Staying focused: A functional account of perceptual suppression during binocular rivalry

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Presenting different images to either eye can induce perceptual switching, with alternating disappearances of each image—a phenomenon called binocular rivalry. We believe that disappearances during binocular rivalry can be driven by a process that facilitates visibility near the point of fixation. As the point of fixation is tied *neither* to a particular stimulus *nor* to a specific eye, indifference to both would be an essential characteristic for the process we envisage. Many factors that influence disappearances during binocular rivalry scale with distance in depth from fixation. Of these, here we use blur. We break the links between this cue and *both* eye of origin and stimulus type. We find that perceptual dominance can track a better focused image as it is swapped between the eyes and that perceptual switches can be driven by alternating the focus of images fixed in each eye. This implies that, as a determinant of suppression selectivity, blur is functionally independent from both eye of origin and stimulus type. Our data and theoretical account suggest that binocular rivalry is not an irrelevant laboratory curiosity but, rather, that it is a product of a functional adaptation that promotes visibility in cluttered environments.

Introduction

When different images project to corresponding regions on the retinas of the two eyes, each image can intermittently disappear such that only one of the two is perceived at a time—a phenomenon known as binocular rivalry (Helmholtz, 1962; Levelt, 1968). It may be tempting to dismiss binocular rivalry as being curious but irrelevant in the context of our daily lives. How often, after all, do we usually encounter completely different images at corresponding points in the two eyes?

The answer is frequently (see Shimojo & Nakayama, 1990, 1994), but this does not normally induce binocular rivalry. For instance, at times, humans try to maximize the probability of seeing without being seen. We do so by exposing the minimal bodily extent (one eye) necessary to see—we peek around corners. When both eyes are open, this creates a situation wherein one eye is selectively occluded and, as a consequence, completely different images project to either eye. However, as interested readers can readily demonstrate for themselves (by placing a fingertip a few centimeters in front of one eye while fixating this text), peeking does not typically induce binocular rivalry. Instead, perception tends to be persistently dominated by that which is closest in depth to the point of fixation (hence, one can still read this text). We are usually only faintly aware of the retinal image projecting from the more proximate object or surface that we are peeking around.

In virtually all viewing conditions, the eyes accommodate at the point of fixation, rendering images of objects and surfaces displaced in depth from fixation relatively blurred. Given the almost complete perceptual suppression of more proximate objects and surfaces when peeking, it is perhaps unsurprising that blur magnitude is negatively correlated with the probability of perceptual dominance during binocular rivalry (Fahle, 1982, 1983; Levelt, 1968) and in possibly related clinical situations (Schor, Landsman, & Erickson, 1987; Shors, Wright, & Greene, 1992).

Because of the manner in which binocular rivalry experiments are usually conducted, with each of the conflicting images presented selectively to either eye, it is unclear if blur biases perception in favor of a particular stimulus (Dorrenhaus, 1975; Logothetis, Leopold, & Sheinberg, 1996) or in favor of information from a specific eye (Blake, Westendorf, & Overton, 1980; Polonsky, Blake, Braun, & Heeger, 2000; Tong & Engel, 2001). We believe that there is a third possibility—that, as a selection criterion, blur can be independent of both eye of origin and stimulus type. Our thoughts are as

follows: The perceptual suppression of the more blurred of two conflicting images (Fahle, 1982, 1983; Levelt, 1968), as experienced while peeking, is consistent with the existence of an evolutionary adaptation that facilitates visibility near the point of fixation. The point of fixation has two interesting characteristics—it is a property that is tied neither to a particular stimulus nor to a specific eye.

Take, for example, the situation where one gazes at a distant object through the leaves of a tree. Because of movement (of either the head or the leaves), the status of the distant object will often fluctuate between being unobscured, thus projecting to corresponding points in both eyes and being obscured from one eye or the other (for a related example, see Ono, Lillakas, Grove, & Suzuki, 2003). Thus, the fixation point can alternate rapidly between projecting to either eye. We can also change our point of fixation between different objects. To promote visibility near the point of fixation, over that of more proximate objects and surfaces, it would therefore be important to discount information concerning both eye of origin and stimulus type and rely instead on a more consistent cue—relative image blur.

