Probing visual consciousness: Rivalry between eyes and images

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During binocular rivalry, one stimulus is visible (dominant), while the other stimulus is invisible (suppressed); after a few seconds, perception reverses. To determine whether these alternations involve competition between the eyes or between the images, we measured suppression depth to monocular probes. We did so in conventional rival stimuli and in rival stimuli swapping between the eyes at 1.5 Hz (both sorts of rivalry were shown either with or without 18-Hz flicker). The conventional conditions cause rivalry that could involve either competition between the eyes or between the images or both. The eye-swapping conditions cause rivalry that could involve competition between the images. Probes were either a small spot or a contrast increment to one of the rival stimuli. Using both yes–no and forced-choice procedures, we found that conventional conditions yielded large suppression depth and that eye-swapping conditions yielded small suppression depth. Weak suppression during image rivalry is consistent with conventional rivalry's involving competition between eyes and between images and flicker-and-swap rivalry's involving little, if any competition between eyes and mainly competition between images.

Keywords: binocular rivalry, visual awareness, visual consciousness, flicker and swap rivalry, stimulus rivalry, visual detection

Introduction

During binocular rivalry, visual consciousness fluctuates randomly between two incompatible stimuli imaged on corresponding retinal regions of the two eyes. One stimulus is visible for few seconds (dominant) while the other stimulus is invisible (suppressed); after a few seconds, visibility reverses. This process continues for as long as one looks. Two broad approaches to the neural processing mediating rivalry can be distinguished: rivalry could involve competition between the representations of the two images tagged with low-level, eye-of-origin information (so-called *eye rivalry*) or between representations of the two images at some higher level of the visual system (so-called *image rivalry*).

To demonstrate eye rivalry, Blake, Westendorf, and Overton (1980) presented a vertical grating to one eye and a horizontal grating to the other and asked the observer to press a key when the vertical grating, say, was exclusively dominant. This key press swapped the gratings between the eyes: observers reported seeing the horizontal grating. Blake et al. concluded that it was the region of an eye that dominates during rivalry, not a particular stimulus.

Similarly, Shimojo and Nakayama (1990) presented a stereogram with an interocularly unpaired region consisting of non-identical patterns to induce rivalry. When that region had a disparity consistent with partial occlusion, they found no rivalry; when that region had the opposite disparity, they found rivalry. Shimojo and Nakayama concluded that rivalry critically depends on which eye receives an unpaired stimulus. Furthermore, Ooi and He (1999), investigating the role of attention in binocular rivalry, found that presenting a pop-out cue to one eye prior to the onset of rivalry made that eye's stimulus dominant in subsequent rivalry. They concluded that dominance during rivalry critically depends on which eye receives the pop-out cue. All these results are consistent with eye rivalry theory (Blake, 1989; Lehky, 1988; Nguyen, Freeman, & Wenderoth, 2001; Wolfe, 1986).

To demonstrate image rivalry, Diaz-Caneja (1928, translated by Alais, O'Shea, Mesana-Alais, & Wilson, 2000) presented a left field of horizontal lines and a right field of concentric semicircles to the left eye and the opposite pattern to the right eye. He found that observers occasionally reported coherent alternations between circles and horizontal gratings, combining these images from the components in the two eyes. Kovács, Papathomas, Yang,

and Fehér (1996) found similar results from complementary patchworks of intermingled photographic images. Logothetis, Leopold, and Sheinberg (1996) extended Blake et al.'s (1980) eye-swapping technique by presenting dichoptic orthogonal gratings that flickered at 18 Hz and swapped between the two eyes every 333 ms. Logothetis et al. found that occasionally a single grating was dominant over multiple alternation periods. They concluded that rivalry is mediated by representations of the images at higher levels of the visual system from which eye-of-origin information has been discarded. It is this form of image rivalry we are concerned with in this paper.

An emerging view about the neural processes mediating rivalry is that eye rivalry and image rivalry are processed at different cortical levels (Blake & Logothetis, 2002). We wondered if we could psychophysically distinguish different depths of suppression during eye and image rivalry. That would be consistent with suppression's acting at different sites in the two forms of rivalry.

Binocular rivalry suppression has traditionally been measured by delivering a probe stimulus to one of the rival stimuli during its dominance and suppression phases. The probe could be a superimposed spot or variation in some aspect of one of the rival stimuli. The difference in the threshold to detect the probe stimulus during dominance and suppression gives an estimate of suppression depth. We define suppression depth as unity minus the ratio of dominance to suppression thresholds. Early experiments showed suppression depths of around 0.3 to 0.5 log units (e.g., Blake & Fox, 1974; Fox & Check, 1966, 1968; Nguyen et al., 2001; Ooi & Loop, 1994; O'Shea & Crassini, 1981; Smith, Levi, Harwerth, & White, 1982; Wales & Fox, 1970).

Previous studies on binocular rivalry suppression have presented one rival stimulus continuously to one eye and the other rival stimulus continuously to the other eye. So as not to presuppose whether this involves eye rivalry or image rivalry, we will refer to such rivalry as *conventional*. We compared suppression in conventional rivalry with that from rivalry when the stimuli swap continuously between the eyes (as in Logothetis et al., 1996). We will refer to such rivalry as *swap*. We found weaker suppression depth during swap rivalry than during conventional rivalry. We will argue later that this is consistent with rivalry's involving processing at multiple stages of the visual system.

Experiment 1

Methods
Observers

Five observers (four males, ROS, DA, DG, and RB, and one female, AP) participated in this experiment after giving their informed consent. All observers had corrected-to-normal visual acuity and normal stereo-acuity. Ages ranged from 22 to 54 years. All the observers were naïve to the aim of the experiment in the sense that none had any idea of what would be found. Of the five observers, four were experienced and one (RB) was an inexperienced psychophysical observer.

Apparatus

Stimuli were generated by an Apple Power Macintosh G4/800 using Matlab in conjunction with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Visual stimuli were displayed on a Sony Trinitron high-resolution, 19-inch, color monitor (CPD-E230) at a viewing distance of 57 cm. The monitor's frame rate was 75 Hz and screen resolution was 1024 × 768 pixels. Its screen was calibrated using a Minolta Chroma meter (model CS-100). Stimuli for the left eye were presented on the left half of the monitor screen and stimuli for the right eye on the right half. The observer used a mirror stereoscope to bring the two views into alignment. Observers responded using the computer keyboard.

Stimuli

We chose the size and spatial frequency of our stimuli to optimize swap rivalry (see Lee & Blake, 1999). The rival stimuli were circular patches of sinusoidal 7 cycle per degree grating with a diameter of 2.34 degrees. We gave the stimuli opposite colors also to optimize swap rivalry (see Logothetis et al., 1996). One was a −45 degree red grating (CIE chromaticity coordinates $x = 0.315$; $y = 0.321$); the other was a +45 degree green grating ($x = 0.270$; $y = 0.347$). The gratings had 50% contrast and a mean luminance of 13 cd/m^2. Stimuli were displayed on an otherwise uncontoured background with a luminance of 0.05 cd/m^2. The experiment was performed in a dark room so that the only significant source of light came from the monitor screen.

