxel size 1.13 x 1.13 x 1 mm). To facilitate the co-registrations, a

high-resolution T1-weighted in-plane anatomical picture was also acquired for all participants, using a fluid attenuated inversion recovery (FLAIR).

2.2 Pre-processing

All fMRI pre-processing and analyses for Experiment One and Two were performed using FSL. We extracted the brain from the skull using the BET toolbox for both the FLAIR and the structural T1 weighted images and these scans were registered to standard space using FLIRT (Jenkinson and Smith, 2001). Prior to conducting the functional connectivity analysis the following pre-statistics processing was applied to the resting state data; motion correction using MCFLIRT (Jenkinson et al., 2002); slice-timing correction using Fourier-space time-series phase-shifting; non-brain removal using BET (Smith, 2002); spatial smoothing using a Gaussian kernel of FWHM 6mm; grand-mean intensity normalisation of the entire 4D dataset by a single multiplicative factor; highpass temporal filtering (Gaussian-weighted least-squares straight line fitting, with sigma = 100 s); Gaussian lowpass temporal filtering, with sigma = 2.8s.

2.3 Low level analysis

We created two spherical seed ROIs, 2 mm in radius, one centered in aSPL and the other in pSPL. The time series of these regions were extracted and used as explanatory variables in a separate subject level functional connectivity analysis for each seed. In these analyses, we also included eight nuisance regressors: white matter (WM), cerebrospinal fluid (CSF), and six motion parameters. The WM and CSF covariates were generated by segmenting each individual's high-resolution structural image (using FAST in FSL). The default tissue probability maps, referred to as Prior Probability Maps (PPM), were registered to each individual's high-resolution structural image (T1 space) and the overlap between these PPM and the corresponding CSF and WM maps was identified. These maps were then thresholded (40% for the SCF and 66% for the WM) and binarized. Finally, these masks were used to calculate the average time course for each aspect of the brain for each individual. The six motion parameters were calculated in the motion-correction step during pre-processing. Movement in each of the three Cartesian directions (x, y, z) and rotational movement around three axes (pitch, yaw, roll) were included for each individual.

At the group-level the data were processed using FEAT version 5.98 part of FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl) and the analyses were carried out using FMRIB's Local Analysis of Mixed Effects (FLAME) stage 1 with automatic outlier detection. Mean displacement was included at the group level as a covariate of no interest. The Z statistic images were then thresholded using clusters determined by $Z>2.3$ and a (corrected) cluster significance threshold of $p=0.05$ (Worsley, 2001).

2.4 Bistable alternation rate experiment

We showed bistable stimuli to participants for trials of 120 seconds in duration and asked them to report their percepts using a computer mouse. One stimulus consisted of oblique gratings (2c/deg, 50% contrast, ±45 deg, 2.3 deg in diameter, smoothed by a raised cosine envelope) shown to opposite eyes (see Figure 1a). The other was a wireframe drawing of a cube, with a face width of two degrees (see Figure 1b), shown to both eyes with no binocular disparity. All stimuli were presented on a gamma-corrected Iiyama VisionMaster Pro 510 CRT monitor with a mean luminance of $32cd/m^2$, and were viewed through a mirror stereoscope to permit presentation of different images to the left and right eyes (where required). The stimuli were surrounded by a dark ring, and a binocular Voronoi texture to promote binocular vergence and fusion (Baker and Graf, 2009).

Participants were instructed to hold down one mouse button whilst they perceived a particular percept (e.g. a left-oblique grating, or the lower face of the cube appearing closer) and the other button when they perceived the alternative percept (e.g. a right-oblique grating, or the upper face of the cube appearing closer). If they could not decide (e.g. because they experienced a piecemeal percept) they were instructed to release both buttons. Each participant completed four 120-second trials for each of the two stimuli, which were displayed in a randomized order across trials. We also switched the orientations of the rivalling stimuli between the eyes on each alternate trial to avoid adaptation and balance any eye dominance effects. Because the dominance durations followed the typical positively skewed gamma distribution (Figure 1c), we calculated the geometric (rather than arithmetic) mean dominance durations and standard deviations, which are shown in Figure 1d.

