



Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Monocular rivalry exhibits three hallmarks of binocular rivalry: Evidence for common processes

Robert P. O'Shea^{a,*}, Amanda Parker^b, David La Rooy^a, David Alais^b

^a Department of Psychology, University of Otago, P.O. Box 56, Dunedin, New Zealand

^b School of Psychology, The University of Sydney, Australia

ARTICLE INFO

Article history:

Received 20 April 2008

Received in revised form 29 December 2008

Keywords:

Monocular rivalry

Binocular rivalry

Colour

Perceptual ambiguity

Vision

Visual suppression

Depth of suppression

ABSTRACT

Binocular rivalry occurs when different images are presented one to each eye: the images are visible only alternately. Monocular rivalry occurs when different images are presented both to the same eye: the clarity of the images fluctuates alternately. Could both sorts of rivalry reflect the operation of a general visual mechanism for dealing with perceptual ambiguity? We report four experiments showing similarities between the two phenomena. First, we show that monocular rivalry can occur with complex images, as with binocular rivalry, and that the two phenomena are affected similarly by the size (Experiment 1) and colour (Experiment 2) of the images. Second, we show that the distribution of dominance periods during monocular rivalry has a gamma shape and is stochastic (Experiment 3). Third, we show that during periods of monocular-rivalry suppression, the threshold to detect a probe (a contrast pulse to the suppressed stimulus) is raised compared with during periods of dominance (Experiment 4). The threshold elevation is much weaker than during binocular rivalry, consistent with monocular rivalry's weak appearance. We discuss other similarities between monocular and binocular rivalry, and also some differences, concluding that part of the processing underlying both phenomena is a general visual mechanism for dealing with perceptual ambiguity.

© 2009 Elsevier Ltd. All rights reserved.

1. Introduction

We experience the visual world in astounding richness and detail, yet our knowledge of how our conscious percepts arise is still quite poor (cf. Chalmers, 1995). One way to learn more about these processes is to study phenomena in which visual consciousness changes without any change in the stimuli being viewed (Crick & Koch, 1995). Such phenomena are known as perceptually multistable and include binocular rivalry (Porta, 1593, cited in Wade, 1996), reversals of the Necker cube (Necker, 1832), of the Rubin face-vase figure (Rubin, 1915), and of the kinetic depth effect (Wallach & O'Connell, 1953), and motion-induced blindness (Bonneh, Cooperman, & Sagi, 2001). Binocular rivalry is a particularly fascinating example, in which visual consciousness fluctuates randomly between two different images presented one to each eye. It has been studied extensively (for reviews see Alais & Blake, 2005; Blake & O'Shea, 2009) and has gone some way to shedding light on how visual awareness arises: conscious visual experience in binocular rivalry is thought to arise from activation, and suppression, of neurons at a succession of stages in the visual system via feed-forward and feedback connections (e.g., Blake & Logothetis, 2002).

Our interest in this paper is in the relationship between binocular rivalry and another phenomenon of perceptual multistability, monocular rivalry. Monocular rivalry was discovered by Breese (1899) in the course of his foundational observations and experiments on binocular rivalry. He found that binocular rivalry-like behaviour also occurred when a red and a green grating were optically superimposed by a prism and presented to a single eye. Breese called it monocular rivalry to distinguish it from binocular rivalry. He reported that monocular rivalry alternations tended to occur at a slower rate than binocular rivalry alternations and that the perceptual alternations were less vivid: "Neither [stimulus] disappeared completely: but at times the red would appear very distinctly while the green would fade; then the red would fade and the green appear distinctly" (p. 43).

One of the unresolved questions in the literature on perceptual multistability is whether common neural mechanisms underlie binocular and monocular rivalry. Rubin (2003), Leopold and Logothetis (1999), and Maier, Logothetis, and Leopold (2005) have proposed that all examples of perceptual multistability represent operations of a single, high-level mechanism. If so, this would tie together diverse multistability phenomena including perception of ambiguous auditory stimuli (e.g., Einhäuser, Stout, Koch, & Carter, 2008), perception of traditional visual ambiguous figures such as the Necker cube (e.g., Meng & Tong, 2004), perception of illusory

* Corresponding author.

E-mail address: r_oshea@otago.ac.nz (R.P. O'Shea).

organisation such as Marroquin patterns (Wilson, Krupa, & Wilkinson, 2000), monocular rivalry, and binocular rivalry.

There are at least three general similarities between monocular rivalry and binocular rivalry that suggest commonality. The basic phenomenology is similar in that both involve periods of alternating dominance. Both forms of rivalry become more vigorous as stimuli are made more different in colour (e.g., Wade, 1975), or in orientation and spatial frequency (e.g., Atkinson, Fiorentini, Campbell, & Maffei, 1973; Campbell, Gilinsky, Howell, Riggs, & Atkinson, 1973; O'Shea, 1998). The two forms of rivalry can influence each other, tending to synchronise their alternations in adjacent regions of the visual field (Andrews & Purves, 1997; Pearson & Clifford, 2005).

