Comparison of stimulus rivalry to binocular rivalry with functional magnetic resonance imaging

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Introduction

When incongruous images are presented to each eye, a type of perceptual bistability known as binocular rivalry occurs. For example, when a horizontal grating is presented to one eye and a vertical grating is presented to the other eye, the observer experiences perceptual alternations between the two gratings rather than a fusion of the patterns. The phenomenon has been studied extensively in the past few decades (Blake, 2001; Levelt, 1965, 1966; see Alais, 2012, for review) as a means to understand early postretinal visual processing (Blake, 1989; Lehky, 1988; Polonsky, Blake, Braun, & Heeger, 2000), the neural correlates of conscious perception (Baker, 2010; Doesburg, Green, McDonald, & Ward, 2009; Engel, Fries, Konig, Brecht, & Singer, 1999; Logothetis & Schall, 1989; Pearson, Tadin, & Blake, 2007), and even certain cognitive disorders (Fox, 1965; Miller et al., 2003; Nagamine et al., 2007; Ngo, Mitchell, Martin, & Miller, 2011). However, despite the wealth of research on this topic, some important aspects of binocular rivalry remain unresolved.

A typical model for binocular rivalry includes mutual competition between monocular neurons in the early visual cortex representing the patterns from each eye. This interocular competition is firmly supported by psychophysical data demonstrating monocular eye-based constraints on rivalry (Blake & Fox, 1974; Blake, Westendorf, & Overton, 1980; Fahle, 1987; Ooi & He, 1999; Shimojo & Nakayama, 1990). However, Logothetis & Schall, 1989; Pearson, Tadin, & Blake, 2007), and even certain cognitive disorders (Fox, 1965; Miller et al., 2003; Nagamine et al., 2007; Ngo, Mitchell, Martin, & Miller, 2011). However, despite the wealth of research on this topic, some important aspects of binocular rivalry remain unresolved.

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thesis, Leopold, and Sheinberg (1996) employed a stimulus featuring rapid interocular swaps of the incongruent images embedded in a high-frequency flicker and demonstrated that similar perceptual alternations can occur despite the rapid interocular swapping. In this stimulus rivalry, sustained periods of pattern dominance persist even during several stimulus swaps.

In order to account for these findings, several recent models of binocular rivalry feature a hierarchical organization with at least two stages of rivalry included: one based on interocular competition of monocular neurons in the primary visual cortex (V1) and a second level of pattern-based rivalry occurring after binocular integration (Dayan, 1998; Freeman, 2005; Gigante, Mattia, Braun, & Del Giudice, 2009; Lehky, 2011; Said & Heeger, 2013; Wilson, 2003, 2007). Wilson (2003) suggested that stimulus rivalry occurs because the rapid transients caused by the flicker and the swapping partially bypass the interocular competition so that sufficient signal can reach the binocular neurons. Once monocular competition is bypassed, neurons attempt to binocularly combine each of the opposing pattern signals. A type of rivalry that is pattern based then results from adaptation and mutual inhibition between pools of binocular neurons representing the opposing images. It would follow from this account that because the binocular neurons receive a reduced signal, lowering the effective contrast, stimulus rivalry is generally characterized by slower alternation rates and reduced perceptual suppression relative to binocular rivalry, and a mixture of the two patterns is more frequently perceived (Bhardwaj, O'Shea, Alais, & Parker, 2008; Kang & Blake, 2008; Lee & Blake, 1999; Said & Heeger, 2013; Stuit, Cass, Paffen, & Alais, 2009). According to this interpretation, stimulus rivalry is not a distinct perceptual phenomenon but rather is just a weaker version of binocular rivalry that occurs only with a limited set of stimulus parameters designed to pass on a strong enough signal for integration at higher level binocular neurons.

In addition to differing in the strength of the first stages of interocular inhibition, it follows from current accounts that stimulus rivalry differs from binocular rivalry with respect to differential reliance on intraocular inhibition. It is known that stimulus rivalry depends on within-eye inhibitory processes to prevent image blending as the patterns of each eye change rapidly due to the swaps, while binocular rivalry does not. The presence of rapid dynamic changes of the image in each eye also partly explains why the alternations in stimulus rivalry are more difficult to perceive than those in binocular rivalry. This within-eye inhibition is likely related to the mechanisms that underlie classic visual masking and rapid serial visual presentation (Brascamp, Sohn, Lee, & Blake, 2013; Keysers & Perrett, 2002; van Boxtel, Knapen, Erkelens, & van Ee, 2008) and reduces perceived effective contrast of rivaling stimuli (e.g., Brascamp et al., 2013). Such mechanisms have been associated with the properties of lateral geniculate nucleus (LGN) neurons and might precede the interocular inhibition in V1 (Baker & Graf, 2009b; Baker, Meese, & Summers, 2007). Thus, these models suggest that the neural activity evoked in the lower tier visual cortex would be reduced for stimulus compared with binocular rivalry despite the increased transients. Finally, it may be important to consider that some stages of rivalry may be common to binocular and stimulus rivalry. For example, both might depend on mutual inhibition processes among pools of binocular neurons in higher tier cortical regions and the systems for attentional control of visual awareness (Ling & Blake, 2012).

In this article, we perform a direct comparison of binocular rivalry and stimulus rivalry using functional magnetic resonance imaging (fMRI), which is important in order to test predictions from current models of binocular rivalry and to determine how stimulus rivalry fits within these models. Previous functional imaging studies have almost exclusively focused on binocular rivalry and have provided evidence for competition at different levels of stimulus representation, consistent with hierarchical models. Most neuroimaging studies report widespread activation across the cortex, including the occipitotemporal, parietal, and frontal areas (e.g., Engel et al., 1999; Lumer, Friston, & Rees, 1998; Pitts & Britz, 2011; Tong, Nakayama, Vaughan, & Kanwisher, 1998), although others have focused on the role of early visual areas (Kamphuisen, Bauer, & van Ee, 2008; Lee & Blake, 2002; Lee, Blake, & Heeger, 2007; Polonsky et al., 2000; Tong & Engel, 2001). Since none of these studies have included a comparison with stimulus rivalry, there is very limited physiological evidence to tease apart the neural substrates for the two versions of rivalry. One study using transcranial magnetic stimulation (TMS) found that stimulation of early visual areas (including V1) affected alternations for binocular rivalry but not for flicker-swap stimulus rivalry (Pearson et al., 2007). A direct comparison between binocular rivalry and stimulus rivalry using fMRI would be valuable to provide support for our idea that stimulus rivalry is a weaker version of binocular rivalry, which can be explained within the context of a hierarchical model. We hypothesized that activation would be higher for binocular rivalry than for stimulus rivalry in early visual areas because of the weaker feed-forward signal for stimulus rivalry as a consequence of interocular inhibition, as discussed above. Furthermore, we also hypothesized that there would be stronger activation for binocular rivalry than for stimulus rivalry in
higher level areas, including in the parietal lobe, reflecting greater attentional engagement, because most subjects report subjectively that the alternations are more vivid and easier to perceive. The perception of stimulus rivalry alternations is less salient in comparison. These observations suggest that comparing binocular and stimulus rivalry while also varying task demands could be informative for characterizing the differences.