3 Results

3.1 Experiment One

We seeded two adjacent parietal regions in the right hemisphere for a set of resting state fMRI

scans collected from 141 participants (Nooner et al., 2012). The network associated with the anterior seed (red button in the upper right panel of Figure 2) involved the occipital lobe, regions of the parietal lobe, and the dorsal surface of the temporal lobe. The network associated with the posterior seed (blue button in the upper right panel of Figure 2) involved lateral regions of temporo-parietal cortex, elements of the temporal lobe, and dorsolateral regions of the prefrontal cortex. We verified the distinctness of these two networks using a large meta-analytic resting state database (*www.neurosynth.org*; Yarkoni et al., 2011), that produced similar (though less extensive) networks, shown in Supplementary Figure S1. It is noteworthy that the connectivity of the aSPL seed was targeted at primary sensori-

motor regions, whereas the connectivity of the pSPL seed region connected with regions of associative cortex (e.g. the temporal lobe and lateral/medial regions of the dorsal prefrontal cortex). These contrasting patterns of connectivity support the hypothesis that these parietal regions have distinct influences on bistable perception because they are functionally connected to different aspects of cortex. In particular, these data suggest that the aSPL connectivity to basic sensory motor information would allow it to integrate lower level sensory information while the connections between the pSPL and regions of associative cortex suggest that it could be important in the top-down coordination of experience.
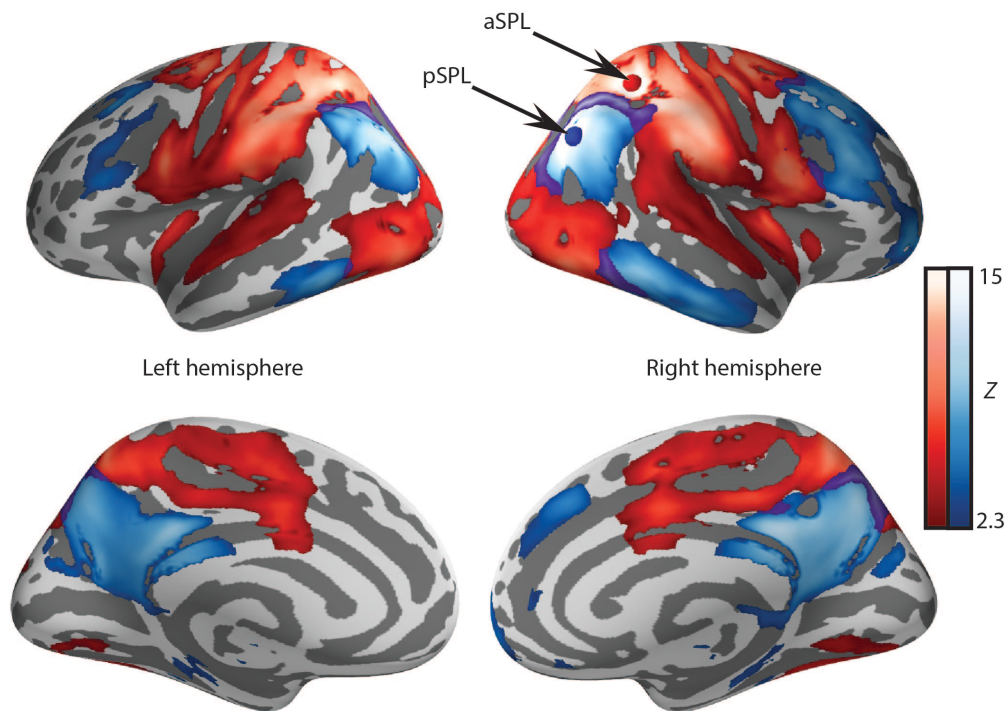

Figure 2: Resting state networks derived from 141 participants. Seed regions were in the anterior superior parietal lobule (aSPL, red button, MNI coordinates: x=36, y=-45, z=51) and in the posterior superior parietal lobule (pSPL, blue button, MNI coordinates: x=38, y=-64, z=32) of the right hemisphere.