There were four different ways these rival stimuli could be presented: (a) static-grating (unchanging, conventional rivalry stimuli), (b) flicker-only (similar to static-grating but flickering on and off at 18 Hz), (c) swap-only (rival stimuli swapping between the eyes at 1.5 Hz), and (d) flicker-and-swap (similar to swap-only but flickering on and off at 18 Hz; this was similar to Logothetis et al.'s, 1996, experiment) as shown in Figure 1. In static-grating and flicker-only conditions, the red grating was always presented to the left eye and the green grating to the right eye.

The probe was monocular luminance spot ($x = 0.268$; $y = 0.313$) subtending 0.16 degrees superimposed on the center of the left eye grating (pulse-probe condition). To avoid abrupt onset/offset of the probe, the probe was ramped on and off using a Gaussian temporal contrast

(a) Static grating

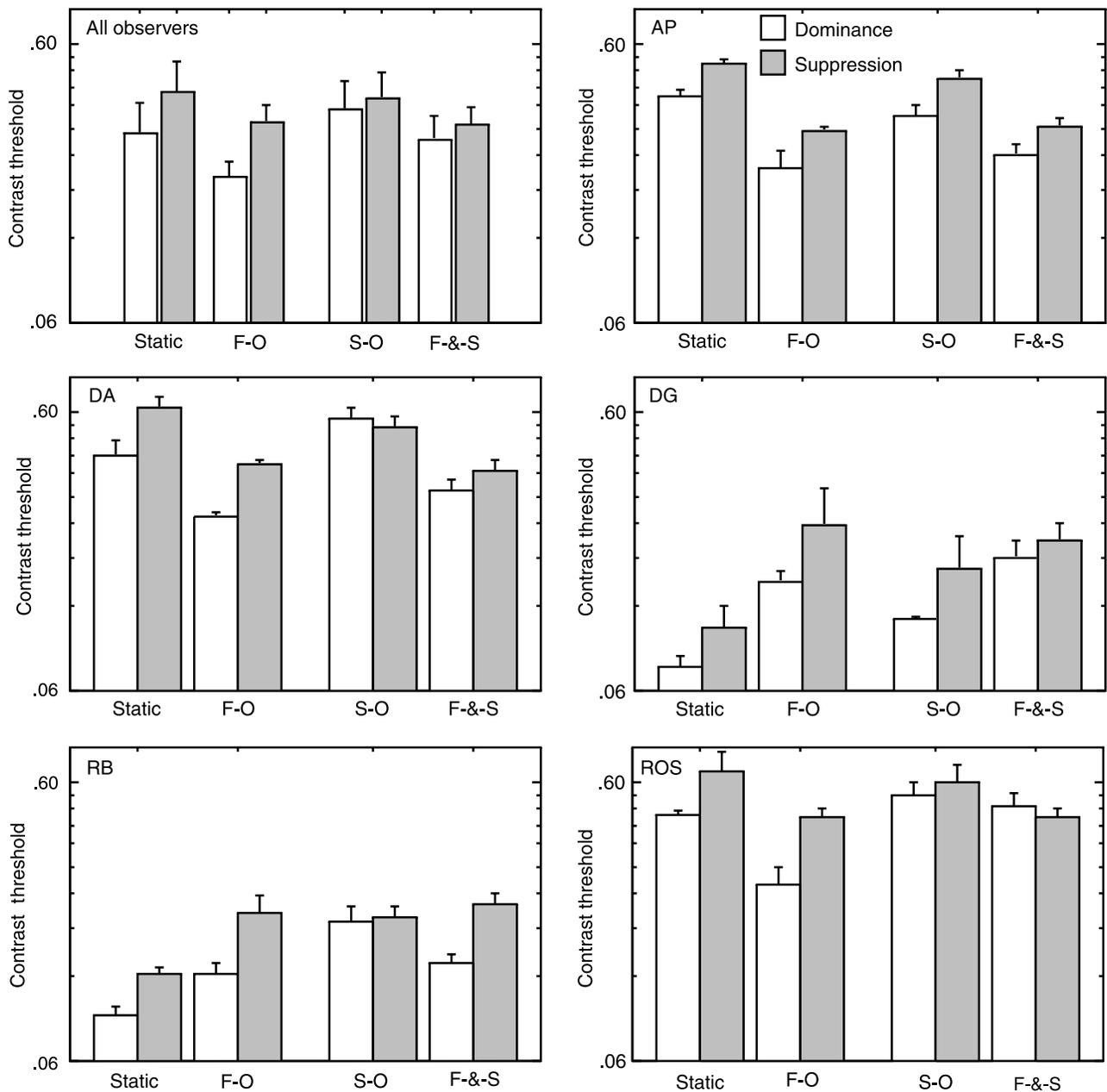(b) Fliker only

(c) Swap only

(d) Flicker-and-swap
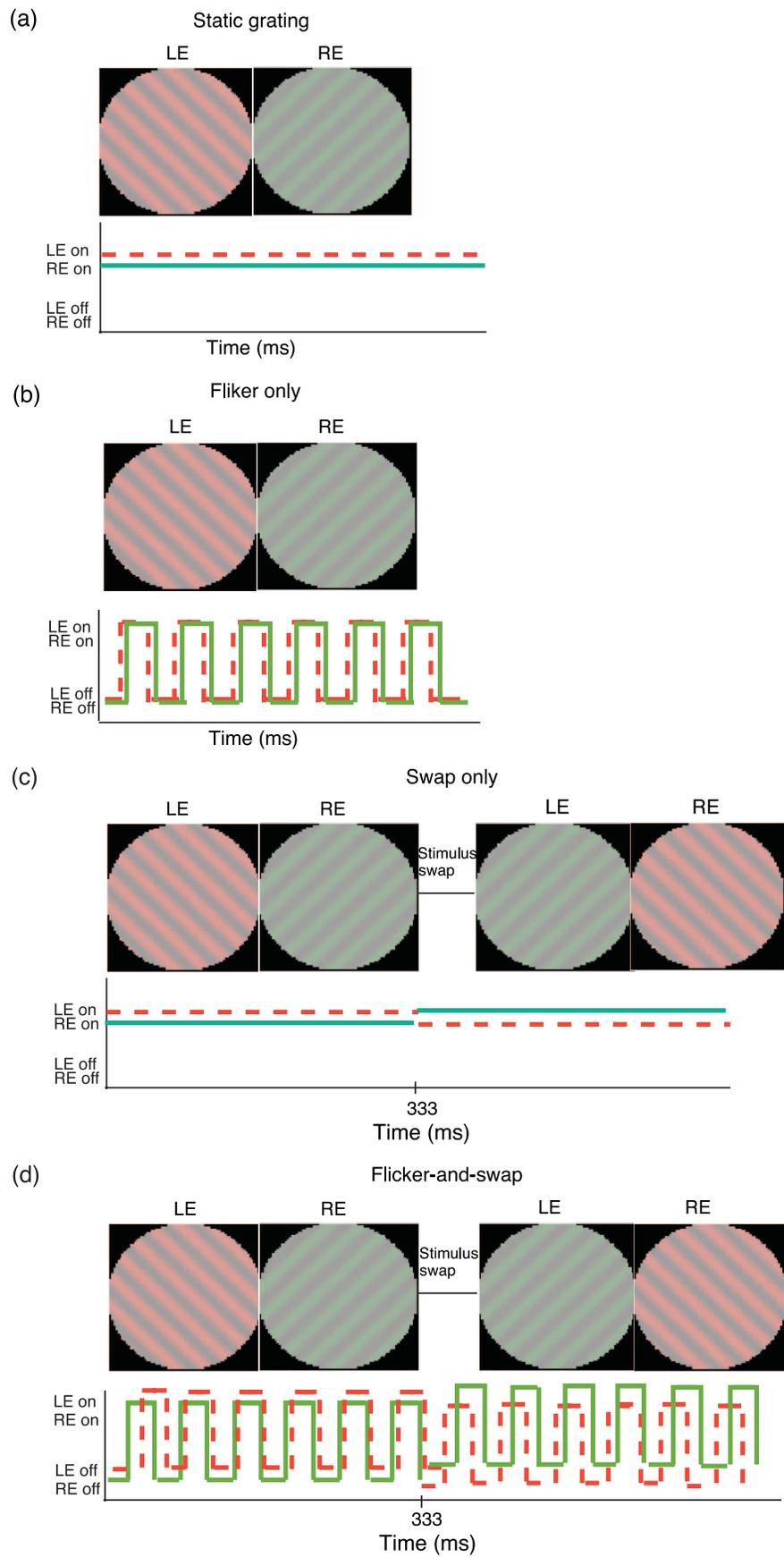
Figure 2. Showing the mean threshold for all observers in the top leftmost plot and individual observer plots for pulse probe in Experiment 1. Static indicates static-grating, F-O indicates flicker only, S-O indicates swap-only and F-&-S indicates flicker-and-swap condition. Error bars show 1 standard error of the mean.