The dominant views concerning binocular rivalry suggest that suppression is related to selections of a particular stimulus (Dorrenhaus, 1975; Logothetis et al., 1996) or to information from a specific eye (Blake et al., 1980; Polonsky et al., 2000; Tong & Engel, 2001). The third possibility—that suppression might be independently related to distance in depth from fixation—is a novel suggestion that has not yet been assessed. We address this possibility using manipulations of image blur, to cue relative distance in depth from fixation, in combination with several image-swapping procedures. These swapping procedures allow us to break the links between (a) relative image blur and eye of origin and (b) relative image blur and stimulus type. By breaking these links, we can establish if image blur can determine suppression selectivity during binocular rivalry independent of information concerning both eye of origin and stimulus type.

Methods

Six observers, of whom three were naïve as to the purpose of the study and the other three being the authors, participated in each of the experiments reported. All observers had normal or corrected-to-normal visual acuity and color vision.

Visual stimuli were generated using Matlab software to drive a ViSaGe stimulus generator (Cambridge Research Systems) and were displayed on a gamma-corrected 21-in. Samsung SyncMaster 1100 p+ monitor (1,024 × 768 resolution; 120 Hz refresh rate). All stimuli were viewed, from a distance of ~78 cm, through an individually

adjusted mirror stereoscope. White fixation points (diameter, ~0.1°) at the center of each image were used to aid convergence in addition to four circular white fusion locks (diameter, ~0.2°) positioned above, below, and to either side (~2.2° of visual angle) of the images presented to either eye.

Images

Four images were derived from grayscale images of a girl and a house. All images subtended ~2.2° of visual angle at the retina. Contrast was linearly reduced from a peak in the middle of the images such that, by a radius of 1.1° of visual angle, the image was reduced to a uniform gray (CIE 1931; $X = 0.28$, $Y = 0.29$, $Z = 66.37$), which was also the color of the display background. This was done to minimize high spatial frequency content at the edges of otherwise blurred images. Image blur was created using a Gaussian function with a space constant subtending 0.2° of visual angle at the retina.

The conflicting images were differently colored to aid identification. *House* images were modulated along an axis from magenta (CIE 1931; $X = 0.43$, $Y = 0.23$, $Z = 23.23$) to cyan (CIE 1931; $X = 0.23$, $Y = 0.31$, $Z = 109.51$). *Girl* images were modulated along an axis from violet (CIE 1931; $X = 0.20$, $Y = 0.11$, $Z = 23.23$) to greenish yellow (CIE 1931; $X = 0.35$, $Y = 0.46$, $Z = 109.51$).

The mean luminance of all images was 66.37 cd/m^2. The RMS contrast of all images was 0.06, expressed in terms of the image modulation axis where the extremes of the axes were considered to have values of ±1 and the midpoint (gray) a value of 0. Normalization of RMS contrasts was ensured by first calculating initial RMS values for each image, based on analysis of each image pixel. We then used the lowest contrast image to calculate appropriate multiples by which to reduce residuals (between pixel luminance values and gray) in the other three images. We then recalculated RMS contrasts for the final four images, which were used in the subsequent experiment, to ensure that they had been properly equated.

It should be noted that blur typically reduces both overall luminance contrast and high spatial frequency content (Fahle, 1982, 1983). However, as RMS contrast was held constant across all images, our results here must primarily be attributed to selective reductions in high spatial frequency content (also see Auxiliary data).