3.2 Experiment Two

To understand the function these networks play in bistable perception, we analyzed resting state scans from a further 26 individuals who also took part in an experiment outside of the scanner to measure their dominance durations for two bistable stimuli (Figure 1a,b). We verified that the same networks were produced from our two parietal seed regions for this independent group

of participants (see Supplementary Figure S2). Dominance durations for both rivalry and the Necker cube conformed to the gamma distribution typically observed with bistable stimuli (Figure 1c). There was a clear correlation (r=0.46, p<0.05) between the geometric mean dominance durations for the two tasks, consistent with previous work (Carter and Pettigrew, 2003) (though see also Gallagher and Arnold, 2014), as shown in Figure 1d.

We regressed mean dominance durations against resting state connectivity from our two seed regions to determine which areas of cortex were involved in determining the dynamics of bistable alternations. We found that the coupling between the aSPL seed and regions of the striatum (green regions in Figure 3a) showed a greater association with faster alternations for the binocular rivalry stimulus (i.e. shorter durations). The striatum is known to be important in relaying prediction error signals to primary regions of cortex (Daw et al., 2011) and might play this role in perceptual decision making (Forstmann et al., 2010; though see also Boekel et al., 2015).

Slower alternations during binocular rivalry were associated with stronger connectivity between the pSPL and regions of the left temporal lobe primarily in the inferior temporal gyrus (ITG, Figure 3b). The ITG constitutes the most anterior aspect of the ventral stream and is hypothesized to code relatively high-level information about stable properties of a stimulus, specifically in the visual modality (Kravitz et al., 2013).

Finally, relatively longer dominance durations in the Necker Cube were associated with stronger coupling between the aSPL and a region of medial cortex in the left hemisphere, at the boundary between the pre-supplementary motor area and the dorsal anterior cingulate cortex (see Figure 3c). This region of cortex is implicated in the coordination of the selection of goal related actions (Domenech and Koechlin, 2015) under conditions when stimulus input is stable.
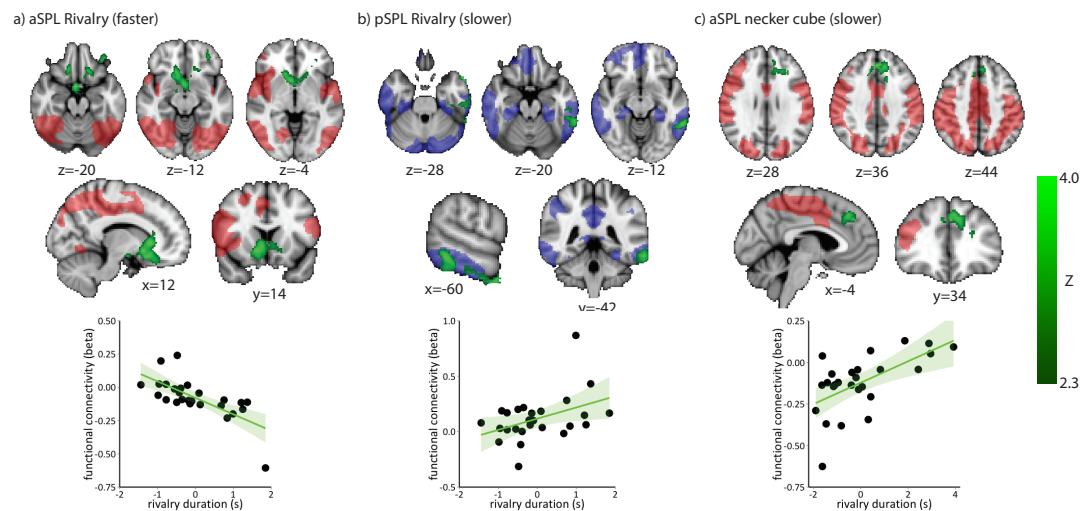