Figure 1. (a) In the static grating condition a −45 deg red grating was presented to the left eye and +45 deg green grating was presented to the right eye throughout the trial. (b) The flicker-only condition was similar to the static grating condition except that the gratings were flickering on and off at 18 Hz. (c) In the swap-only condition the −45 deg red grating was presented to the left eye and the +45 deg green grating was presented to the right eye but after each 333 ms the stimuli were interchanged between eyes. (d) In the flicker-and-swap condition, the gratings were flickering on and off at 18 Hz and exchanging between the eyes every 333 ms.

envelope with a half-height full-width of 108 ms. When the rival stimuli flickered at 18 Hz, the probe also flickered at 18 Hz. To check whether differences between the temporal frequency of the probe and of the rival stimuli might affect the results, we also tested static and swap-only conditions with a probe that flickered at 18 Hz (flicker-probe condition).

Procedure

Each observer participated in at least four sessions of data collection. A single session consisted of all the four major

rivalry conditions for blocks of dominance and suppression. The order of the test conditions within a session was randomized and the order of testing dominance and suppression was random for each observer then alternated over sessions.

The luminance of the probe was varied using an adaptive QUEST procedure (Watson & Pelli, 1983) to find the 75% threshold level for detecting the probe. On 50% of the trials, the probe was presented and on the remaining 50% of the trials the probe was not presented. Two interleaved staircases comprising 20 trials each were used. These staircases were preceded by four practice trials. We presented the probe to the center of the −45 degree red grating in the left eye. If a probe presentation was triggered immediately after the −45 degree red grating switched to the left eye, then the probe was shown to the left eye. Otherwise, presentation was delayed until the next switch of the −45 degree red grating to the left eye. This meant a random delay of 13–560 ms during the swap conditions. We incorporated similar random delays into the non-swap conditions (a and b).

Observers controlled the onset of the probe with a key press. The observers were asked to trigger the probe stimulus only when the −45 degree red grating was completely dominant or completely suppressed. If, after deciding to press the key, the observer's perception reversed before the key could be pressed, we asked the observers to abort the trial by pressing another key. A correct response was indicated by a single short tone and an incorrect response with two short tones. We gave feedback to help observers reach and maintain optimal performance.

Analyses

We expressed threshold luminances as contrasts with the mean luminance of the grating on which the probe was superimposed. In our initial statistical analyses of these thresholds and of the thresholds in the other experiments, we found that their variances were correlated with their means, violating the assumption of homogeneity of variance made by analysis of variance (ANOVA). To restore homogeneity of variance, here and elsewhere, we log-transformed contrast thresholds. To calculate suppression depths, we subtracted from unity the ratio of untransformed dominance to untransformed suppression thresholds. Suppression depths, therefore can range from 0 (no suppression) to 1 (complete suppression). We also analyzed these data with ANOVA.

Results and discussion

We conducted a within-subject ANOVA on log thresholds with swap (swap/no-swap), flicker (flicker/no-flicker), and state (dominance/suppression) as factors. The analysis showed two significant effects that can be seen in Figure 2:

Thresholds were higher during suppression than during dominance, $F(1,4) = 133.53$, $p < .0001$. This difference was greater when the stimuli were not swapping than when they were swapping between the eyes, $F(1,4) = 8.49$, $p < .05$.

We then calculated the overall suppression depth for the four test conditions; these are plotted in Figure 3. A two-factor, within-subjects ANOVA showed the only significant effect was that suppression was deeper under no-swapping conditions (static-grating and flicker-only) than under swapping conditions (swap-only and flicker-and-swap), $F(1,4) = 8.23$, $p < .05$. Suppression depth was significantly greater than zero for static-grating and flicker-only conditions, $t(4) = 18.63$ and 13.41, $ps < .001$, but not for swap-only and flicker-and-swap conditions, $t(4) = 1.64$ and 2.10, $ps > .05$.

We also analyzed the flickering probes in the same way. Their results were essentially the same: strong suppression depth for conventional rivalry, weak suppression depth for swap rivalry, $F(1,4) = 8.04$, $p < .05$.

All the observers showed a suppression depth of about 0.3 for the conventional rivalry conditions agreeing with the previous research (Fox & Check, 1966, 1968; Nguyen et al., 2001; Ooi & Loop, 1994; O'Shea & Crassini, 1981; Smith et al., 1982; Wales & Fox, 1970). All the observers showed weaker suppression depth of about 0.1 for swap rivalry. We could think of two possible explanations for weak suppression during swap rivalry.