Although monocular and binocular rivalry are similar in these three respects, this is by no means an exhaustive list of possible comparisons. Here we test whether monocular rivalry shares three other hallmarks of binocular rivalry. First, binocular rivalry can occur between any two images, providing they are sufficiently different. For example, Porta (1593, cited in Wade, 1996) observed rivalry between two different pages of text. Wheatstone (1838) observed rivalry between two different alphabetic letters. Galton (1907) observed rivalry between pictures of different faces. Yet monocular rivalry has always been shown between simple repetitive stimuli such as gratings, leading some to suppose that such stimuli are necessary for monocular rivalry (e.g., Furchner & Ginsburg, 1978; Georgeson, 1984; Georgeson & Phillips, 1980; Maier et al., 2005). In Experiments 1 and 2, we show that monocular rivalry occurs between complex pictures of faces and houses. We demonstrate this in Fig. 1.

Second, binocular rivalry has a characteristic distribution of dominance times, a gamma distribution, and the duration of one episode of dominance cannot be predicted by any of the preceding



Fig. 1. Illustration of one of the monocular-rivalry stimuli from Experiment 2: a red face and a green house. To experience monocular rivalry stare approximately at the centre of the image, say at the bridge of the face's glasses. Be patient! Monocular rivalry takes a while to develop. But after a time, 10–30 s or so, you will notice fluctuations in the relative clarity of the two images. You may even see one of the two images become exclusively visible briefly, along with brief composites in which different parts of the images appear in different parts of the visual field. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ones (e.g., Fox & Herrmann, 1967; Levelt, 1967). Yet the distribution and predictability of episodes of monocular rivalry dominance are unknown. In Experiment 3, we show that the temporal periods of monocular rivalry are similar to those of binocular rivalry: gamma distributed and stochastic.

Third, binocular rivalry suppression is accompanied by a characteristic loss of visual sensitivity. When a stimulus is suppressed during binocular rivalry and becomes invisible, stimuli presented to the same retinal region are also invisible, provided the new stimuli are not so abrupt or so bright as to break suppression (e.g., Fox & McIntyre, 1967; Nguyen, Freeman, & Alais, 2003; Norman, Norman, & Bilotta, 2000; Wales & Fox, 1970). This is usually demonstrated by showing a loss of sensitivity during periods of suppression relative to periods of dominance, however it is unknown whether monocular rivalry also shows such suppression effects. In Experiment 4, we show that monocular rivalry does indeed produce threshold elevations during suppression, although the effect is weaker than in binocular rivalry.

The experiments in this paper have been published individually in abstract form (O'Shea, Alais, & Parker, 2005, 2006; O'Shea and LaRooy, 2004). Here we draw these experiments together and give their details to provide evidence for similarities between monocular rivalry and binocular rivalry.

2. Experiment 1

Maier et al. (2005) reviewed studies of monocular rivalry, and concluded that monocular rivalry occurs only between simple, faint, repetitive images, such as low-contrast gratings. They observed, however, that alternations in clarity could occur between complex images, such as the surface of a pond and a reflection on it of a tree, although they did not measure rivalry with such stimuli. Boutet and Chaudhuri (2001) optically superimposed two faces that differed in orientation by 90°. They reported that the two faces alternated in clarity in a rivalry-like way, but they did not measure rivalry conventionally. They forced observer's choices about whether one or two faces was seen after brief stimulus presentations of 1–3 s. Monocular rivalry, however, usually takes several seconds, or even tens of seconds, before oscillations become evident (e.g., Breese, 1899). We decided to measure monocular rivalry with complex images in a conventional way, by showing observers optically superimposed images for 1-min trials, and asking them to track their perceptual alternations using key presses. We used images of a face and a house. Moreover, we explicitly compared monocular rivalry with binocular rivalry for identical stimuli over a range of stimulus sizes. We chose to manipulate size because, at least with gratings, it has powerful effects on binocular rivalry (e.g., Blake, Fox, & Westendorf, 1974; Breese, 1899, 1909; O'Shea, Sims, & Govan, 1997).

3. Method

3.1. Observers

One female and three males volunteered for this experiment after giving informed consent: HF (age 23), DLR (age 33), and RS (age 24) had some experience as observers; ROS (age 50) was a highly trained observer. All had normal or corrected-to-normal vision. All observers were right handed. HF and RS were naive as to the purpose of the experiment.

3.2. Stimuli and apparatus

Stimuli were digitized photographs of ROS's face and part of his house on plain backgrounds, similar to that shown in Fig. 1 except

that they were greyscale. Stimuli were 0.77°, 1.54°, 3.08°, 6.16°, and 12.32° of visual angle square. The smaller images were all scaled-down versions of largest image (800 × 800 pixels) and scaling was done using NIH Image software. (Scaling from large to small minimises spatial frequency distortions that can arise when scaling from small to large). They were surrounded by two bright vertical bars, each 0.5° wide, as tall as the stimulus, and separated from the edge of the stimulus by 0.5°; these were to help observers align the stimuli binocularly. Stimuli were displayed on two identical Sony Trinitron, 19-in., colour monitors with a spatial resolution of 1152 × 870 pixels and a frame rate of 75 Hz. Each eye of the observer viewed only one monitor from a distance of 1 m through a mirror stereoscope. The experiment was controlled by a Power Macintosh 8600 computer running specially written software (Handley, Bevin, & O'Shea, 2005).