One major challenge to performing a comparison between binocular and stimulus rivalry is their aforementioned differences in alternation rates as well as different spatial frequency and luminance contrast tuning (Bonneh, Sagi, & Karni, 2001; Lee & Blake, 1999). However, van Boxtel et al. (2008) recently demonstrated that controlling certain temporal factors of the swap stimulus (e.g., the length of time between swaps) can minimize differences in both alternation rates and reported rivalry percepts relative to binocular rivalry, even diminishing differences in the effect of spatial frequency. Similar to Kang and Blake (2008), the authors also found that disrupting dichoptic presentation—in this case, by including a blank period—shortly before an image swap promoted stimulus rivalry more effectively than the earlier flicker-swap stimulus. In keeping with Wilson’s (2003) model, van Boxtel et al. (2008) interpreted their results as reflecting specific temporal constraints necessary for a swapping stimulus to bypass the interocular competition typical of binocular rivalry. More practically, their findings allow experimenters to match alternation rates for binocular and stimulus rivalry with the same level of stimulus contrast. Such a matched approach is ideal for a direct neurophysiological comparison of these two types of perceptual rivalry.

Informed by the stimulus parameters of van Boxtel et al. (2008), we used functional imaging to investigate blood oxygen level–dependent (BOLD) response differences between closely matched binocular rivalry and stimulus rivalry tasks for the first time. In order to control for differences that may result simply from increased responses to rapid dynamic visual stimulation compared with a static dichoptic display, we presented binocular rivalry images that blanked at the same rate as the image swap rate of the stimulus rivalry images. Additionally, we employed several control conditions that allowed us to specifically investigate BOLD activity corresponding to perceptual rivalry rather than activity related to stimulus changes or to motor responses. Finally, in order to assess the possible differential roles of voluntary attention and visual awareness, we compared rivalry types during both passive viewing conditions and a more effortful active task requiring button presses.

### Method

#### Subjects

Six healthy adults (four females, two males) participated in all experiments. Two were authors (A. B. and L. K.) and four were naive to the hypotheses of the study. The subjects were university students or postdoctoral fellows. All were right handed and had normal or corrected-to-normal acuity and stereoscopic thresholds better than 30 arc s, measured using the Titmus stereo test (Stereo Optical, Chicago, IL). The subjects provided informed consent and were remunerated for their time. The experiments were approved by the Research Ethics Board of the McGill University Health Centre (Protocol NEU-08-03).

#### Display

All stimuli were presented using a MacBook Pro Laptop (Intel Core 2 Duo) Macintosh computer (1024 × 768 resolution, 120-Hz refresh rate, 8 bits/pixel gray scale, Apple, Cupertino, CA). Stimuli were generated and displayed using Matlab, version 2008 and Psychtoolbox Version 3 software and a Matrox (Dual Head 2Go Analogue Edition, Matrox Graphics, Inc., Dorval, Quebec, Canada) splitter graphics card. Dual liquid-crystal display (InFocus LP 540, InFocus Corporation, Milton, Ontario, Canada) projectors and linear polarizers (Edmund Optics, Barrington, NJ) were used for dichoptic projection (Thompson, Farivar, Hansen, & Hess, 2008). The subjects wore linear polarizers with complementary polarization on their eyepieces. The stimuli were back projected from the liquid-crystal display projectors onto a screen (Eclipse II, Reversa World SL, Bugansvillas, Spain) at the rear end of the fMRI scanner bore at a viewing distance of 134 cm, and subjects viewed stimuli through a mirror attached to the head coil. The display was gamma corrected using a color look-up table so that after calibration the stimulus had a mean luminance of 32 cd/m² and a peak luminance of 64 cd/m² viewed through the polarizers. The same display equipment and viewing condition parameters were used for both fMRI scan sessions and psychophysical sessions, including the same viewing distances.

#### Stimulus conditions

Figures 1 and 2 depict the stimuli used for the two rivalry types. All conditions featured oblique left–right sinusoidal grating stimuli (spatial frequency of 1.4 cpd...
and Michelson contrast of 80\%). Orthogonal orientations were used (45°, -45°). The stimulus was displayed as a 3.5° × 3.5° square patch on the mean luminance background, with a 0.2° fixation cross at the center. In different conditions, blank periods were introduced periodically by removing the stimulus and showing the background luminance. Note that the stimulus rivalry condition that we used is not conventional flicker and swap rivalry (Lee & Blake, 1999; Logothetis et al., 1996) because we did not use the high-frequency 19-Hz flicker but rather used short blanking periods, which has been shown to promote stimulus rivalry just as easily (van Boxtel et al., 2008). To avoid confusion, we thus reserve the term flicker for those high (19 Hz) frequencies.

**Binocular rivalry (fMRI active and passive scans)**

In the binocular rivalry condition (Figures 1B and 2A), the sinusoidal grating stimulus was displayed with a constant interocular orientation difference of 90°. In order to match the temporal transients that occurred during the stimulus rivalry condition, the images were periodically blanked at the same rate. The time period for displaying the stimulus was 90 ms, followed by a blank period of 60 ms. Hence, the total pattern repetition period was 150 ms, corresponding to a blanking rate of 6.67 Hz.