Procedure: Experiment 1

In the first experiment, three types of image pairs were presented: both focused (see Figures 1D and 1E), both blurred (Figures 1F and 1G), and different pairs wherein one of the two images was focused and the other one was blurred (Figures 1H and 1I).
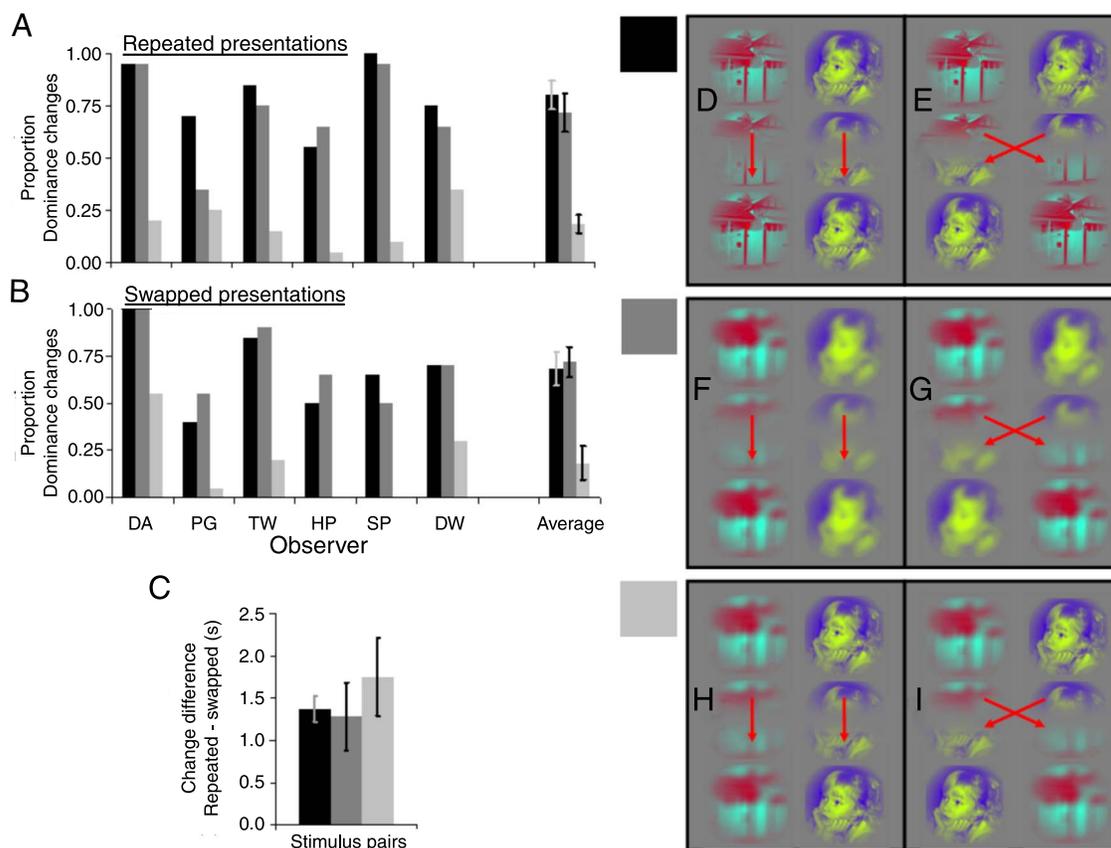
Figure 1. Results and stimuli used in Experiment 1. (A) Proportions of perceptual dominance changes following disruptions after which images were repeated in the same eyes. Data are shown for each observer and for each type of image pair. Average proportions are also shown with the associated standard error between the individual proportions. (B) Proportions of perceptual dominance changes following presentation disruptions during which the conflicting images were swapped between the eyes. (C) Difference between perceptual dominance change latencies following repeated and swapped stimulus presentations, averaged across those trials where perceptual dominance changes were reported. Positive values indicate that dominance changes were faster when the conflicting images were swapped as opposed to being repeated. (D–I) Depictions of different stimulus trials (see main text for descriptions).

Each trial started with the presentation of an image pair, one to either eye. One of these two images was nominated as the target, for which the observer should wait for and then signal perceptual dominance (meaning that the other image had completely disappeared). The focused image was always the target for different pairs.