The room was entirely dark, with the monitors as the sole light source. Presenting superimposed images of the face and house to both eyes created monocular rivalry. Presenting the image of the face and house separately to each eye created binocular rivalry. The luminance of the stimuli on each screen was 10 cd/m², and that of the vertical bars was 30 cd/m². Otherwise the screens were dark (0.2 cd/m²). The standard deviation of the luminances in the two images was 2.45 cd/m² for the face and 3.44 cd/m² for the house.

3.3. Procedure

There were two sessions each containing a block of 10 binocular rivalry trials and a block of 10 monocular-rivalry trials. In each block, observers received two presentations of the images at each of the five image sizes. During binocular rivalry trials, one presentation of each stimulus size was of the face to the left eye and the house to the right eye, and the other was of the opposite arrangement. Order of trials was random within blocks. Order of blocks was counterbalanced over observers and over sessions.

Each trial lasted for 60 s and was followed by an inter-trial interval of at least 45 s. Observers reported their perception of either the face or house by pressing the 'Z' or '?' keys, respectively. They pressed a key whenever, and for as long as, a particular stimulus exceeded a criterion level of visibility. For binocular rivalry, this criterion was that an image was exclusively visible over at least 95% of the field. For monocular rivalry, this criterion was that an image appeared to be at least twice as clear as the other, or was exclusively visible over at least two-thirds of the field (we call this a 66% visibility criterion).

The experimental sessions were preceded by sufficient practice trials to enable each observer to respond consistently to both sorts of rivalry.

4. Results and discussion

All observers found it easy to press keys to signal their perception of the two images in both monocular and binocular rivalry. They also commented on some of their unusual perceptions. During binocular rivalry, they sometimes described *composites*, in which one image would replace the other over a few moments. For example, one might briefly see the left half of the face on the left side of the screen and the right half of the house on the right side of the screen before the face would then wipe out the remaining image of the house. More amusingly, one might briefly see the face with one eye replaced by the house's window. Such composites are a common property of binocular rivalry, and have been studied by Wilson, Blake, and Lee (2001). Observers reported similar composites during monocular rivalry.

We quantified rivalry in three ways. First, we counted the number of times each key was pressed to obtain a *rate* measure of riv-

alry. Second, we counted the cumulative time each key was pressed to obtain a measure of *dominance time*. Third, we averaged the time of each individual key press to obtain a measure we call *period*.

We analysed these data with three-factor, within-subjects ANOVAs (the factors were type of rivalry, size, and image reported). There was a significant effect of size on rate, $F(4, 12) = 12.29$, $p < .001$, such that rate increased with size of the images (see Fig. 2). All observers showed this pattern of results. An increasing alternation rate with image size is opposite to the usual finding with simple stimuli such as gratings (e.g., Breese, 1899; O'Shea et al., 1997). Critically, there was no difference between monocular and binocular rivalry in the shape of the function relating size to rate.

There was also one significant effect for dominance time: the face was seen for longer than the house, $F(1, 3) = 10.64$, $p < .05$. The mean dominance time for the face was 12.44 s (SD = 9.95 s) and that for the house was 6.90 s (SD = 5.47 s). This could have arisen from a general preference for faces over other stimuli in rivalry (e.g., Beloff & Beloff, 1959; Engel, 1956) or from some preference for the spatial frequencies of the face image over the house image (cf. Lumer, Friston, & Rees, 1998; Tong, Nakayama, Vaughan, & Kanwisher, 1998). But it is not important for our purposes, because there were no other significant effects or interactions for this measure, showing that this advantage for the face was consistent over size and over type of rivalry.

There were no significant effects for period. These were similar over stimuli, over sizes, and over the two sorts of rivalry.

The increase in the rate of alternations with size for both sorts of rivalries is consistent with the idea that rivalry between complex stimuli is mediated by interactions among neurons in higher-level visual areas such as the inferotemporal cortex (Alais & Melcher, 2007; Sheinberg & Logothetis, 1997). Not only are such neurons responsive to coherent visual objects, such as the house and face stimuli used here, their receptive fields are far larger than those at earlier levels of the visual system (Gross, Bender, & Rocha-Miranda, 1969; Yoshor, Bosking, Ghose, & Maunsell, 2007) and would therefore be preferentially activated by the larger rival stimuli.

One possible alternative explanation is that image size is correlated with spatial-frequency content. This might seem plausible because with grating stimuli, monocular rivalry is usually strongest at low spatial frequencies (Kitterle & Thomas, 1980; Mapperson & Lovegrove, 1984; O'Shea, 1998). But grating stimuli contain only a single spatial frequency, whereas our images are complex with a very broad spatial frequency spectrum that follows a fractal (1/f) amplitude profile. Such images are scale invariant (e.g., Field,

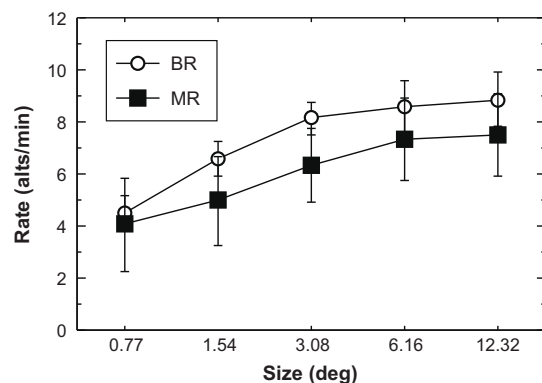


Fig. 2. Plot of binocular rivalry (BR) and monocular-rivalry (MR) rate (the number of episodes of dominance of each image per minute) against size of the images. The vertical bars show ± 1 standard error of the mean.