**Stimulus rivalry (fMRI active and passive scans)**

In the stimulus rivalry condition (Figures 1C and 2B), the interswap period, or period between two successive stimulus swaps between the eyes, was 150 ms. During each 150-ms period, the stimulus was displayed for 90 ms, followed by a blank period of 60 ms. Hence, the blanking frequency was 6.67 Hz. We chose these particular stimulus parameters from pilot studies that indicated that it was possible to obtain stimulus rivalry with similar alternation rates to binocular rivalry using these values, as found by other researchers (van Boxtel et al., 2008).
Figure 2. Schematic illustration of the active task stimulus conditions in the fMRI experiment. Color is used only to increase the legibility of the diagram; the actual stimuli were monochromatic, as shown in Figure 1. Right-leaning gratings are depicted in red, while left-leaning gratings are depicted in green. The orange hands indicate button presses made by the subjects. For binocular rivalry (A), the gratings blanked on and off at a rate of 6.67 Hz, but the orientation of the grating shown to each eye did not change.
Stimulus rivalry (B) featured the same dynamics, but the gratings were swapped between eyes on every cycle. For replay (C), nonrivalrous matched stimuli alternated at a rate determined individually for each subject and each scan based on the preceding rivalry blocks. For the matched control condition (D), the asterisks are used to indicate the slightly longer blank periods that subjects were instructed to detect. Note also the fast monocular changes in the matched control condition.

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**Binocular rivalry replay (fMRI active scans only)**

The binocular rivalry replay condition (Figure 2C) was a control condition with stimulus changes determined by the button press data from each participant’s immediately preceding fMRI binocular rivalry blocks. The subject viewed matched stimuli in each eye that alternated physically in orientation to mimic the perceptual experience during rivalry. In this condition, there was no interocular orientation difference, so no actual rivalry occurred. As in the binocular rivalry condition there was similar blanking (6.67 Hz) but no swapping.

**Stimulus rivalry replay (fMRI active scans only)**

The stimulus rivalry replay condition (Figure 2C) was a control condition with stimulus changes determined by the button press data from each participant’s preceding stimulus rivalry blocks. Again, the subject viewed matched stimuli in each eye that alternated physically in orientation to mimic the perceptual experience during rivalry, but no perceptible rivalry occurred. Just like the binocular rivalry replay condition, there was similar blanking (6.67 Hz) but no swapping.

**Matched control (fMRI active and passive scans)**

The matched control condition (Figure 2D) was similar to the stimulus rivalry condition, using the same temporal dynamics for the swap presentation, except that there was never any interocular orientation difference and therefore no perceptible rivalry alternations. The condition was included to measure the activity for stimulus rivalry that might be related to rapid changes in monocular spatial information rather than rivalry per se. Unlike the other conditions, the blanking period was longer than average (200 ms instead of 60 ms) every second or two. This was done so that during the active scan conditions the subject could be given the task to hit a key every time a longer blank period was observed. Each subject’s key press data were used to determine precisely when these longer blanking periods occurred. This allowed a matched comparison with the other active task conditions.

**Matched binocular rivalry (fMRI passive scans only)**

The matched binocular rivalry condition was an additional nonrivalrous, passive control condition with stimuli similar to binocular replay, but there was no task (not shown in figures). Extended blocks consisted of either left oblique or right oblique gratings, and the only transients were the blanks. This was intended as a low-level control for the stimulus properties of binocular rivalry and was used only for the purpose of region of interest (ROI) definition (see below).

**Psychophysical tests**

Before each subject attended the scanning session, behavioral responses to the rivalry stimuli were measured via psychophysical test sessions. Alternation rates were measured for binocular rivalry and stimulus rivalry conditions with the left–right oblique sinusoidal grating stimuli. Subjects reported perceptual alternations continuously over two separate 90-s trials, alternately pressing two different keys. Subjects pressed the first key once the left oblique stimulus component was exclusively visible over at least two thirds of the stimulus or if a composite was perceived. Subjects pressed the second key once the right oblique stimulus component appeared to be exclusively visible using the same criterion. A second set of trials was carried out in which the meaning of the keys was reversed (i.e., the first key was pressed if the left oblique was exclusively visible, while the second key was pressed if the right oblique or composite was perceived). This was done to confirm whether subjects had a dominant eye and to measure the time that a composite was perceived. Subjects performed eight repetitions of the rivalry task with each stimulus condition.

**Functional magnetic resonance imaging**

**Acquisition of fMRI data**

All images were acquired using a 3T MR scanner (Siemens, Munich, Germany) with a 32-channel head coil (20 channels for retinotopic mapping) at the Montreal Neurological Institute. Functional whole-brain images were acquired using a T2*-weighted gradient echo echo-planar imaging sequence (38 slices, repetition time = 2500 ms, echo time = 30 ms, field of
view (FOV) = 192, voxel size = 3 × 3 × 3 mm). Functional images for retinotopic mapping were acquired with a T2*-weighted sequence, with slices oriented perpendicular to the calcarine sulcus (28 slices, repetition time = 2000 ms, echo time = 30 ms, FOV = 128, voxel size = 4 × 4 × 4 mm). Anatomical images were acquired using a T1-weighted magnetization-prepared rapid gradient-echo sequence optimized for contrast between gray and white matter (176 slices, repetition time = 2300 ms, echo time = 2.98 ms, FOV = 256, voxel size = 1 × 1 × 1 mm).

**Active task scans**

A block design comprising 30-s stimulus blocks in a pseudorandomized sequence was used. The first half of the run consisted of a block of binocular rivalry and a block of stimulus rivalry. There were also single blocks of two other stimulus conditions not analyzed in this article. Subjects used a button box to report when their dominant percept switched to that of a left oblique or right oblique grating (following the procedure described above). During the second half of each scan run, a rivalry replay block was presented for each of the previous rivalry conditions from the first half of the run, similar to the manner in which rivalry replay has been used in previous studies (e.g., Lumer et al., 1998). In these replay conditions, the stimulus itself switched between the two possible grating orientations that were perceived during rivalry alternations, duplicating the exact temporal sequence of the button presses from the first half of the run (Figure 2C). There was also a block of the matched control condition, presented in the latter part of the scan, in which there were fast stimulus changes but no perceptible rivalry (Figure 2D). Each subject’s rivalry key press data, taken from earlier in the same scan, were used to determine the timing of events for detection. Finally, one block of each run was a blank baseline condition. During the first 0.8 s of each stimulus block, central fixation markers (“X,” “O,” or “+”) were superimposed on the stimulus to aid fixation and indicate which task needed to be performed. Thus, there was a total of 11 blocks in each scan run for a total length of 330 s. These were presented in pseudorandomized order with the constraint that all rivalry replay blocks were in the latter half of the scan. Each subject participated in a total of eight of these scan runs.