After perceptual dominance had been signaled, the contrast of the two images was linearly ramped off (to zero, mean gray) and on again over 100 ms—creating flicker in each eye. During this disruption the images were either swapped between the eyes (see Figures 1E, 1G, 1I) or they remained and were therefore repeatedly shown to the same eyes (see Figures 1D, 1F, 1H). The trial was terminated either when the observer indicated, via a second button press, that perceptual dominance had changed (such that the previously dominant image had completely disappeared) or after a further 5 s had passed.

Each observer completed two trial runs. During each trial run, the six experimental conditions (see Figure 1) were each presented 10 times in random order. Observer data were averaged across the two trial runs. As exclusive perceptual dominance of the nominated target image could take some time to emerge at the start of each trial, during this period we counterphased the contrast of either image at a rate of 1 Hz to avoid retinal adaptation effects. This created an impression of each image alternating with its photo negative. Contrast counterphasing ceased as soon as the observer reported that exclusive perceptual dominance of the target image had been achieved.

Procedure: Experiment 2

In Experiment 2, five types of stimulus presentation were used, including both blurred (see Figure 2A), both focused (Figure 2B), girl focused and house blurred (Figure 2C), house focused and girl blurred (Figure 2D), and focus swapped (Figure 2E). During Presentation Styles A–D, conflicting images were simply swapped between the eyes at a rate of 1 Hz. During Presentation Style E, the girl and house images were presented to the same eyes throughout the stimulus presentation. However,
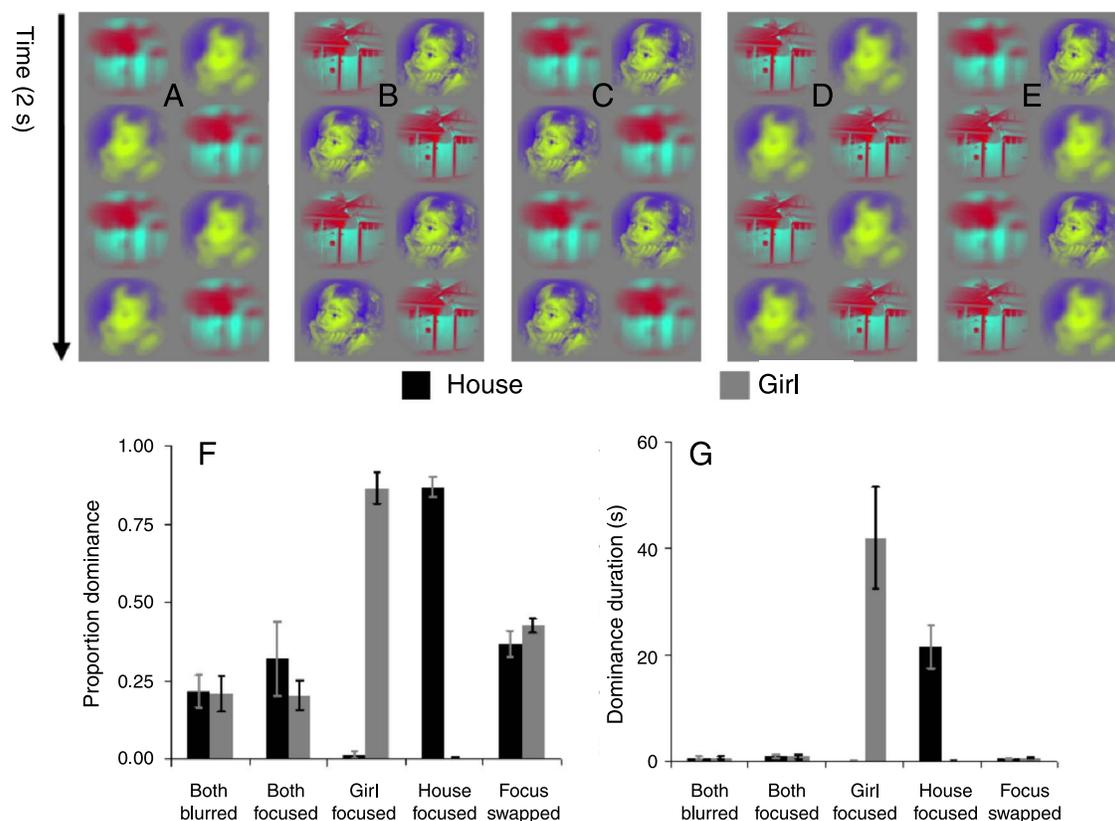
Figure 2. Results and stimuli used in Experiment 2. (A–E) Depictions of different stimulus presentation styles. See main text for descriptions. (F) Proportions of stimulus presentations during which exclusive perceptual dominance was reported. (G) Average durations for which exclusive perceptual dominance persisted during 1-min stimulus presentations. Error bars indicate ±1 *SE*.