1994; Ruderman & Bialek, 1994) Complex images therefore show the same complex mix of spatial frequencies at all sizes of images.

Of more central importance for our purposes is that both monocular rivalry and binocular rivalry, which is robust over a very large range of spatial frequencies (O'Shea et al., 1997), exhibited the same trend of increasing alternation rate with increasing image size. Given this, the similar trends shown in Fig. 2 may be indicative of common mechanisms in monocular and binocular rivalry. We further test this idea in the next experiment by assessing the effects on the two sorts of rivalries of adding colour differences to the two rivaling images.

5. Experiment 2

Monocular rivalry does not require coloured stimuli (e.g., Experiment 1), but its alternation rate is faster when stimuli have complementary colours (Campbell & Howell, 1972; Rauschecker, Campbell, & Atkinson, 1973; Wade, 1975). Similarly, binocular rivalry does not require coloured stimuli, but its alternation rate is also faster when the rival stimuli have complementary colours (Hollins & Leung, 1978; Thomas, 1978; Wade, 1975). The only studies we are aware of in which the effects of colour on monocular and binocular rivalry were compared in the same experiment with the same observers' viewing grating stimuli came to different conclusions. Kitterle and Thomas (1980) found that colour affected monocular but not binocular rivalry whereas Knappen, Kanai, Brascamp, van Boxtel, and van Ee (2007) found that colour affected monocular and binocular rivalry similarly. In Experiment 2, we also examine the role of colour on binocular and monocular rivalry but extend it to include complex broadband images.

6. Method

The Method of Experiment 2 was very similar to that of Experiment 1. The differences were that a second set of stimuli, that used by Tong et al. (1998) was added, and one of the male observers (RS) from Experiment 1 did not participate. All stimuli were 6.16° square. Tong et al.'s stimuli were similar to those of Experiment 1, except that they comprised a different male face (younger, clean-shaven, and without glasses) and a different house (older, of a Georgian style, and showing more elaborate architectural details). Pixel luminances in Tong et al.'s face and house had standard deviations of 3.22 cd/m² and 4.98 cd/m², respectively. There were 12 binocular rivalry and 12 monocular-rivalry trials in which observers again tracked their rivalry alternations. In four repetitions of each pair of stimuli the images were achromatic, in four the face was red (CIE $x = .315$, $y = .321$) and the house green (CIE $x = .270$, $y = .347$), and in four the face was green and the house red. Mean luminances of all stimuli (colour and greyscale) were the same as that in Experiment 1. See Fig. 1 for an illustration of one of the monocular-rivalry stimuli.

7. Results and discussion

Again observers had no trouble recording perceptual alternations in monocular and binocular rivalry, and again they reported episodes of composites for both types of rivalry.

We analysed the same three measures of rivalry with four-factor, within-subjects ANOVAs (the factors were type of rivalry, colour, stimulus set, and image reported). The only significant effect was colour on rivalry rate, $F(1,2) = 19.87$, $p < .05$, such that the alternation rate was greater with coloured images than with achromatic images (see Fig. 3). All observers showed this pattern of results. The difference between the rates for monocular and binocular rivalry was not significant, $F(1,2) = 5.19$, $p > .15$.

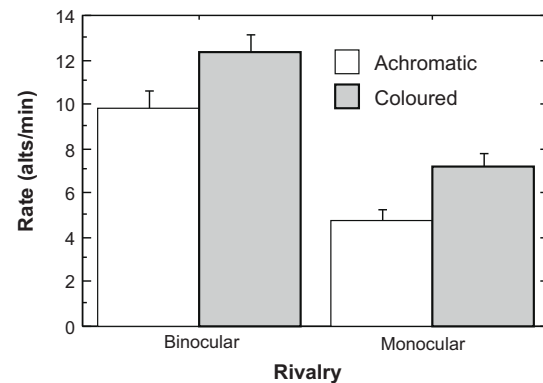


Fig. 3. Plot of binocular rivalry and monocular-rivalry rate (the number of episodes of dominance of each image per minute) for achromatic and for coloured images. The vertical bars show ± 1 standard error of the mean.

Fig. 3 shows that adding colour differences to two complex rivaling images increases the rate of both monocular and binocular rivalry (the interaction between type of rivalry and colour was not significant, $F(1,2) = 0.03$) without consistently affecting the other measures of rivalry. This is different from the result of Kitterle and Thomas (1980) who found that colour enhanced monocular rivalry between gratings, but did not enhance binocular rivalry. Although it is possible that this indicates a difference between simple and complex stimuli, we suspect that there is some other explanation, especially because others did find that colour differences enhanced binocular-rivalry rates with gratings (Hollins & Leung, 1978; Thomas, 1978; Wade, 1975). For example, Kitterle and Thomas's binocular-rivalry rates for achromatic stimuli were about four times greater than their monocular-rivalry rates. Possibly, then, a ceiling effect limited the scope for binocular rivalry to be enhanced by coloured stimuli.