**Passive viewing scans**

In the passive viewing runs, a block design comprising 15-s stimulus blocks was used. The binocular rivalry and stimulus rivalry stimuli were identical to those in the scans with a task. In addition, the matched control condition was used in which there were fast stimulus changes but no dichoptic patterns (Figure 2D). As in the active conditions, the occasional longer blank periods were based on each subject’s key press data taken from an active scan earlier in the fMRI scan session. However, no key presses occurred during any of these passive scans. A fourth condition was the matched binocular rivalry that consisted simply of matched orientations in the two eyes, either left or right oblique. A fifth condition was the blank baseline condition. Two other conditions are not reported here. Three repetitions of each of these seven block types were shown in pseudorandomized order for a total of 21 blocks lasting 315 s. Each subject participated in two of these runs, which were averaged together for analysis.

**Retinotopic mapping and the localization of visual area MT+ and lateral occipital complex**

Retinotopic mapping was carried out in a separate session. The stimuli for retinotopic mapping consisted of high-contrast, chromatic, flickering checkerboard patterns of two specific types. The rotating wedge stimulus swept through polar angles, and the expanding–contracting ring stimulus mapped eccentricity. There were four acquisition runs for each subject: eccentricity mapping (fovea to periphery and vice versa) and polar mapping (clockwise and counterclockwise). The polar mapping runs consisted of eight cycles (full-field rotation of the wedge) lasting a total of 512 s. The eccentricity mapping runs consisted of eight cycles of expanding or contracting rings lasting a total of 512 s. Both stimuli attempted to compensate for the cortical magnification factor by increasing in size as they approached the periphery (Sereno et al., 1995). The eccentricity stimuli traversed space with a logarithmic transformation. A central fixation marker was present at all times, and subjects were required to perform a task monitoring the orientation of the fixation marker to aid fixation stability. These retinotopic mapping runs were used to define foveal regions of interest for V1, V2, and V3, defined as the region of occipital pole activated in the central 5.3° of visual angle. Area V3A was also defined using these scans. Subjects also performed two runs of cortical motion area MT+ (middle temporal area) localization (256 s) consisting of eight 16-s epochs of low-contrast stationary rings and eight 16-s epochs of moving rings (Tootell et al., 1995). In addition, subjects performed two runs of lateral occipital complex localizer scans consisting of six blocks of photographs of objects alternating with six blocks of scrambled objects (textures created by randomly scrambling these pictures into 400 blocks) as well as a blank baseline condition at the beginning and end of the scan run. Each block was 20 s in duration, and 40 images were shown successively.
in each block. Regions of interest were defined by a $t$ test ($p < 10^{-4}$) that detected regions that were significantly more activated when subjects viewed photographs of objects compared with scrambled objects (Grill-Spector et al., 1998). This resulted in a bilateral region of contiguous voxels on the lateral surface of the brain near the lateral occipital sulcus and in ventral occipitotemporal regions extending into the posterior and mid fusiform gyrus and occipitotemporal gyrus.

**Additional regions of interest**

Additional regions of interest were defined as areas of contiguous voxels using statistical subtractions as follows (false discovery rate [FDR] = 0.01 in all cases). A superior parietal (SP) area was defined bilaterally as an area more strongly activated by the passive binocular rivalry condition than the matched binocular rivalry condition (passive scans). Similarly, the temporoparietal junction (TPJ) was defined as an area in the inferior parietal lobe more strongly activated by the passive binocular rivalry condition than the matched binocular rivalry condition from the passive scans (right hemisphere only). A ventral temporal (VT) area was defined bilaterally as an area more strongly activated by the active binocular rivalry condition than the active matched control condition.

**Data analysis**

BrainVoyager QX Version 2.1.2.1545 (Brain Innovation, Maastricht, The Netherlands) was used for all functional data analyses as well as for the creation of inflated and flattened cortical representations. The anatomical and functional scans were analyzed in BrainVoyager using the standard processing sequence in this software package, described as follows. The anatomical scans were used to create surface reconstructions of each subject’s cerebral cortex. The computed cortical surface representation was inflated and then flattened. Each subject’s reconstructed folded cortical representation was normalized to spherical coordinate space and aligned to a target brain (chosen as an individual subject) using cortex-based alignment (Goebel, Hasson, Lefé, & Malach, 2004). The cortex-based alignment was performed in order to obtain a good match between corresponding brain regions for the group-level statistical data analysis. Before analysis of the functional scans, the first two volumes of every scan were discarded. All functional images were subjected to a standard set of preprocessing steps: (a) three-dimensional motion correction, (b) slice timing correction, (c) linear trend removal using a high-pass filter, (d) transformation of the functional data into Talairach coordinate space (Talairach & Tournoux, 1988), and (e) coregistration to anatomical images. A voxel-by-voxel, fixed-effects general linear model was used for analysis. The functional results were then viewed on an individual’s cortical surface, producing maps of statistical significance ($t$ tests with an FDR of $p < 0.05$), which were spatially smoothed. In addition, we separately analyzed the BOLD signal changes within our regions of interest using a fixed-effects general linear model analysis.