First, suppression during swap rivalry could be intrinsically weak. We will consider this explanation further in the later experiments. Second, the probe we used might have
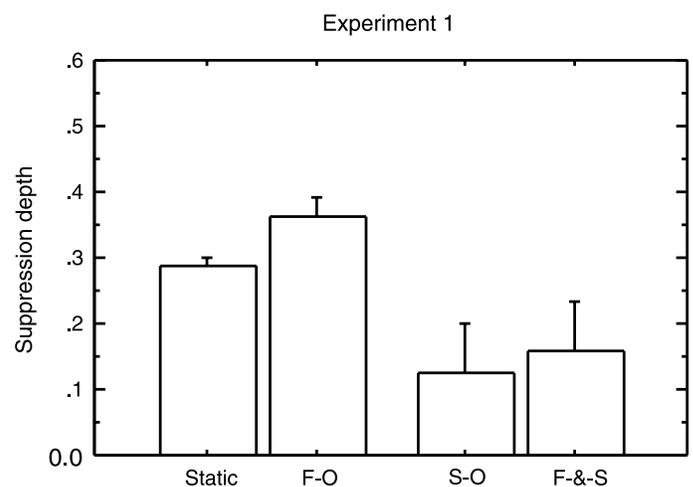

Figure 3. Showing the suppression depths for each condition tested in Experiment 1. Suppression depth is one minus the ratio of dominance to suppression thresholds. A value of 0 indicates no suppression. Static indicates static-grating, F-O indicates flicker only, SO indicates swap-only and F-&-S indicates flicker-and-swap condition. Error bars show 1 standard error of the mean. Both conventional rivalries yielded deeper suppression than the swap rivalries.

escaped suppression: we used a spot as a probe. Although Fox and colleagues have shown that suppression during eye rivalry is not spatially selective (Blake & Fox, 1974; Fox & Check, 1966, 1968, 1972; Wales & Fox, 1970), perhaps the suppression of swap rivalry is spatially selective.

To test these ideas, we conducted Experiment 2 in which we used a probe comprising a change to one of the rival gratings. By making the probe the same as the rival stimuli, we ensured that it must be detected by the neurons processing the rival stimuli.

Experiment 2

Method

The method was the same as in Experiment 1 with the following changes. Three observers from Experiment 1 (ROS, DG, and RB) and two new observers (one male HCH and one female BW) participated. Ages ranged from 22 to 58 years. All the observers except for observers ROS
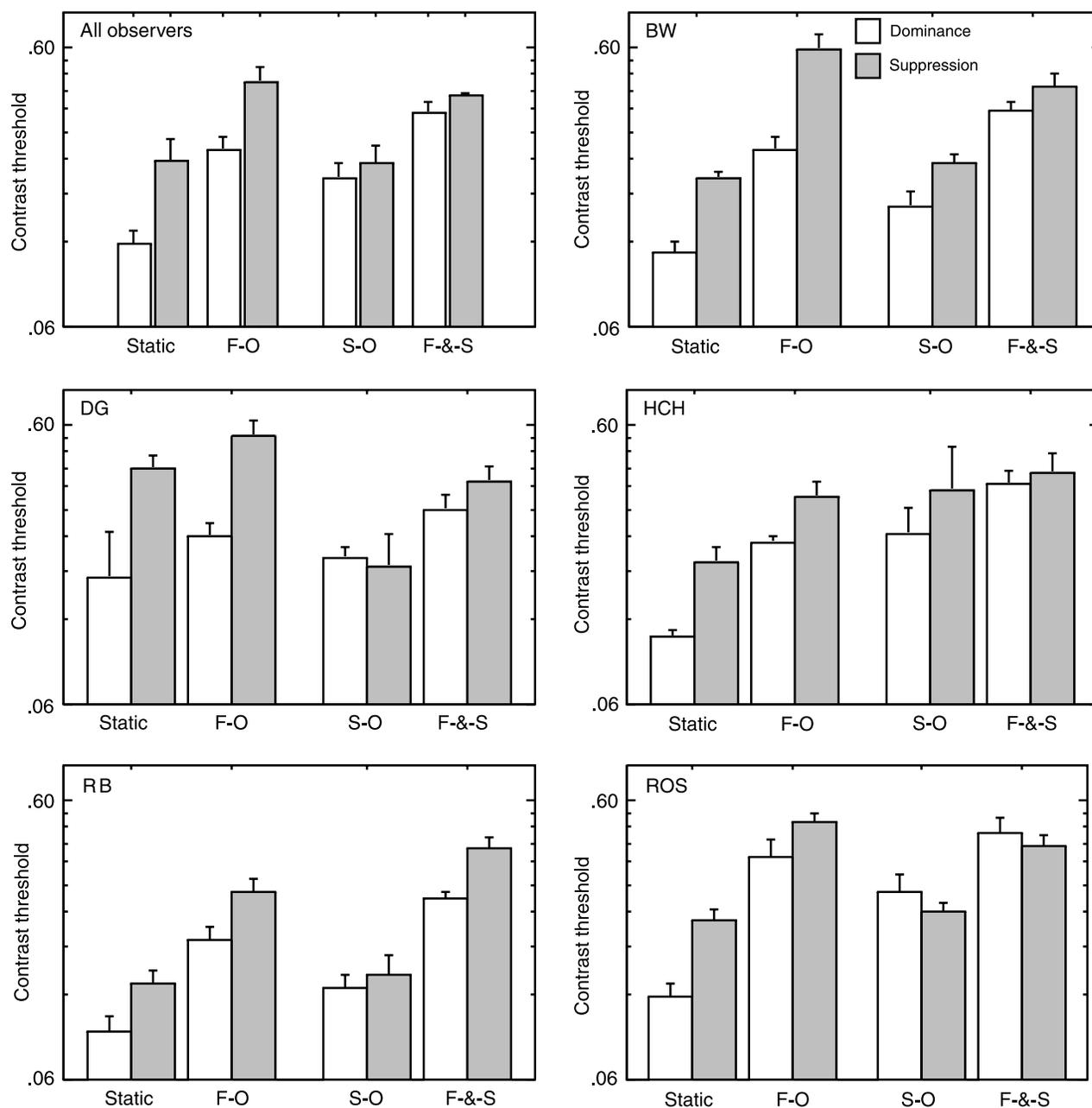

Figure 4. Showing the mean threshold for all observers in the top leftmost plot and individual observer plots when the probe was a contrast increment in Experiment 2. Static indicates static-grating, F-O indicates flicker only, S-O indicates swap-only and F-&-S indicates flicker-and-swap condition. Error bars show 1 standard error of the mean.

and RB were naïve to the aim of the experiment. Of the five observers, four were experienced and one (BW) was an inexperienced psychophysical observer. The gratings had a contrast of 25% to avoid ceiling effects when adding the probe. The probe was a superimposed red grating with the same phase, spatial frequency, size, and orientation as the red test grating. The probe was presented with the same Gaussian temporal profile as used in Experiment 1.

Results and discussion

We analyzed the data in the same way as in Experiment 1. There was a main effect of flicker, $F(1,4) = 56.77$, $p < .01$: thresholds with flickering rival stimuli were higher than with non-flickering rival stimuli. This probably arose because the high-temporal-frequency flicker masked the low-temporal-frequency probe (Cass & Alais, 2006).

Thresholds were once again higher during suppression than during dominance, $F(1,4) = 35.21$, $p < .01$. Critically, there was also an interaction between swap and state, $F(1,4) = 16.25$, $p < .05$, plotted in Figure 4. As in Experiment 1, it arises because thresholds are higher during suppression than during dominance, and this difference is bigger in conventional rivalry than in swap rivalry.