In any case, we are confident that with complex stimuli, adding different colours to different complex images does enhance both binocular and monocular rivalry. This is consistent with some general rivalry mechanism that assesses the degree of difference between representations of two images and instigates rivalry accordingly. Adding different colour to different images adds another dimension along which the stimuli differ, which would be expected to lead to more vigorous rivalry. In a related vein, adding colour to rival images also tends to reduce piecemeal rivalry, because it adds a unifying attribute to each image and tends to lead to more coherent alternations.

By concentrating on overall rivalry alternation rates in the first two experiments, we have ignored the finer-grained temporal dynamics of rivalry. In Experiment 3, we will conduct a comparison of monocular and binocular rivalry on a finer temporal scale.

8. Experiment 3

The temporal dynamics of binocular rivalry have been well studied. For example, Levelt (1968) showed that the distribution of dominance times approximates a gamma function. Moreover, Levelt demonstrated that the duration of one episode of dominance of one image cannot be predicted from the duration of any of the previous episodes, meaning that each dominance episode is a statistically independent sample from an underlying population distribution of dominance times. We set out to determine whether monocular rivalry also conforms to these principles, comparing it with binocular rivalry dynamics measured on identical binocular-rivalry stimuli. In this we were following the example of van Boxtel, van Ee, and Erkelens (2007) who used similar comparisons to

argue that binocular rivalry and dichoptic masking share similar processing.

Essentially all of the studies of the temporal properties of binocular rivalry have used simple repetitive stimuli such as gratings. For comparability with these studies, we use grating stimuli for both monocular and binocular rivalry.

9. Method

9.1. Observers

Three of the authors acted as observers, along with four inexperienced observers who were unaware of the aims of the experiment. All observers had normal vision.

9.2. Apparatus

The computer controlling this experiment was a Macintosh G5, running Matlab 7.0.4 scripts that used the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Stimuli were displayed on a 14-in. DiamondPro monitor showing 800 × 600 pixels at a 90 Hz vertical refresh rate (75 Hz for observers DL, ROS, SM, SS). Stimuli were shown one on each side of the screen and viewed via a mirror stereoscope at a viewing distance of 57 cm.

9.3. Stimuli

Stimuli were two orthogonal square-wave gratings, one red and the other green, oriented $\pm 45^\circ$ to vertical. The gratings had a spatial frequency of 2.2 cycles/deg with a Michelson contrast of 8% and were placed in a circular aperture subtending 4.6° . Gratings had a mean luminance of 31.30 cd/m²; the background had the same luminance. The gratings were superimposed and visible to both eyes for monocular rivalry conditions; the gratings were presented one to each eye for binocular rivalry conditions.

9.4. Procedure

For both binocular and monocular rivalry, the observer's task was similar to that in Experiments 1 and 2: to track episodes of perceptual dominance of one and the other stimuli by pressing keys on the computer keyboard. There were two trials lasting up to 5 min for each viewing condition. Viewing condition was alternated for each observer over trials; each observer started with a different condition.

10. Results and discussion

We analysed the records of rivalry in two ways. First, we plotted distributions of dominance periods to which we fitted a gamma distribution. However, we also tried fitting a gamma distribution to the reciprocal of dominance duration (alternation rate), following Brascamp, van Ee, Pestman, and van den Berg's (2005) recommendation that the gamma distribution provides a better fit to alternation rates than to the more commonly used dominance durations. When we compared fits to both types of data using the Kolmogorov–Smirnov goodness-of-fit test (the cumulative functions for this test were calculated without binning the data), we found they fitted equally well. Using a critical *p*-value of 0.10 (as in Brascamp et al., 2005), we found that three out of 14 distributions of duration data were significantly different from the best-fitting gamma distribution. For the same analysis based on the rate data, the outcome was the same: three out of 14 distributions differed significantly from the best fit. Although Brascamp et al. did find rate-based fits to be better (based on nearly 200 distributions),

there was no difference in our small sample. For this reason, and to make it easier to relate our findings to the previous literature (where duration-based fits have been the standard), we show distributions of dominance periods together with best-fitting gamma distributions of the following form:

$$f(t|k, \lambda, a) = a \frac{1}{\lambda^k \Gamma(k)} t^{k-1} e^{-\frac{t}{\lambda}}$$

where *k* is the “scale” parameter, λ is the “shape” parameter, and *a* scales the height (amplitude) of the distribution.

Fig. 4 shows the distributions of dominance periods separately for monocular and binocular rivalry for four observers (the results of the other three observers were similar). We show the fitted gamma functions with their parameters. The parameters of all fits are remarkably similar, showing that monocular and binocular rivalry exhibit globally similar alternation dynamics.

Second, we computed autocorrelations between the recorded dominance sequence and the same sequence offset by various time lags in order to test the sequential independence of rivalry dominance times. Fig. 5 shows the autocorrelation analyses from the same four observers for binocular and monocular rivalry. The correlation is arbitrarily 1.0 when there is no lag, and the error bars show 95% confidence intervals (computed from 1000 iterations of a bootstrapping procedure). Similar to binocular rivalry (Levelt, 1968) there is no systematic tendency in monocular rivalry for a given dominance duration to be related to the previous dominance duration, or to dominance durations several phases earlier. Over the seven observers tested at 12 phase lags for monocular and binocular rivalry (a total of 168 points), there are only nine significant deviations from zero – about what would be expected from type I errors with our 95% confidence intervals ($9/168 = 0.053$).