Figure 3: Regions associated with alternation rates. In each panel the red or blue shading shows the resting state networks derived in Figure 2, and the green shading shows regions that correlate with alternation rates. Panel (a) shows significant clusters where connectivity with the aSPL was associated with faster alternation rates during binocular rivalry. Panel (b) shows clusters from the pSPL seed associated with slower rivalry alternations. Panel (c) shows significant clusters where connectivity with the aSPL was associated with slower Necker cube alternations. Each subplot shows three axial slices, one saggital slice and one coronal slice, with MNI coordinates given below each image. The scatterplots show the relationship between dominance durations and connectivity (y-values are fMRI beta parameter estimates). In axial and coronal slices the left hemisphere is shown on the right of the image.

4 Discussion

We found evidence that anterior and posterior regions of superior parietal cortex which influence bistable perception in opposing directions do so because of differences in their functional architecture. Our seed region in the pSPL exhibited connectivity with regions of parietal and lateral prefrontal cortex whose specialism is in the extraction of higher order features of sensory input (Duncan, 2010; Goldman-Rakic, 1988). This functional network is consistent with prior fMRI studies that have found a relationship between alternations and activity in similar regions of fronto-parietal cortex (Kleinschmidt et al., 1998; Knapen et al., 2011; Lumer and Rees, 1999; Sterzer and Kleinschmidt, 2007; Watanabe et al., 2014; Weilnhammer et al., 2013). Importantly, Experiment Two found that connectivity between pSPL and ventral aspects of the temporal lobe was enhanced for individuals who experienced slower rivalry alternations. This brain region is important in visual aspects of semantics (Squire et al., 2004; Visser et al., 2010) and activity there is suppressed when an image is rendered invisible by rivalry suppression (Fang and He, 2005).

Together these data are consistent with the claim that the pSPL is part of a distributed functional system that helps stabilize a specific interpretation of low-level perceptual input.

In contrast to the pSPL, the aSPL was connected to regions of sensori motor cortex that are thought to serve functions more closely tethered to sensory input (Buckner and Krienen, 2013). Importantly, our data show that strong aSPL connectivity with the striatum was linked to shorter rivalrous durations. Given the potential role of the striatum in prediction error (Forstmann et al., 2010), this pattern of heightened connectivity suggests that during binocular rivalry, a specific percept may remain dominant as long as the competing low-level input is suppressed. Consistent with this interpretation of our data, recent work has shown that increasing the reward associated with a particular stimulus, a manipulation that increases the magnitude of a prediction error signal, increases the dominance of that particular stimulus (Marx and Einhauser, 2015).
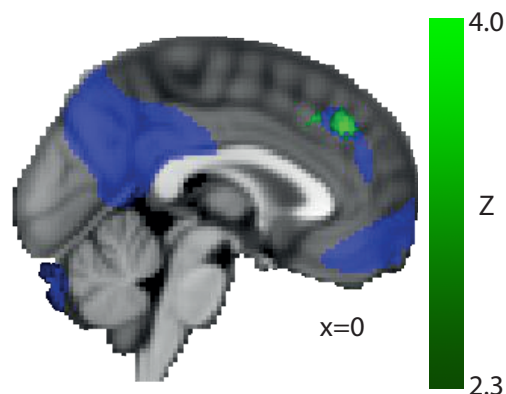

Figure 4: Overlap between the pSPL resting state network from Figure 2 (purple) and the connectivity between the aSPL region associated with slower Necker cube reversals (green; see Figure 3c).