the girl and house images alternated between being focused and blurred at a rate of 1 Hz—such that one of the two was always focused whereas the other was blurred.

During each stimulus presentation, observers tracked their percept by pressing one of three response buttons to indicate when they were (a) exclusively seeing the *girl,* (b) exclusively seeing the *house,* or (c) either unsure which image they were seeing or they were seeing patches of both.

Each observer completed two trial runs. During each trial run, the five experimental conditions were each presented for a period of 1 min in a random order. Observer data were averaged across these two trial runs.

The data reported relate to performances in each experimental condition averaged across observers.

Results

Experiment 1

Figures 1A and 1B show proportions of trials during which perceptual dominance changed following presentation

disruptions, for both *repeated* and *swapped* presentations, respectively. In both cases perceptual dominance changed less frequently for *different* pairs than it did for either pairs of *blurred* images [*repeated* $t(5) = 9.68$, $p < 0.001$; *swapped* $t(5) = 7.68$, $p = 0.001$] or *focused* images [*repeated* $t(5) = 11.175$, $p < 0.001$; *swapped* $t(5) = 4.63$, $p = 0.006$].

We observed stable perceptual dominance of the better focused image on most of the trials that involved different image pairs (see Figures 1A and 1B). When dominance changes did occur, we found that they happened faster following swapped relative to repeated stimulus presentations [blurred $t(5) = 8.96$, $p < 0.001$; focused $t(5) = 3.22$, $p = 0.024$; *different* $t(3) = 3.8$, $p = 0.032$; see Figure 1C], an observation that is consistent with previous findings (Blake et al., 1980). Note, however, that the reduced degrees of freedom in the latter case signify that two of our six observers never reported a perceptual dominance change when a dominant focused image was swapped with a suppressed blurred image (see Figure 1B).

Experiment 2

Figure 2F shows the proportions of stimulus presentations for which exclusive perceptual dominance, of either

the *girl* or *house,* persisted. Proportions during which observers were unsure of which image they were seeing or during which they reported seeing patches of both can be surmised by the difference between the summed girl and house proportions and 1. Each image (house/girl) exclusively dominated perception for equal proportions of the stimulus presentation when both images were blurred, $t(5) = 0.21$, $p = .845$, focused, $t(5) = 0.85$, $p = .434$, and when the focus of images fixed in each eye was swapped, $t(5) = 1.46$, $p = .204$. However, when the girl was focused and the house was blurred, $t(5) = 14.42$, $p < .001$, or when the girl was blurred and the house was focused, $t(5) = 24.70$, $p < .001$, the focused image exclusively dominated perception for a much greater proportion of the stimulus presentation.

Figure 2G shows the average durations for which exclusive perceptual dominance of either the girl or the house persisted during stimulus presentations. Dominance durations did not differ significantly from 500 ms—the physical duration for which an image (see Figures 2A–2D) or focal property (see Figure 2E) persisted in either eye when both images were blurred, girl: $t(5) = 0.69$, $p = .522$; house: $t(5) = 0.62$, $p = .560$), focused, girl: $t(5) = 1.08$, $p = .328$; house: $t(5) = 1.34$, $p = .238$, and when the focus of images fixed in each eye was swapped, girl: $t(5) = 2.36$, $p = .065$; house: $t(5) = 2.01$, $p = .101$. However, when the girl was focused and the house was blurred, and when the house was focused and the girl was blurred, the focused images exclusively dominated perception for significantly longer than 500 ms, girl focused: $t(5) = 4.37$, $p = .007$; house focused: $t(5) = 5.22$, $p = .003$, and blurred images dominated perception for significantly less than 500 ms, girl blurred: $t(5) = 6.32$, $p = .001$; house blurred: $t(5) = 6.61$, $p = .001$.