In summary, the results of this experiment show that monocular rivalry possesses the characteristic temporal dynamics of binocular rivalry. The remaining hallmark of binocular rivalry is that there is an objectively measurable suppression of vision of one or the other images. In Experiment 4, we will search for the same suppression in monocular rivalry.

11. Experiment 4

One technique commonly used to study binocular rivalry has been to measure the depth of suppression. This is done by measuring the detection threshold for a probe stimulus presented to an eye during suppression, and comparing it against the threshold for the same probe measured during dominance (Blake & Camisa, 1979; Blake & Fox, 1974; Fox & Check, 1972; Wales & Fox, 1970). Generally, for simple stimuli such as gratings and contours, probe sensitivity is reduced during suppression to about 60% of the level measured during dominance (Fox & McIntyre, 1967; Nguyen et al., 2003; Norman et al., 1999; Wales & Fox, 1970).

Surprisingly, the probe technique has never been used to assess the depth of monocular-rivalry suppression. We set out to do so. Of course, it is not possible to use monocular probes (as done in binocular rivalry probe experiments) for monocular rivalry because the rivaling stimuli are both present in the same eye. Instead, our approach was to use a contrast increment of one of the monocular-rivalry stimuli as a probe. Again, for comparability with previous research, we used orthogonal gratings as rivalry stimuli. Gratings were red or green, oriented $\pm 45^\circ$ to vertical. We briefly and smoothly pulsed the contrast of the red grating according to a temporal Gaussian profile, varying the amplitude of the pulse to find the threshold. These thresholds were measured during dominance and suppression to quantify suppression depth for monocular rivalry. As a comparison, we also measured suppression depth for the same stimuli under binocular rivalry conditions.

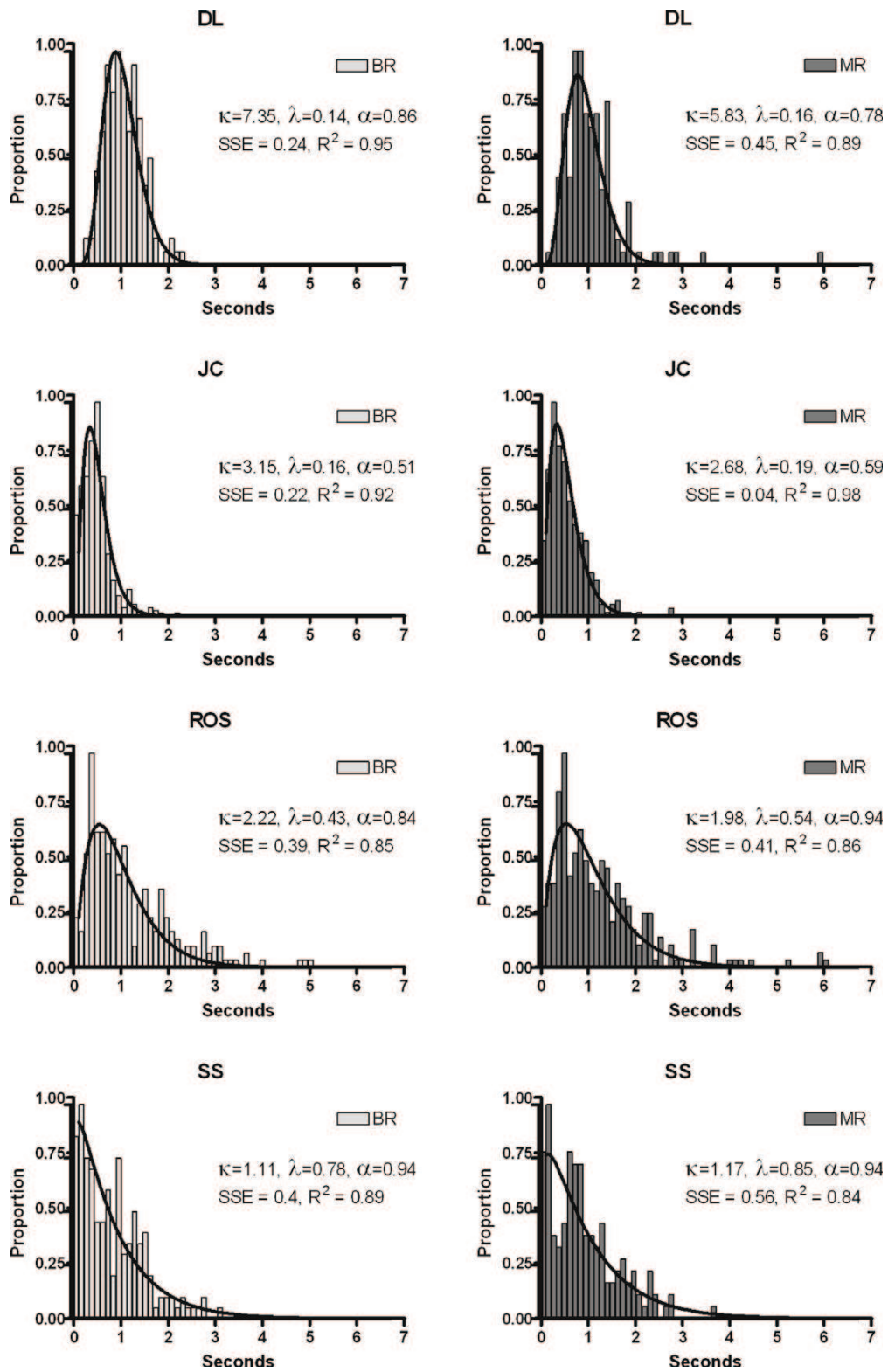


Fig. 4. Distributions of dominance durations for four observers for binocular rivalry (left panels) and for monocular rivalry (right panels). The continuous plot shows that best-fitting Gamma distribution fitted to the data. The periods were binned into 125 ms intervals.