We show suppression depths in Figure 5. The only significant effect was swap, $F(1,4) = 16.30$, $p < .05$, arising from deeper suppression during conventional rivalry than during swap rivalry. Suppression depth was significantly greater than zero for static-grating and flicker-only conditions, $t(4) = 11.32$ and 5.99 ps $< .05$, but not for swap-only and flicker-and-swap conditions, $t(4) = 0.99$ and 1.85 ps $> .05$.
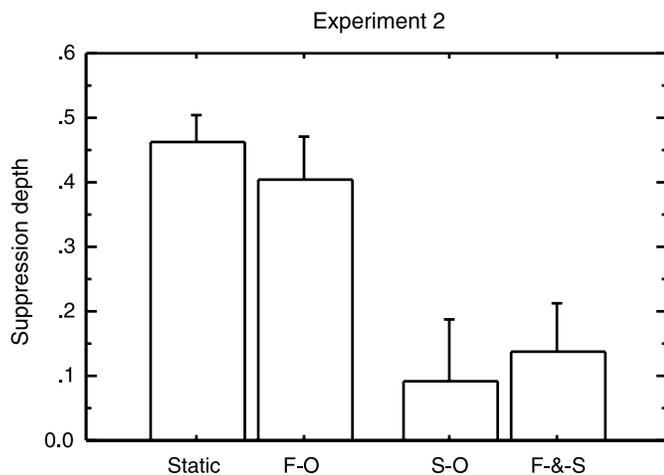

Figure 5. Showing the suppression depths for each condition tested in Experiment 2. Static indicates static-grating, F-O indicates flicker only, S-O indicates swap-only and F-&-S indicates flicker-and-swap condition. Error bars show 1 standard error of the mean. Conventional rivalry yielded deeper suppression than swap rivalry.

The results of Experiment 2 were similar to Experiment 1. Once again all the observers showed typical suppression depths, around 0.4, for conventional rivalry but weak suppression depths, around 0.2, for swap rivalry. This suggests that the weak suppression we found in both experiments for swap rivalry is not because the probe was processed by different neurons from those processing the rival stimuli.

Before we can conclude that suppression during swap rivalry is intrinsically weak, we need to address one other alternative explanation. It is possible that the yes–no procedure we used in Experiments 1 and 2 allowed different response criteria to operate in different conditions. This is plausible because Caetta, Gorea, and Bonneh (2007) recently found different response criteria to reporting probes delivered during dominance and suppression in motion-induced blindness, a perceptually bistable phenomenon in which peripheral dots superimposed in a globally moving background disappear and reappear (Bonneh, Cooperman, & Sagi 2001). In Experiment 3, we compared the yes–no procedure of Experiments 1 and 2 with a forced-choice procedure for detecting probes.

Experiment 3

Method

The method was the same as in Experiment 2 with the following changes. There were three observers from earlier experiments (RB, DG, and HCH) and two new observers (MJB, a male, and UR, a female). Ages ranged from 26 to 58 years. All the observers except for observer RB were naïve to the aim of the experiment. Of the five observers, four were experienced and one (MJB) was an inexperienced psychophysical observer. Observer MJB had 4–6 prism diopters of exophoria for near, although he had no trouble maintaining binocular alignment of the rival stimuli. The gratings were red horizontal and green vertical. We tested only static-grating rivalry and flicker-and-swap rivalry using the same yes–no procedure of the previous experiments. The probe during the yes–no procedure was a superimposed red grating of the same phase, spatial frequency, size, and orientation as the red test grating. We refer to this as the yes–no task (Y/N). The probe during two-alternative forced-choice procedure was a superimposed red grating of the same phase, spatial frequency and orientation presented either to the top or to the bottom half of the red test grating for both sorts of rivalry aligned with a zero crossing to avoid sharp edges. In this procedure, observers pressed an upper or lower key to record their responses. We refer to this as the up-down task (U/D). The probe was presented with the same Gaussian temporal profile as used in Experiments 1 and 2.

Results and discussion

We show mean contrast increment thresholds in Figure 6. Thresholds were lower during static than during flicker-and-swap, $F(1,4) = 614.85$, $p < .0001$. This is consistent with what we found in Experiment 2: The flicker of the stimuli masked the probe.

Threshold were once again higher during suppression than during dominance, $F(1,4) = 92.49$, $p < .001$. Thresholds obtained with the U/D task were lower than with the Y/N task, $F(1,4) = 92.49$, $p < .01$. This is typical of forced-choice procedures (Macmillan & Creelman, 1991). Type of task did not, however, interact with any other factors.
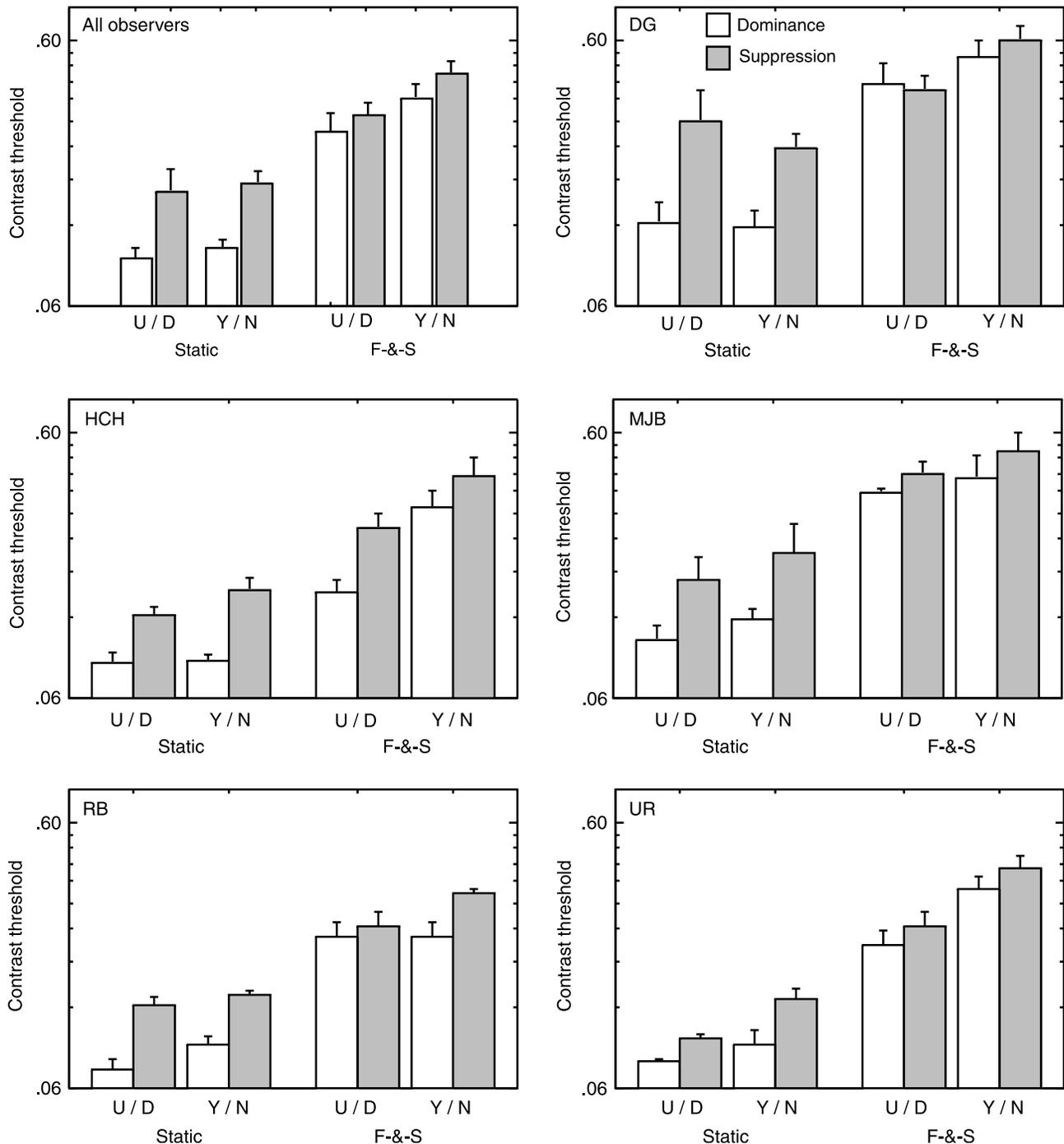