Discussion

Our data show that better focused images can dominate perception across a single disruption during which the two images are swapped between the eyes. Better focused images also dominated perception for prolonged periods as conflicting images were repeatedly swapped between the eyes at a rate of 1 Hz. Both findings demonstrate an independence of suppression selectivity from information concerning eye of origin. The latter finding is particularly striking as the average period for which better focused images exclusively dominated perception (~30 s) far exceeded the durations (0.5 s) for which they were shown to either eye.

We have also shown that perceptual switching can be driven by alternating the relative focus of images (girl/house) presented to the same eyes throughout a stimulus presentation. In these circumstances, perception tends to be exclusively dominated by whichever image is better focused—whether that image is of a girl or a house. This demonstrates an independence of suppression selectivity from information concerning image type (i.e., girl or house).

In combination, our results show that suppression selectivity during binocular rivalry can be determined by relative focus (Fahle, 1982, 1983; Levelt, 1968) independently from information concerning both eye of origin (Blake et al., 1980; Polonsky et al., 2000; Tong & Engel, 2001) and stimulus type (Logothetis et al., 1996; Dorrenhaus, 1975). We suggest that this observation is consistent with binocular suppression being driven by an evolutionary adaptation, prevalent in daily life, which facilitates visibility near the point of fixation.

Most binocular rivalry experiments have used conflicting images that are equally focused. This situation may be somewhat peculiar as real-world situations will tend to enforce characteristic patterns of blur difference between conflicting and unmatched retinal images—the images of objects and surfaces closer in depth to the point of fixation will be less blurred. We suggest that the fluctuations of perceptual dominance that are characteristic of binocular rivalry experiments track the brain's attempts to determine which of the two conflicting images is closest to the point of fixation. These fluctuations are likely to be driven by small changes in the adaptive states of competitive neural populations (Blake, Westendorf, & Fox, 1990; Lehky, 1988; Wilson, Blake, & Lee, 2001) that are sufficient to bias the determination of relative depth. It is also probable that these interactions are influenced by multiple distributed processes occurring at different levels of the visual hierarchy (Blake & Logothetis, 2002; Lee & Blake, 1999; Tong, 2001; Watson, Pearson, & Clifford, 2004). We anticipate that existing models of binocular rivalry would require only minor changes to account for our data.

Blur-related reductions in high spatial frequency content are obviously central to our functional account of binocular suppression. However, this is not the only stimulus feature implicated by the real-world situations we invoke. When the point of fixation is selectively occluded from either eye, the retinal image of the more proximate obstructing surface will be relatively blurred. Blurring an image also tends to reduce luminance and chromatic contrasts (Fahle, 1982, 1983). In the absence of differential blur, these properties could be used to determine which, of a pair of conflicting images, is probably closest in depth to the point of fixation—thus explaining their influence on suppression selectivity (Kovacs, Papathomas, Yang, & Feher, 1996; Levelt, 1968; Mueller & Blake, 1989; Pearson & Clifford, 2004). However, we hasten to point out that blur-related reductions in high spatial frequency content can be a strong and independent determinant of perceptual dominance during binocular rivalry (Fahle, 1982, 1983; Levelt, 1968; see Auxiliary data for further evidence).

Our thesis is similar to the concept of *signal strength,* which is a multidimensional construct with contributions

from several stimulus properties, including image blur (Levelt, 1968). However, we believe that the *signal* is directly related to a familiar stimulus property that is important in our daily lives—distance in depth from the point of fixation. The novelty of our data is that it shows that suppression selectivity during binocular rivalry can be independent of *both* information concerning eye of origin and stimulus type. This implies that blur does not bias perceptual dominance in favor of either of these factors but, rather, that it contributes to the strength of an independent signal relating to distance in depth from fixation.