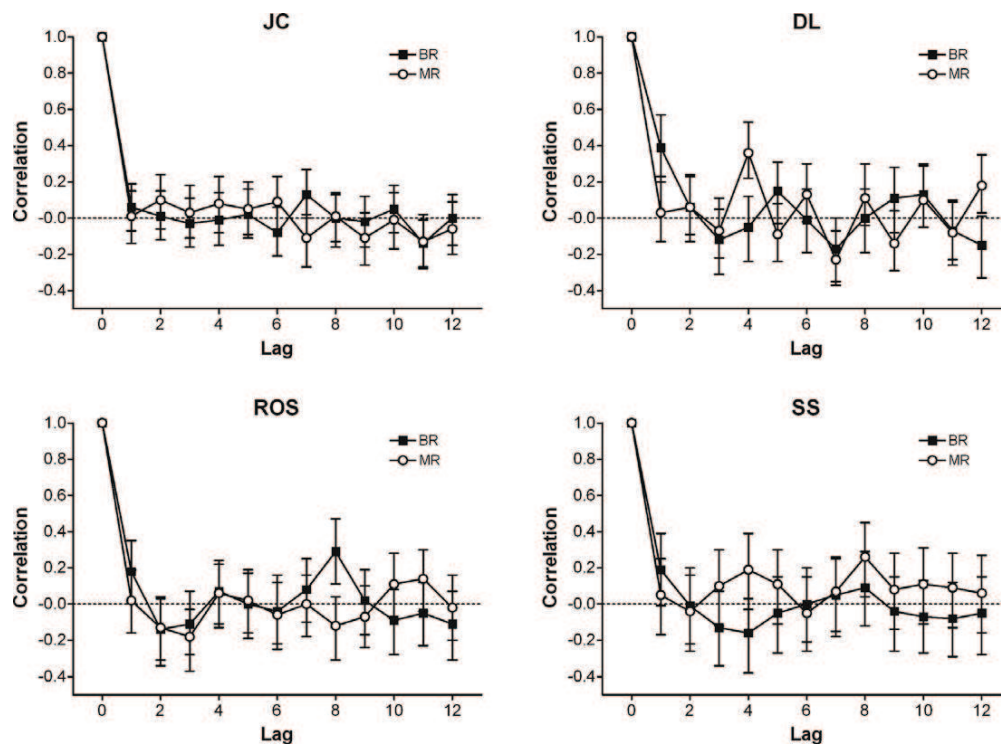


Fig. 5. Results of the autocorrelation analysis for four observers for binocular rivalry (open circles) and for monocular rivalry (filled squares). Apart from the arbitrarily perfect autocorrelation when the signal was not lagged, there were no statistically significant deviations from zero. 95% confidence intervals, calculated using Fisher's r -to- Z' method, were erected around the correlation at each non-zero lag. All included a correlation of zero.

12. Method

The Method was similar to that of Experiment 3 with the following exceptions. Observers were the three authors who participated in Experiment 3 and JC, who also participated in Experiment 3. Instead of tracking monocular or binocular rivalry, observers pressed a key either whenever the red or the green grating was dominant, using similar response criteria: at least 95% visibility for binocular rivalry and at least 66% visibility for monocular rivalry. Randomly on 50% of trials this caused a probe, a contrast increment, to appear briefly on the red grating. Observers then made another keypress to say whether the probe appeared or not. Feedback was given for correct and incorrect responses. The probe followed the first keypress by 150 ms, and had a Gaussian profile over time (with a half-width of 67 ms) to ensure the probe was smooth and free of transients. The Gaussian amplitude had a variable peak that was controlled by an adaptive QUEST procedure (Watson & Pelli, 1983) involving two randomly interleaved staircases to find the contrast increment threshold for the probe. Each QUEST was preceded by four practice trials and comprised 40 trials. Observers responded to at least four QUESTs in each of four conditions (probe presented during dominance vs suppression and monocular vs binocular rivalry). Observers alternated between dominance and suppression conditions, and alternated between monocular and binocular rivalry. Starting condition was counter-balanced over sessions and over observers.

13. Results and discussion

Before discussing the thresholds, it is important to note that the phenomenology of probe detection in the two sorts of rivalry differed in the same way as the rivalries differed. The essential character of binocular rivalry is that its perceptual alternations are of

visibility, whereas those of monocular rivalry are of clarity. During binocular rivalry, a suppressed stimulus is invisible. Observers agreed there were three basic experiences when such a stimulus was probed. For low-contrast probes, the probe was invisible too. Observers pressed the key to say that no probe was presented, and were surprised when the feedback told them of their error. For intermediate-contrast probes, the probe would sometimes cause the rival stimulus to break suppression partially, so that the pulse could be seen on the parts of the previously suppressed grating. For high-contrast probes, the probe would cause the rival stimulus to break suppression, so that the contrast pulse could be seen on the previously suppressed grating.