**Results**

**Behavioral measures**

Figure 1D shows the mean dominance durations and alternation rates computed from the key press data for the binocular rivalry and stimulus rivalry tasks during the psychophysical tests and during the fMRI sessions. Although the psychophysical sessions conducted before scanning yielded no significant difference between the two rivalry types (duration = 1.78 s for binocular versus 1.69 s for stimulus), $t(5) = -0.75$, $p > 0.05$, we found that during the fMRI sessions stimulus rivalry yielded dominance durations that were significantly shorter than binocular rivalry, $t(5) = -2.6$, $p < 0.05$. The mean dominance durations for binocular rivalry and stimulus rivalry during the fMRI sessions were 1.77 s and 1.52 s, respectively. We note that less data were collected overall during fMRI sessions and were collected over a greater number of shorter epochs. These results were similar for alternation rates. The mean for all subjects during the psychophysical tests was 0.64 alternation/s for binocular rivalry and 0.66 for stimulus rivalry. This difference was not significant, $t(5) = -0.57$, $p > 0.05$. During the fMRI scans the respective means were 0.58 and 0.70 alternation/s, and the difference was not significant, $t(5) = -2.08$, $p > 0.05$. With regard to mixed percepts, the mean percentage was 10% for binocular rivalry and 14% for stimulus rivalry, and there was no significant difference between the conditions, $t(5) = 0.95$, $p > 0.05$.

**fMRI comparison of binocular rivalry to stimulus rivalry in active and passive conditions**

Figure 3A shows activation maps depicting subtractions of stimulus rivalry from binocular rivalry for both active and passive viewing conditions. Overall, the activation for binocular rivalry was stronger than for stimulus rivalry in all brain regions, with no negative values indicating stronger activation of
stimulus rivalry for either of the subtractions (which would be colored blue–green). Thus, this global pattern fits with our expectations based on models of binocular rivalry that stimulus rivalry is not a distinct perceptual phenomenon but rather a weaker version of binocular rivalry. Right parietal regions in particular show a large bias for binocular rivalry, especially in the passive viewing condition. This includes the SP and inferior parietal cortex, also known as the TPJ. Figure 3B shows plots of differences in percentage signal change between the two rivalry conditions for nine ROIs that include the SP and TPJ along with retinotopic and higher tier regions such as the lateral occipital complex and the VT cortex. As detailed in the Method section, all the ROIs were defined based on data that were entirely independent of the current subtractions, except for SP, TPJ, and VT. TPJ and SP were defined based on passive binocular rivalry data because their response was maximal. Thus, the lower response seen for stimulus rivalry and during active viewing should be compared with this benchmark. Nevertheless, as Figure 3B indicates, the activity in all...
the ROIs was stronger for binocular rivalry than for stimulus rivalry for all comparisons in both active and passive conditions. The 18 one-way analyses of variance (ANOVA) for the ROIs in the left and right hemispheres and active conditions were all statistically significant, with $F$ test values ranging from 2.58 to 36.10 ($p < 0.00001$). Likewise, the 18 one-way ANOVA for the ROIs in the passive conditions were also all statistically significant, with $F$ test values ranging from 1.55 to 36.70 ($p < 0.05–0.00001$). The differences during active viewing (pink bars) were small but reached significance in all comparisons ($ts = 2.33–4.68; p < 0.05–0.0001$) except for right V1, left V3, and bilateral V3A and MT+. Given that V3A and MT+ have both been associated previously with binocular integration, the lack of significant differences is notable and may indicate an aspect of processing common to both types of rivalry (see Discussion). Nevertheless, the differences between binocular and stimulus rivalry were much stronger for passive viewing (blue bars), and all comparisons were significant ($ts = 2.50–7.25; p < 0.05–0.0001$) except for left MT+. The large differences in V1 to V3, SP, and TPJ are prominent. This suggests that the activity normally produced by passive viewing of alternations is weak for stimulus rivalry but that with the addition of attention, awareness, and decision demands from active tasks, stimulus rivalry activation more closely resembles binocular rivalry. The question of which regions in the network reflect the activity most closely related to stimulus rivalry per se is addressed in the following section by means of comparison with the nonrivalrous replay task.

**fMRI comparison of binocular rivalry and stimulus rivalry with replay conditions**

Figure 4A shows brain maps indicating areas in which activation for binocular rivalry and stimulus rivalry was greater than their respective replay conditions. Figure 4B shows plots of differences in percentage BOLD signal change between the rivalry and respective replay conditions for nine ROIs. The replay conditions were based on each participant’s key press data recorded during their rivalry scans, so they consisted of stimulus changes precisely matching what was viewed earlier in the scans for the rivalry blocks. The participants also made key press responses during the replay conditions. These subtractions thus reveal activation that is related to the rivalrous perception per se, removing the influence of stimulus changes or motor responses. The maps indicate a consistently greater spread and extent of activation for binocular rivalry than for stimulus rivalry, as was expected on the basis of our predictions from models that stimulus rivalry is a weaker version of binocular rivalry. While differences between binocular rivalry and replay were significant for all ROIs tested ($ts = 2.98–6.39; p < 0.01–0.0001$), the differences between stimulus rivalry and replay did not reach significance in left V1, left and right V2, right V3, or TPJ (other ROIs: $ts = 2.29–7.34; p < 0.05–0.0001$). In other words, the BOLD signal in V1 to V3 and in the TPJ was low for stimulus rivalry conditions regardless of the presence of dichoptic stimulation and interocular conflict. This was clearly not the case for binocular rivalry, and there were prominent differences from replay in a number of areas, with the largest in V1 to V3 and the VT.

**fMRI comparison of binocular rivalry and stimulus rivalry with matched control in active and passive conditions**

The previous two comparisons allowed us to contrast the effects of viewing condition on both types of rivalry or the effects of rivalry type during active tasks. In this section we consider the matched, nonrivalrous control condition with fast stimulus changes (Figure 2D) that was available in our design for both types of rivalry and for both viewing conditions. Figure 5 shows the difference in percentage signal change of activity between both binocular rivalry and stimulus rivalry versus the matched control condition in nine ROIs. This is shown for both active and passive viewing conditions, which differed only in terms of the button press task.

Considering first the active tasks (shown with pink bars) for both types of rivalry, the BOLD signal generally exceeded the matched control, with prominent differences in V1 to V3 and area VT. It might be noted that, overall, this pattern of activity for the rivalry tasks versus the control task is similar to that produced for the rivalry tasks versus the replay tasks (Figure 4). In general, both of those comparisons are intended to isolate the processing specific to rivalrous, competitive alternations by removing the stimulus- and task-related effects. The main difference between the replay and control tasks is the inclusion of rapid stimulus transients (mimicking stimulus rivalry) for the matched control task (Figure 2D). Presumably, this difference explains why the differential signal in some areas (e.g., V3A and MT+) is reduced in Figure 5 compared with Figure 4 and somewhat higher in V1 to V3. We could attribute the former to motion sensitivity and the latter to some monocular masking.