Compared with resolving binocular rivalry, viewing a Necker cube involves overcoming incongruency in perceptual input at a relatively higher level. Connectivity between the aSPL and a region of dorso-medial prefrontal cortex was enhanced for participants with relatively longer dominance durations for the Necker cube. This region of pre-frontal cortex is implicated in the top-down coordination of cognition and action (Botvinick et al., 2004). Importantly, this region overlaps with the connectivity patterns of the pSPL (see Figure 4) suggesting that it is functionally connected to information arising in a bottom up manner from sensori-motor cortex and in a top down manner from information in associative cortex (see also Watanabe et al., 2014). This convergence of information would be especially important in allowing perceptual incongruity to be resolved at relatively complex levels such as that which occurs while viewing the Necker Cube.

Recently, a study using dynamic causal modelling delineated a network involving the right hemisphere parietal regions studied here (aSPL and pSPL) and motion area V5 (Megumi et al., 2015). The connectivity in this network accurately predicted individual alternation rates for a bistable structure from motion stimulus (see also Watanabe et al., 2014). We did not find significant connectivity with V5 using our resting state method, though this is likely because our stimuli were static, and so are unlikely to activate this motion-sensitive region of visual cortex. That we found no significant connectivity to early visual areas might suggest that the contribution of these regions to bistable alternation rates is determined by factors other than connectivity, such as neurotransmitter levels (van Loon et al., 2013).

4.1 Summary and conclusions

Building on prior investigations using techniques such as TMS, our study demonstrates the complex role that the SPL plays in maintaining a unified perceptual experience in the face of perceptual ambiguity. Anterior aspects are important in regulating low-level visual incongruity through interactions with sensori motor regions as well as limbic structures (such as the striatum). Posterior aspects, by contrast, may stabilize perceptual input through connectivity to regions of associative cortex including ventral aspects of the temporal lobe and elements of domain general prefrontal cortex. Importantly, these two systems may act in tandem to facilitate a unified perceptual interpretation in the face of more complex perceptual uncertainty (such as that which occurs while viewing the Necker Cube).

The participation of the larger SPL in a diverse and heterogeneous set of functional networks as our data shows indicates that it acts as a *hub* regulating the balance of neural processing. It is already known that this region of cortex is a member of a rich 'club' of regions whose connectivity allows them to integrate neural processing in an influential manner (van den Heuvel and Sporns, 2011). The heterogeneous nature of this pattern, coupled with its distinct psychological consequences, explains why disrupting adjacent regions of the SPL using TMS can have different and apparently contradictory consequences on rivalry durations. More generally, its role as a hub would allow the

SPL to stabilize perceptual experience on one of several possible perceptual interpretations that a complex environment can afford.

5 Author Contributions

DHB: Conceived the experiments, collected data, analysed data, wrote the paper
TK: Analysed data, wrote the paper
DDC: Analysed data, wrote the paper
KWN: Collected data, analysed data
JS: Conceived the experiments, collected data, analysed data, wrote the paper

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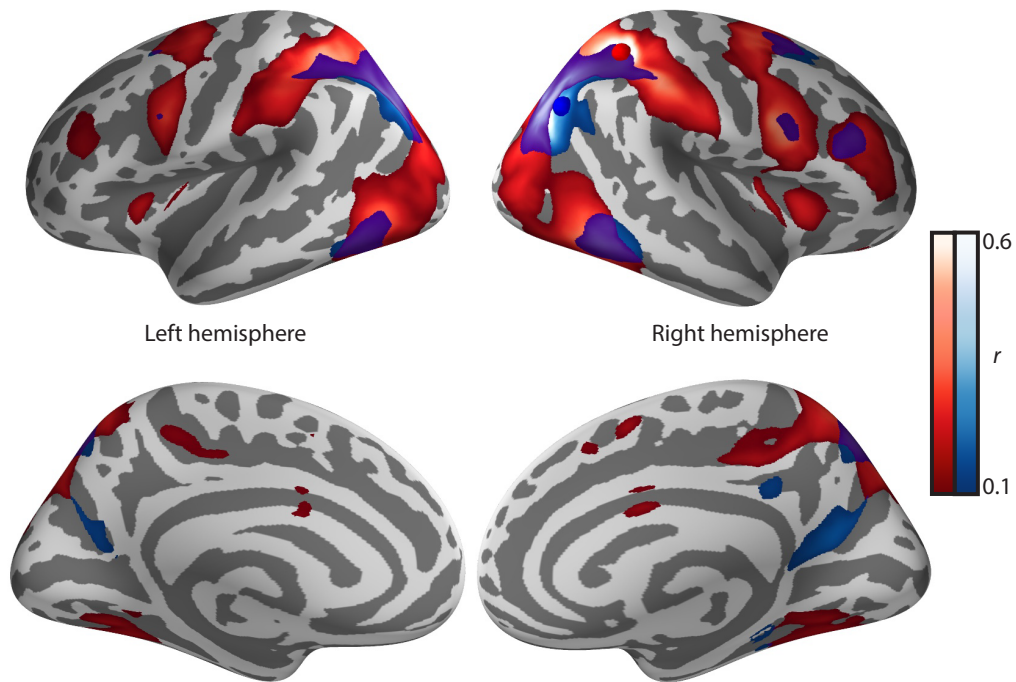
Supplementary materials