Figure 6. Showing the mean threshold for all observers in the top leftmost plot and individual observer plots for Experiment 3. Static indicates static-grating, and F-&-S indicates flicker-and-swap condition. U/D (Up/Down) shows results for the forced-choice task; Y/N (Yes/No) shows results for the task used in the previous experiments. Error bars show 1 standard error of the mean.
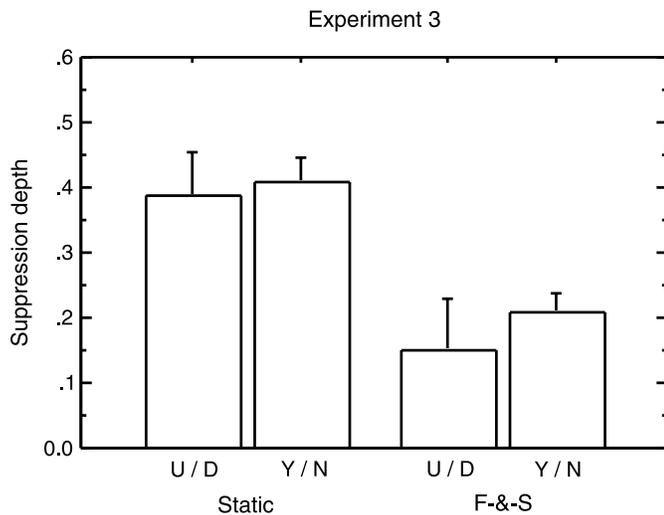
Figure 7. Showing the suppression depths for each condition tested in Experiment 3. Static indicates static-grating, and F-&-S indicates flicker-and-swap condition. U/D (Up/Down) shows results for the forced-choice task; Y/N (Yes/No) shows results for the task used in the previous experiments. Error bars show 1 standard error of the mean.

Critically, as in the previous two experiments, there was a significant interaction between condition and state, $F(1,4) = 7.31$, $p = .05$, because thresholds were higher during suppression than during dominance, and this difference was bigger with conventional rivalry stimuli than with swap rivalry.

We show suppression depths in Figure 7. The only significant effect was condition, $F(1,4) = 7.93$, $p < .05$, arising from deeper suppression during conventional rivalry than during swap rivalry. In the Y/N task (the same as used in Experiments 1 and 2) suppression depth was significantly greater than zero for conventional rivalry and also, for the first time, for swap rivalry, $t(4) = 11.97$ and 7.26 $ps < .01$. In the U/D task, suppression depth was significantly greater than zero for conventional rivalry, $t(4) = 5.93$, $p < .01$, but not for swap rivalry, $t(4) = 1.92$ $p > .05$.

There are two implications of results of this experiment. First, we cannot attribute the weak suppression we have consistently found for swap rivalry to our choice of response task. We found the same weak suppression with a forced-choice task. Second, the weak suppression we have measured for swap rivalry really is weak. We might have been tempted to conclude from the statistical results of Experiments 1 and 2 that there was no suppression in swap rivalry at all. But in this experiment, we found a significant, albeit weak depth of suppression for swap rivalry with the same task as used in the previous experiments.

General discussion

By measuring suppression depth in conventional rivalry and in swap rivalry, we have found evidence that we will

argue is consistent with suppression acting at least two different sites for the two sorts of rivalry, an early site for conventional rivalry, involving eye rivalry, and a later site for swap rivalry involving image rivalry.

Before we do that, we address the possibility that a single low-level mechanism is responsible for both eye and image rivalry. Lee and Blake (2004) proposed this for image rivalry in which a patchwork of two images in presented to one eye, and the opposite patchwork is presented to the other (Kovács et al., 1996). Lee and Blake (2004) asked their observers to report dominance of a particular region of the display by a key press. The key press swapped the region between the two eyes on half of the trials. On these trials, they found that observers reported seeing the previously suppressed stimulus. They concluded that dominance during rivalry is a combination of zones of dominance within or between eyes that gives rise to either conventional rivalry or to image rivalry. But the swap rivalry we have studied must be different from these patchwork displays because visibility of one image endures over many swaps of the images between the eyes.

Polonsky, Blake, Braun, and Heeger (2000) have argued that neuronal mechanisms of V1 are responsible for conventional binocular rivalry. They induced rivalry between high-contrast and low-contrast gratings, finding increased fMRI activity in V1 when the high-contrast grating was dominant and decreased fMRI activity when the low-contrast grating was dominant. Tong and Engel (2001) made a similar argument while measuring fMRI activity evoked by rivalry between grating stimuli presented to the blind spot of the contralateral eye and to the corresponding region of space of the ipsilateral eye. Haynes, Deichmann, and Rees (2005) and Wunderlich, Schneider, and Kastner (2005) confirmed the involvement of V1, but also found fMRI activity in the lateral geniculate nucleus (LGN) correlated with observers' percepts during binocular rivalry. But none of these studies rules out a higher-level mechanism also operating. In fact, both Haynes et al. and Wunderlich et al. proposed that the modulation of LGN activity by rivalry arises from feedback from some higher mechanism. A similar argument could be made for the other studies.

A single early site for binocular rivalry was challenged by a series of microelectrode studies of monkeys by Logothetis and colleagues. They found that in V1, where monocular neurons might be found, there are very few cells whose activity is directly correlated with the animal's perceptual experience (Leopold & Logothetis, 1996); most cells' activity is indifferent. Yet at higher cortical regions, they found increasing numbers of cells whose activity is correlated with perceptual experience (Logothetis, 1998; Logothetis & Schall, 1989; Sheinberg & Logothetis, 1997). Also when Tong, Nakayama, Vaughan, and Kanwisher (1998) showed observers images of a face and a house as rival stimuli they found increased fMRI activity in the appropriate high levels of the visual system

correlated with dominance: the fusiform face area and the parahippocampal place area respectively.

This raises the possibility that there is a single mechanism, but that it is higher in the visual system (Logothetis et al., 1996). But we can rule this out too. The crucial evidence that eye and image rivalry are processed at two different levels comes from Pearson, Tadin, and Blake (2007). They presented flickering stimuli that swapped between the eyes to elicit image rivalry, and similar stimuli that did not swap between the eyes to elicit eye rivalry. These stimuli were essentially similar to our swap and conventional rivalries. Pearson et al. found that transcranial magnetic stimulation over early visual areas shortened dominance durations during conventional rivalry but had very little effect on swap rivalry. They concluded that eye and image rivalry are mediated at different stages of visual processing.