During passive viewing (shown with blue bars), both types of rivalry showed weaker activation relative to the control in V1 to V3 (especially in the right hemisphere). This suggests that an overall attentional enhancement of activity in V1 to V3 occurs when active
decisions are required. For passive stimulus rivalry, except for a small SP response, activation was either no different from the control (V1, left V2 and V3, V3A, TPJ, VT, left MT+) or significantly less than the control stimulus, especially in the right V2 and V3. This reinforces the conclusions from both Figures 3 and 4 that when no task is required, stimulus rivalry produces a low BOLD signal for many ROIs. We suggest that this distinctively low (negative) differential response in V1 to V3 for stimulus rivalry may reflect the cumulative effects of inhibition from monocular masking as well as the mutual interocular inhibition.

For passive viewing, the largest positive differential activation is in SP. Therefore, both types of rivalry yielded an overall dissociation across the two viewing conditions. Namely, outside of the early visual cortex, the strongest activity during active tasks was found in the VT, while the strongest activity during passive viewing was in the SP. Moreover, the inverse was also true: Activity in the VT was comparatively weak in passive conditions, while activity in the SP was relatively weak in active conditions. Finally, it is notable that the pattern of activation for the TPJ was quite distinctive. Similar to the SP region, the TPJ was
Discussion

Summary of findings

In this experiment, we used fMRI to compare cortical activation during binocular rivalry tasks versus stimulus rivalry tasks. This is the first study to directly compare the two forms of rivalry in a functional imaging paradigm using parameters from van Boxtel et al. (2008) to approximately match these stimuli with respect to temporal properties and alternation rates. Additionally, in order to address the roles of attention and task demands in viewing the competing visual patterns, we compared rivalry in active tasks versus passive viewing conditions. To constrain our investigation to activation related to rivalry itself rather than to the changing stimulus or to motor activity, we employed replay blocks with pattern alternations identical in their timing to each participant’s rivalry percepts (based on button response data from earlier in the scan) and compared the BOLD activation for rivalry versus replay. Finally, we included a matched control condition with fast changes in monocular stimulation applied to both viewing conditions.

Overall, we observed that activation for binocular rivalry was stronger and more widespread than that for stimulus rivalry; this is consistent with our conception of stimulus rivalry as a weaker version of binocular rivalry rather than a distinct perceptual phenomenon.
There was greater activation for binocular rivalry relative to stimulus rivalry in early visual areas V1 to V3, the VT cortex, and the parietal cortex, including the bilateral superior (SP) and right inferior parietal cortex (TPJ). Comparisons with replay tasks showed stronger activity for the binocular rivalry task in all regions tested, while activity for the stimulus rivalry task did not differ greatly from its replay task in the early visual cortex or in TPJ, suggesting that the recruitment of these areas for stimulus rivalry is similar to what is required for basic visual stimulus processing. Consistently, comparisons with the matched control task reveal a similar pattern of activation in the early visual cortex and in the VT for both types of rivalry for active viewing—with binocular rivalry yielding the strongest activity—and reduced activity in these regions for passive viewing. Interestingly, the superior and inferior parietal regions were actually stronger during passive viewing than the active task, and these effects were greatly pronounced for binocular rivalry. Thus, the results fit with our expectations that there is a weaker feed-forward signal for stimulus rivalry in early visual areas and that the activation remains weaker in higher level areas, such as the parietal cortex, which are likely involved in salience and attentional modulation (Carmel, Walsh, Lavie, & Rees, 2010; Corbetta, Patel, & Shulman, 2008; Kanai, Bahrami, & Rees, 2010; Kanai, Carmel, Bahrami, & Rees, 2011; Ling & Blake, 2012; Zaretskaya, Anstis, & Bartels, 2013; Zaretskaya, Thielscher, Logothetis, & Bartels, 2010).

Relation to models of rivalry

Our findings provide support for models that assume that stimulus rivalry is a weaker form of binocular rivalry, which is consistent with a hierarchical model with competition between representations at different levels. The reduced activation for stimulus rivalry compared with binocular rivalry in early visual areas provides evidence that stimulus rivalry lacks a robust feed-forward signal from early visual regions, as early as V1 (Freeman, 2005; Wilson, 2003; see also Brascamp et al., 2013). This occurs despite much greater monocular stimulus changes for stimulus rivalry, indicating that the weaker signal of stimulus rivalry derives from \textit{intraocular} constraints (Bhardwaj & O’Shea, 2012; Brascamp et al., 2013) that may include a precortical origin (Baker & Graf, 2009b; Baker et al., 2007). These fast monocular dynamic changes also make stimulus rivalry alternations harder to perceive. This is consistent with the view that monocular neurons do in fact play an important role in stimulus rivalry (Brascamp et al., 2013; van Boxtel et al., 2008). The presence of flicker in stimulus rivalry generally reduces effective contrast (Brascamp et al., 2013), and this has been postulated to affect interocular competition in a fashion analogous to physical contrast (e.g., Baker & Graf, 2009a; Paffen, Alais, & Verstraten, 2006; Pearson & Clifford, 2005a). The results are also consistent with models of stimulus rivalry that include a partial bypassing of early \textit{interocular} competition due to equivalent mutual inhibition of monocular neurons (Freeman, 2005; Wilson, 2003) so that perceptual alternations are driven by binocular neurons in higher tier regions, but this presumably leads to a weaker signal overall and alternations that are harder to perceive (Bhardwaj et al., 2008). In comparison with stimulus rivalry, binocular rivalry may trigger greater interocular competition at the monocular level as well as greater image-based competition at the binocular level (Freeman, 2005; Tong, Meng, & Blake, 2006; Wilson, 2003). This appears to result in a more robust BOLD signal that propagates from lower to higher regions of the cortex during binocular rivalry. In support of this distinction, deactivation of the early visual cortex via TMS has been found to alter binocular rivalry but not stimulus rivalry (Pearson et al., 2007).