Figure S1: Networks derived from the Neurosynth dataset (*www.neurosynth.org*) with seeds placed in the same regions of the superior parietal lobule as detailed in the main paper (red and blue buttons). Colour intensity here corresponds to Pearson's *r* values indicating the strength of connectivity with the seed regions.
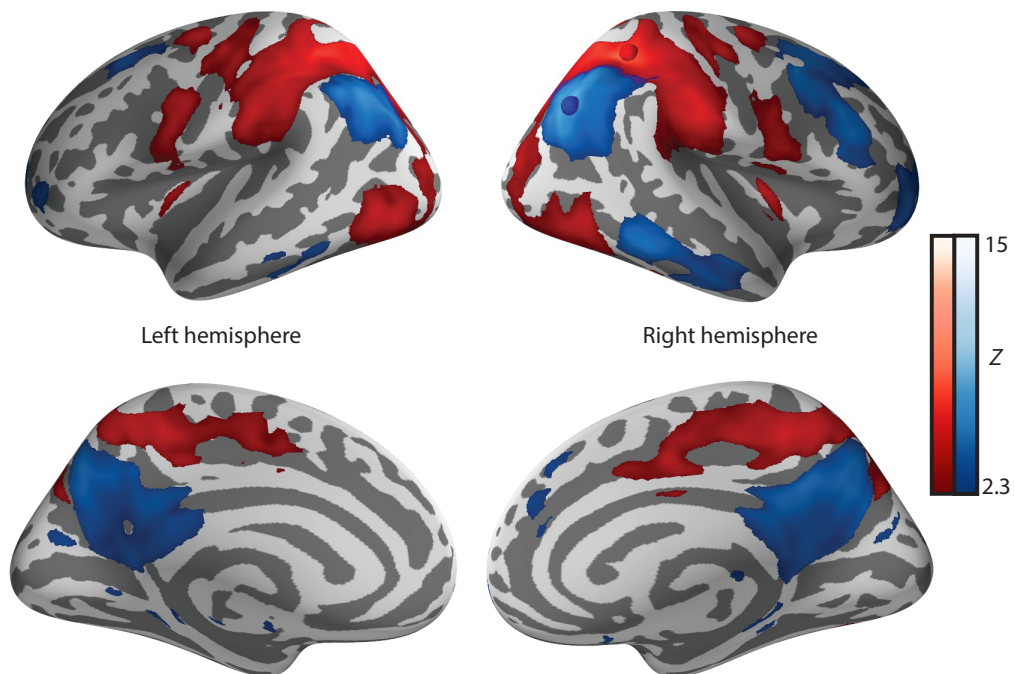

Figure S2: Networks derived from a second data set of 26 participants. Seeds were placed in the same regions of the superior parietal lobule as detailed in the main paper (red and blue buttons). The networks have the same layout as those shown in Figure 2.