If there are two (or more) sites for conventional and for swap rivalry, there are two possibilities for how rivalry suppression is mediated. Although our data cannot distinguish between these possibilities, they do place constraints on models of rivalry.

First, suppression for conventional rivalry could be mediated solely at the early, eye-rivalry site and suppression for swap rivalry could be mediated solely at the later, image-rivalry site. Wilson's (2003) model is an example of such a two-stage mechanism. He proposed early monocular competitive neurons that provide input to later binocular neurons. He also proposed weak excitatory feedback from the binocular to the monocular level. According to Wilson, during conventional rivalry, competition at the monocular stage generates rivalry alternations, the binocular stage simply inheriting the activity of its monocular inputs and requiring no further suppression. During swap rivalry, according to Wilson, the temporal transients bypass the competition at the first stage and the competition at the second stage produces rivalry alternations. If suppression is mediated at mutually exclusive sites for the two sorts of rivalry, then our results suggest that suppression at the earlier site must be stronger than at the later site.

Second, suppression for conventional rivalry could be mediated at both early and later sites and suppression for swap rivalry stimuli could be mediated at only the later site (Wolfe, 1996). If suppression accumulates as information passes from the early to later sites, then our results imply that the major component of suppression for conventional rivalry is at the early stage. Nguyen et al.'s (2001; Nguyen, Freeman, & Wenderoth, 2003) model, although not constructed with swap rivalry in mind, is an example of such a multi-stage model. They proposed that rivalry involves two or more sites of suppression. Mutual inhibition between the visual pathways of each eye occurs at an early stage of monocular and binocular neurons and at later stages of feature-selective neurons in higher cortex. Suppression starts at the early stages and is augmented at later stages. During conventional rivalry

probe sensitivity is mediated at the monocular neuronal stage and perception of the rival stimuli at the feature selective stage. Nguyen et al. proposed weak suppression at the monocular level and stronger suppression at the later stage, consistent with the small loss of sensitivity to probes (i.e., suppression depths of around 0.4) compared with the total perceptual loss of the suppressed field (implying suppression depths of 1.0). If we modify Nguyen et al.'s model so that the probe sensitivity is mediated partly at the monocular level and partly at the binocular level (similar to Wilson's, 2003, model), and if we assume that swapping the stimuli between the eyes bypasses inhibition at the monocular level, then the probe undergoes suppression only at the binocular stage consistent with the weak suppression depth we found for swap rivalry.

Nguyen et al.'s (2001, 2003) notion that suppression accumulates as information passes up the visual system can also account for different suppression depths from rival stimuli differing in complexity. Alais and Melcher (2007) found suppression depth of around 0.7 when the two rival stimuli were faces and around 0.4 when one was a face and the other a grating. Alais and Parker (2006) found similar results, when the rival stimuli were either faces or global motion or combination of face and global motion. They concluded that complex stimuli undergo suppression at monocular and binocular levels of V1 and also at specialized higher regions. For example, when the two rival stimuli are faces they also undergo suppression at the fusiform face area. When the two rival stimuli are a face and a grating, the grating confines suppression to V1, consistent with shallow suppression.

Alternations in visual consciousness occur with other multistable phenomena such as monocular rivalry (Breese, 1899) and motion-induced blindness (Bonneh et al., 2001). O'Shea, Alais, and Parker (2005, 2006) have recently measured the depth of suppression in monocular rivalry. They found it to be weak, around 0.1, similar to the level we have found for swap rivalry. This raises the intriguing possibility that monocular rivalry is a form of image rivalry like swap rivalry. The two sorts of rivalry also share some suggestive similarities: First, monocular rivalry and flicker-and-swap rivalry do not require that eye-of-origin information be retained (unlike conventional binocular rivalry). Second, flicker-and-swap rivalry is promoted by interspersing monocular rivalry stimuli between the swapping stimuli (Kang & Blake, 2006). Third, flicker-and-swap rivalry is enhanced at low contrast (Lee & Blake, 1999) and so is monocular rivalry (O'Shea & Wishart, 2007).

The reason flicker-and-swap rivalry is enhanced at low contrast may be because high-level neurons are contrast invariant. That is, their contrast–response functions are much steeper initially with a longer saturated plateau than that of lower-level neurons. Sclar, Maunsell, and Lennie (1990) compared contrast–response functions from macaque lateral geniculate, primary visual cortex, and middle

temporal visual area (MT) and found they progressively steepened. A magnetic resonance imaging study (Avidan et al., 2002) showed steeper contrast–response functions in the human brain along the ventral visual pathway from V1 through V2, V4/V8, and LO. Because of this tendency towards early saturating contrast response curves, there is no reason to expect that a high-level flicker-and-swap rivalry process should behave more vigorously at high contrast. Indeed, it would be mainly at low contrast, before reliable responses are elicited, that a high-level process would be least stable.

Caetta et al. (2007) measured the dominance and suppression threshold during motion-induced blindness. They found a suppression depth of 0.5 (personal communication), much stronger than we have found for flicker-and-swap rivalry. Although this suggests differences between these two forms of image rivalry, we note that motion-induced blindness requires the stimuli to be in peripheral vision, whereas we have measured suppression depth for central vision. As far as we are aware, there have been no studies of suppression depth as a function of eccentricity for conventional rivalry.

Conclusions

We have shown that suppression depth is stronger during conventional rivalry and weaker during swap rivalry. This is consistent with suppression's being mediated at both early and later sites of the visual system for conventional rivalry and being mediated weakly, if at all, at the early site and mainly at the later site for swap rivalry.

Acknowledgments

References

Alais, D., & Melcher, D. (2007). Strength and coherence of binocular rivalry depends on shared stimulus complexity. *Vision Research, 47,* 269–279. [PubMed]

Alais, D., O'Shea, R. P., Mesana-Alais, C., & Wilson, I. G. (2000). On binocular alternation. *Perception, 29,* 1437–1445. [PubMed]

Alais, D., & Parker, A. (2006). Independent binocular rivalry processes for motion and form. *Neuron, 52,* 911–920. [PubMed] [Article]

Avidan, G., Harel, M., Hendler, T., Ben-Bashat, D., Zohary, E., & Malach, R. (2002). Contrast sensitivity in human visual areas and its relationship to object recognition. *Journal of Neurophysiology, 87,* 3102–3116. [PubMed] [Article]

Blake, R. (1989). A neural theory of binocular rivalry. *Psychological Review, 96,* 145–167. [PubMed]

Blake, R., & Fox, R. (1974). Binocular rivalry suppression: Insensitive to spatial frequency and orientation change. *Vision Research, 14,* 687–692. [PubMed]

Blake, R., & Logothetis, N. K. (2002). Visual competition. *Nature Reviews, Neuroscience, 3,* 13–21. [PubMed]

Blake, R., Westendorf, D. H., & Overton, R. (1980). What is suppressed during binocular rivalry? *Perception, 9,* 223–231. [PubMed]

Bonneh, Y. S., Cooperman, A., & Sagi, D. (2001). Motion-induced blindness in normal observers. *Nature, 411,* 798–801. [PubMed]

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision, 10,* 433–436. [PubMed]

Breese, B. B. (1899). On inhibition. *Psychological Monographs, 3,* 1–65.