Readers familiar with binocular rivalry research may have noticed marked differences between some of the presentation protocols used here and those previously used to encourage perceptual dominance of an image as it is swapped between the eyes. Using equally focused images, it seems that this effect can only be obtained if the conflicting images are also flickered (∼18 Hz) while being swapped between the eyes (Lee & Blake, 1999; Logothetis et al., 1996). Evidently, this is not true when one of the conflicting images is better focused. In these circumstances, simply swapping the conflicting images between the eyes at a rate of 1 Hz can be sufficient. This robust indifference to information concerning eye of origin would be essential to facilitate persistent visibility near the point of fixation, which can alternate rapidly between projecting to either eye.

Of the two dominant accounts of binocular rivalry, our thesis has more in common with the view that suppression is related to selections of a particular stimulus (Dorrenhaus, 1975; Logothetis et al., 1996) rather than to information from a specific eye (Blake et al., 1980; Polonsky et al., 2000; Tong & Engel, 2001). However, our thesis differs from the former account as we believe that perceptual dominance is biased in favor of a stimulus property, relative focus, as opposed to an abstract interpretation or scene representation (Logothetis et al., 1996). Although the point of focus is often conceived of as being a low-level stimulus property, it can alternate rapidly between projecting to either eye; hence, indifference to eye of origin would be essential to promote its persistent visibility. Our data and proposal may therefore help to elucidate *why* perceptual dominance can track an image as it is swapped between the eyes, once the link between image type and eye of origin has been broken (Dorrenhaus, 1975; Logothetis et al., 1996).

Our data support the conclusion that suppression selectivity during rivalry is functionally independent from information concerning eye of origin. However, this does not dictate that the competition (to determine relative proximity to fixation) is necessarily mediated at higher levels of the visual hierarchy. Rather, it is entirely probable that the competition is mediated by activity at early monocular processing stages (Blake, O'Shea, & Mueller, 1992; O'Shea & Corballis, 2003; Polonsky et al., 2000; Tong & Engel, 2001). Alternatively, monocular

processing could be influenced by higher level processes via feedback (Haynes, Deichmann, & Rees, 2005; Watson et al., 2004). Our data speak to the function and selectivity of suppression during binocular rivalry, not to the neural locus.

Conspicuously absent in our account has been any mention of a number of other phenomena in which perception can flip between alternate states without changing retinal input (for recent reviews, see Blake & Logothetis, 2002; Kim & Blake, 2005; Long & Toppino, 2004). These other phenomena, which will not be described here, have been theoretically linked to binocular rivalry primarily because the durations between perceptual alternations can be strikingly similar (Andrews & Purves, 1997; Carter & Pettigrew, 2003; Miller et al., 2000). We believe that our functional account of binocular rivalry may play some role in situations that are related to ambiguity concerning relative depth (Andrews & Purves, 1997; Bonneh, Cooperman, & Sagi, 2001; Necker, 1832; Wallach & O'Connell, 1953). We would attribute to tangential factors any similarity between binocular rivalry and perceptual phenomena that are unrelated to depth. For instance, different phenomena are likely to be influenced by fluctuations in the adaptive states of diverse neural populations, and the timings of such fluctuations might be similar.

Conclusions

The extent of research concerning binocular suppression, spanning at least the past 160 years, is daunting. We would not pretend that our observations here provide a comprehensive account of the great number of documented perturbations of the phenomenon. We believe, however, that we have shown that perceptual suppression during binocular rivalry can be driven by a functional adaptation relevant to real-world situations. This proposal complements other attempts to identify the functional characteristics of suppression during binocular rivalry (Fahle, 1982, 1983; Forte, Peirce, & Lennie, 2002; Leopold, Maier, Wilke, & Logothetis, 2005; Shimojo & Nakayama, 1990, 1994). We would hope that closer attention to these characteristics, and most especially to the processes influenced by image blur, will guide future attempts to identify and understand the neural correlates of visual awareness.

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