The results also showed greater activation for binocular rivalry than for stimulus rivalry in higher level areas such as the right hemisphere parietal cortex. At these higher tier areas the activity presumably does not reflect direct competition between different stimulus representations, but rather is more likely related to the role these areas play in attention, awareness, and modulation of rivalry percepts in lower level areas, including possibly both the maintenance of the current perceptual state during rivalry and switching to a new percept (Carmel et al., 2010; Corbetta et al., 2008; Doesburg et al., 2009; Doesburg, Kitajo, & Ward, 2005; Kanai et al., 2010, 2011; Ling & Blake, 2012; Williams, Elfar, Eskandar, Toth, & Assad, 2003; Zaretskaya et al., 2010, 2013). The results are in harmony with TMS studies that implicated a causal role for right parietal areas in the modulation of perceptual states during rivalry alternations. Our region of interest SP was defined functionally and, as such, included the regions of the SP cortex reported by Kanai et al. (2011) as well as the cortex anterior to the intraparietal sulcus. Thus, this includes two separate areas in which TMS has been found to affect rivalry rates in different directions—either increasing or decreasing rates. Moreover, for binocular rivalry, our observed activity in region SP was notably stronger in the right hemisphere than in the left—which is also compatible with the lateral specificity observed by Kanai et al. (2010, 2011), Carmel et al. (2010), and Zaretskaya et al. (2010, 2013)—yet this trend is not clear for stimulus rivalry. This fits with our overall hypothesis from rivalry models that stimulus rivalry is simply a weaker form of binocular rivalry that occurs under a small subset of stimulus parameter conditions.
Our novel demonstration of pervasively lower BOLD activity for stimulus rivalry compared with binocular rivalry not only provides support for particular models of rivalry as described above but also provides evidence against other types of rivalry models. Specifically, these data contradict the predictions of models in which the two types of rivalry are more or less equally driven by a common pattern-based (binocular) perceptual selection mechanism. Based on these types of concepts or models, we might have expected no significant differences between the two rivalry types, particularly at higher tier processing areas such as those in the VT cortex (Leopold & Logothetis, 1999; Sheinberg & Logothetis, 1997; van Boxtel et al., 2008). Indeed, some authors have even speculated that the role of higher tier areas would be greater for stimulus rivalry than for binocular rivalry, although this remains a topic of debate (Bartels & Logothetis, 2010; Brascamp et al., 2013; Pearson & Clifford, 2005b; van Boxtel et al., 2008). Instead, we advocate the view that stimulus rivalry is a weaker form of binocular rivalry, and no aspect of our data suggests any specialized cortical mechanisms for stimulus rivalry.

The role of cortical mechanisms for binocular rivalry

The role of perceptual suppression

We did not measure perceptual suppression per se in this study, and thus we make no attempt to discuss suppression (i.e., visual awareness) and specifically assign it to particular cortical regions. Furthermore, we acknowledge that just measuring the average BOLD signal (e.g., from V1) during extended periods of rivalry does not allow us to disentangle the separate roles of excitation versus inhibition (subtractive or divisive) in the complex circuit that underlies rivalry (e.g., Said & Heeger, 2013). We can only assume that the BOLD signal provides one global index that reflects a balance between excitation and inhibition (Boorman et al., 2010, 2015; Brocke, Schmidt, Irbacher, Cichy, & Brandt, 2008; Muthukumaraswamy, Edden, Jones, Swettenham, & Singh, 2009; Muthukumaraswamy, Evans, Edden, Wise, & Singh, 2012; Schäfer et al., 2012; Shmuel, Augath, Oeltermann, & Logothetis, 2006). We believe that this index is informative but far from exhaustive (e.g., Fesi & Mendola, 2015). An illustration that it is possible to derive estimates of suppression using functional imaging comes from the study of a related phenomenon called continuous flash suppression, in which one eye is shown a static stimulus while the other eye is shown a dynamically changing stimulus. Thus, the interocular inhibition is not equivalent because of the rapid transients presented only to one eye. This greatly increases the suppression of the other eye’s image to the point that rivalrous alternations occur rarely, if at all, and perceptual suppression is even greater than in binocular rivalry (Tsuchiya & Koch, 2005; Tsuchiya, Koch, Gilroy, & Blake, 2006). Several fMRI studies of continuous flash suppression have convincingly demonstrated a correlation between perceptual suppression and reduced BOLD activation in early visual areas (Watanabe et al., 2011; Yuval-Greenberg & Heeger, 2013) as well as the temporal and parietal cortex (Fang & He, 2005; Hesselmann, Hebart, & Malach, 2011; Jiang & He, 2006).

The role of binocular integration

The only exceptions to the finding of stronger activation for binocular rivalry than for stimulus rivalry were areas V3A and MT+. In these two regions, both types of rivalry yielded equally strong activity during active viewing. This differs from earlier findings for monocular pattern rivalry, where activation was consistently less than binocular rivalry in these areas across several contrast settings (Buckthought, Jessula, & Mendola, 2011). Both of these findings are compatible with the interpretation of those regions as being sensitive to binocular interactions and stereoscopic depth information (Brouwer, Tong, Hagoort, & van Ee, 2009; Chandrasekaran, Canon, Dahmen, Kourtzi, & Welchman, 2007; DeAngelis & Newsome, 1999; Welchman, Deubelius, Conrad, Bülthoff, & Kourtzi, 2005). This would suggest robust activity whenever binocular (i.e., dichoptic) information must be integrated or resolved. However, the results for passive rivalry were not as clear cut, given that activity in these two areas for binocular rivalry did exceed stimulus rivalry. In addition, activity for passive binocular rivalry exceeded the matched control condition in V3A and MT+, unlike for stimulus rivalry. Therefore, without the active task-related effects that generally minimized the differences between stimulus and binocular rivalry, V3A and MT+ also showed the overall bias in favor of binocular rivalry. We note in passing that one alternate interpretation of the weak or absent bias in favor of binocular rivalry for MT+ and V3A is that these areas are known to have saturated contrast response functions, so they might be less sensitive to a difference in the perceived effective contrast for the two rivalry types discussed in the previous sections.