Caetta, F., Gorea, A., & Bonneh, Y. (2007). Sensory and decisional factors in motion-induced blindness. *Journal of Vision, 7*(7):4, 1–12, http://journalofvision.org/7/7/4/, doi:10.1167/7.7.4. [PubMed] [Article]

Cass, J., & Alais, D. (2006). Evidence for two interacting temporal channels in human visual processing. *Vision Research, 46,* 2859–2868. [PubMed]

Fox, R., & Check, R. (1966). Forced-choice form recognition during binocular rivalry. *Psychonomic Science, 6,* 471–472.

Fox, R., & Check, R. (1968). Detection of motion during binocular rivalry suppression. *Journal of Experimental Psychology, 78,* 388–395. [PubMed]

Fox, R., & Check, R. (1972). Independence between binocular rivalry suppression duration and magnitude of suppression. *Journal of Experimental Psychology, 93,* 283–289. [PubMed]

Haynes, J. D., Deichmann, R., & Rees, G. (2005). Eye-specific effects of binocular rivalry in the human lateral geniculate nucleus. *Nature, 438,* 496–499. [PubMed] [Article]

Kang, M.-S., & Blake, R. (2006). How to enhance the incidence of stimulus rivalry [Abstract]. *Journal of*

Vision, 6(6):46, 46a, http://journalofvision.org/6/6/46/, doi:10.1167/6.6.46.

Kovács, I., Papathomas, T. V., Yang, M., & Fehér, A. (1996). When the brain changes its mind: Interocular grouping during binocular rivalry. *Proceedings of the National Academy of Sciences of the United States of America, 93,* 15508–15511. [PubMed] [Article]

Lee, S. H., & Blake, R. (1999). Rival ideas about binocular rivalry. *Vision Research, 39,* 1447–1454. [PubMed]

Lee, S. H., & Blake, R. (2004). A fresh look at interocular grouping during binocular rivalry. *Vision Research, 44,* 983–991. [PubMed]

Lehky, S. R. (1988). An astable multivibrator model of binocular rivalry. *Perception, 17,* 215–228. [PubMed]

Leopold, D. A., & Logothetis, N. K. (1996). Activity changes in early visual cortex reflect monkeys' percepts during binocular rivalry. *Nature, 379,* 549–553. [PubMed]

Logothetis, N. K. (1998). Single units and conscious vision. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 353,* 1801–1818. [PubMed] [Article]

Logothetis, N. K., Leopold, D. A., & Sheinberg, D. L. (1996). What is rivalling during binocular rivalry? *Nature, 380,* 621–624. [PubMed]

Logothetis, N. K., & Schall, J. D. (1989). Neuronal correlates of subjective visual perception. *Science, 245,* 761–763. [PubMed]

Macmillan, N. A., & Creelman, C. D. (1991). *Detection theory: A user's guide*. New York: Cambridge University Press.

Nguyen, V. A., Freeman, A. W., & Alais, D. (2003). Increasing depth of binocular rivalry suppression along two visual pathways. *Vision Research, 43,* 2003–2008. [PubMed]

Nguyen, V. A., Freeman, A. W., & Wenderoth, P. (2001). The depth and selectivity of suppression in binocular rivalry. *Perception & Psychophysics, 63,* 348–360. [PubMed] [Article]

Ooi, T. L., & He, Z. J. (1999). Binocular rivalry and visual awareness: The role of attention. *Perception, 28,* 551–574. [PubMed]

Ooi, T. L., & Loop, M. S. (1994). Visual suppression and its effect upon color and luminance sensitivity. *Vision Research, 34,* 2997–3003. [PubMed]

O'Shea, R. P., Alais, D., & Parker, A. (2005). The depth of monocular-rivalry suppression. *Australian Journal of Psychology, 57,* 66.

O'Shea, R. P., Alais, D., & Parker, A. (2006). The depth of suppression during monocular rivalry and binocular rivalry. *Perception, 35,* 9.

O'Shea, R. P., & Crassini, B. (1981). The sensitivity of binocular rivalry suppression to changes in orientation assessed by reaction-time and forced-choice techniques. *Perception, 10,* 283–293. [PubMed]

O'Shea, R. P., & Wishart, B. (2007). Contrast enhances binocular rivalry and retards monocular rivalry. *Australian Journal of Psychology, 59,* 51–52.

Pearson, J., Tadin, D., & Blake, R. (2007). The effects of transcranial magnetic stimulation on visual rivalry. *Journal of Vision, 7*(7):2, 1–11, http://journalofvision.org/7/7/2/, doi:10.1167/7.7.2. [PubMed] [Article]

Pelli, D. G. (1997). The ViedoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10,* 437–442. [PubMed]

Polonsky, A., Blake, R., Braun, J., & Heeger, D. J. (2000). Neuronal activity in human primary visual cortex correlates with perception during binocular rivalry. *Nature Neuroscience, 3,* 1153–1159. [PubMed]

Sclar, G., Maunsell, J. H., & Lennie, P. (1990). Coding of image contrast in central visual pathways of the macaque monkey. *Vision Research, 30,* 1–10. [PubMed]

Sheinberg, D. L., & Logothetis, N. K. (1997). The role of temporal cortical areas in perceptual organization. *Proceedings of the National Academy of Sciences of the United States of America, 94,* 3408–3413. [PubMed] [Article]

Shimojo, S., & Nakayama, K. (1990). Real world occlusion constraints and binocular rivalry. *Vision Research, 30,* 69–80. [PubMed]

Smith, E. L., Levi, D. M., Harwerth, R. S., & White, J. M. (1982). Color vision is altered during the suppression phase of binocular rivalry. *Science, 218,* 802–804. [PubMed]

Tong, F., & Engel, S. A. (2001). Interocular rivalry revealed in the human cortical blind-spot representation. *Nature, 411,* 195–199. [PubMed]

Tong, F., Nakayama, K., Vaughan, J. T., & Kanwisher, N. (1998). Binocular rivalry and visual awareness in human extrastriate cortex. *Neuron, 21,* 753–759. [PubMed] [Article]

Wales, R., & Fox, R. (1970). Increment detection thresholds during binocular rivalry suppression. *Perception & Psychophysics, 8,* 90–94.

Watson, A. B., & Pelli, D. G. (1983). QUEST: A Bayesian adaptive psychometric method. *Perception & Psychophysics, 33,* 113–120. [PubMed]

Wilson, H. R. (2003). Computational evidence for a rivalry hierarchy in vision. *Proceedings of the National Academy of Sciences of the United States of America, 100,* 14499–14503. [PubMed] [Article]

Wolfe, J. M. (1986). Stereopsis and binocular rivalry. *Psychological Review, 93,* 269–282. [PubMed]

Wolfe, J. M. (1996). Resolving perceptual ambiguity. *Nature, 380,* 587–588. [PubMed]

Wunderlich, K., Schneider, K. A., & Kastner, S. (2005). Neural correlates of binocular rivalry in the human lateral geniculate nucleus. *Nature Neuroscience, 8,* 1595–1602. [PubMed] [Article]