The role of attention

Another important result in our study was the clear difference in activation for both binocular and stimulus rivalry that we observed for active rather than passive viewing conditions. Recall that although the alternation rates for the two types of rivalry were quite similar,
the alternations were easier to perceive for binocular rivalry than for stimulus rivalry. Introducing a task that increased attentional demands caused the observers to monitor and closely observe the alternations. This apparently had the effect of increasing activation levels for both types of rivalry (in V1 to V3 and the VT), although stimulus rivalry signals remained less than for binocular rivalry. Thus, the BOLD signal would correlate positively with presumed effort in those regions. However, for binocular rivalry we also found that some regions (SP and TPJ) were actually more strongly activated by passive viewing than by the active task (a situation that never occurred for stimulus rivalry). Therefore, instead of a BOLD effect that might reflect effort, these signals might be a reflection of a relatively more spontaneous or automatic feed-forward salience effect.

Corbetta et al. (2008) has proposed that the cortical networks for visual attention are divided broadly into dorsal frontoparietal networks for top-down selection and ventral frontoparietal networks for stimulus-driven selection. The dorsal parietal regions include the intraparietal sulcus and SP cortex, and so the activity in our SP ROI may partially reflect endogenous biasing for perceptual selection. In contrast, the ventral parietal regions (overlapping with the TPJ) are thought to be modulated by stimulus-driven attentional shifts, such as the appearance of new objects at unattended locations, and unexpected events. In accord with this interpretation, the TPJ region has also been implicated in the individuation of the objects in a visual scene (Xu & Chun, 2009). Interestingly, this region is recruited even when the cues to individuation are task irrelevant (Xu & Chun, 2007). This task-independent selectivity seems compatible with our findings for passive viewing of binocular rivalry. The strong rivalry-specific activity in the TPJ suggests a bottom-up visual salience selection process, which may serve as a cue for individuation in the context of ambiguous visual input. In other words, the visual system may treat each binocular rivalry alternation more like a new object event than in the case of stimulus rivalry. We note that TPJ activity has been observed for several types of perceptual bistability other than binocular rivalry (Inui et al., 2000; Kleinschmidt, Büchel, Zeki, & Frackowiak, 1998; Raemaekers, van der Schaf, van Ee, & van Wezel, 2009; Slotnick & Yantis, 2005; Sterzer, Russ, Preibisch, & Kleinschmidt, 2002), suggesting that the activation is due to changing object information in these ambiguous images. The fact that stimulus rivalry and monocular pattern rivalry (Buckthought et al., 2011) recruit dorsal but not ventral parietal regions such as the TPJ suggests that they both are highly dependent on top-down selection processes and may indicate that their pattern alternations are not interpreted as object related.

Finally, one finding that seems to be general to both binocular rivalry and stimulus rivalry is the modest but consistent double dissociation of activity in regions VT and SP relative to the matched control task for active versus passive viewing. In the VT—particularly the left hemisphere—the differences in activity for rivalry versus control are strongest during active viewing and are weaker during passive viewing. In contrast, the differences are strongest in SP during passive viewing and are weaker during active viewing. Keeping in mind that we refer only to relative differences here, this dissociation is consistent with previous interpretations of the two regions. As mentioned earlier, parietal regions are regarded as important for attentional selection processes that are relatively task independent (Corbetta et al., 2008; Xu & Chun, 2009). The VT cortex, however, is often implicated in tasks involving the categorization of objects or pattern information (Gauthier et al., 2000; Kanwisher, McDermott, & Chun, 1997; Kriegeskorte et al., 2008), and so the strong engagement of these regions during active viewing may reflect top-down categorization of the visual information as well as decisional processes related to the task. Our findings here may hint at distinct contributions of these different areas to the general phenomenon of perceptual rivalry (cf. Logothetis et al., 1996), but further experiments would be useful to test this generalization more directly.

**Limitations**

One possible limitation of our study was an unexpected significant difference in dominance durations between the two rivalry tasks during the fMRI sessions despite earlier psychophysical tests to ensure matched rates. Specifically, the alternations for stimulus rivalry were modestly faster than those for binocular rivalry despite the fact that, in general, stimulus rivalry tends to produce slower alternations than stimulus rivalry despite the fact that, in general, stimulus rivalry tends to produce slower alternations for previous flicker-and-swap versions (Bhardwaj et al., 2008; Kang & Blake, 2008; Lee & Blake, 1999; Stuit et al., 2009). While it is possible that the BOLD activation differences we observed between the two rivalry tasks in fact reflect this difference of alternation rates, this seems unlikely. For instance, a faster alternation rate does not necessarily indicate a weaker or more variable percept (Fox & Check, 1972). More important than this, however, is the fact that stimulus rivalry yielded pervasively weaker activation in the visual cortex than binocular rivalry despite the slightly faster alternations and despite featuring more frequent changes of monocular stimulus features via the interocular swapping of the gratings. Finally, a control analysis in which we compared the whole-brain activation levels for the two replay conditions (matched respectively for binoc-
ular and stimulus rivalry alternation rates) showed no differential activation in the occipital, temporal, or parietal cortices. Because of this, we interpret the weak activity for stimulus rivalry as reflecting real differences in visual processing compared with binocular rivalry rather than something specific to our experimental setup.

Conclusions

We performed the first direct comparison of binocular and stimulus rivalry using a functional imaging paradigm. The results were important in order to characterize how stimulus rivalry fits within hierarchical models of binocular rivalry. We found that responses to binocular rivalry were stronger than those to stimulus rivalry, particularly in the early visual cortex and parietal cortex, and particularly during passive viewing. While binocular rivalry yields robust activation throughout the brain even in the absence of a task, stimulus rivalry seems to be maintained primarily via higher tier ventral regions of the cortex, and a task is required. Moreover, unlike during binocular rivalry, the recruitment of the TPJ during stimulus rivalry could not be distinguished from activity for non-rivalrous controls. We find that only binocular rivalry produces perceptually vivid alternations, the associated increased activation of the early visual cortex, and the coordinated engagement of dorsal stream regions for selection of salient visual information, even if a task is not performed. Thus, this study is significant in providing physiological evidence that stimulus rivalry is not a distinct perceptual phenomenon but instead is a weaker version of binocular rivalry that fits within a hierarchical model of rivalry.

Keywords: visual cortex, inhibition, suppression, stereopsis, competition, attention, bistable

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