During monocular rivalry a suppressed stimulus is still visible but its visibility is reduced. This means the experience of the probe was necessarily different from that in binocular rivalry. Observers could not agree on different qualitative experiences of the probe; all felt that there was no phenomenal suppression at all! It was only when the results were collated that the small but significant effect of suppression emerged (see below). That is not to say detection of the probe during monocular-rivalry suppression or dominance was easy; it was hard. The probe resembled the naturally occurring fluctuations in the visibility of the suppressed stimulus.

We analysed the mean thresholds for the four observers using a two-way, within-subjects ANOVA. This found both main effects (rivalry type: monocular vs. binocular; and rivalry phase: dominance vs. suppression) to be significant, but critically there was an interaction between them, $F(1,3) = 21.12$, $p < .05$. The thresholds are shown in the upper panel of Fig. 6. Suppression depths are shown in the lower panel of Fig. 6. Suppression depth is calculated by subtracting from unity the ratio of the dominance threshold to the suppression threshold. A suppression depth of zero (i.e., the complete absence of suppression) would occur if suppression and dominance thresholds were equal. Suppression depths ap-

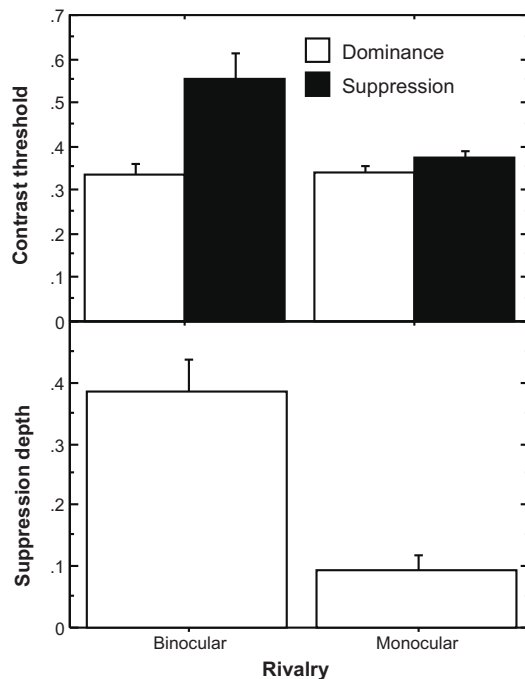


Fig. 6. Upper panel. Average thresholds for the four observers for detecting the contrast increment during dominance and during suppression, for both binocular rivalry and monocular rivalry. Lower panel. The dominance and suppression thresholds from the upper panel expressed as suppression depth (i.e., one minus the dominance-to-suppression ratio). Error bars show 1 standard error of the mean.

proach unity (i.e., very strong suppression) when suppression thresholds are much greater than dominance thresholds. For binocular rivalry, typical suppression depths are around 0.40 (e.g., Fox & McIntyre, 1967; Nguyen et al., 2003; Norman et al., 2000; Wales & Fox, 1970); the lower panel of Fig. 6 shows that the suppression depth we measured for binocular rivalry is consistent with this value. Suppression depth for monocular rivalry is much weaker at around 0.10. Nevertheless, this value is significantly greater than zero, $t(3) = 4.67$, $p < .05$.

It could be argued that the weaker suppression depth of monocular rivalry than binocular rivalry is because observers used a more liberal criterion of invisibility for the former. We used this criterion to equate, as far as possible, the number and durations of rivalry periods. The results of Experiments 1 and 2 show that we were largely successful. The essential character of monocular rivalry is that episodes of suppression are seen as reductions in the clarity of the suppressed stimulus. It is possible that if we had asked our observers to wait for the rare instances of monocular rivalry that reached a 95% criterion of visibility, we would have measured deeper suppression. Nevertheless, we conclude that the thresholds we have measured are an accurate indication of the depth of suppression during typical monocular rivalry.

14. General discussion

Our main question was whether similar neural mechanisms underlie monocular and binocular rivalry. Our experiments showed that the two phenomena do exhibit important similarities. In Experiments 1 and 2, we demonstrated that both kinds of rivalry can occur between complex images, and that they are affected similarly by the size of the rivaling images, as well as by their colours in quantitatively similar ways. In Experiment 3, we illustrated the similar temporal dynamics of the two sorts of rivalry, showing that

both exhibit a gamma distribution of dominance durations with comparable parameters and that neither shows any temporal correlation of one episode of visibility with any of the preceding episodes. In Experiment 4 we demonstrated that both sorts of rivalry involve suppression of visual sensitivity to the non-dominant stimulus, albeit to a very different degree. These qualitative and quantitative (with the exception of suppression depth) similarities between monocular and binocular rivalry are consistent with the idea that their underlying processes involve common neural mechanisms (cf. Leopold & Logothetis, 1999; O'Shea, 1998; Papathomas, Kovács, Fehér, & Julesz, 1999).

There are other similarities between monocular and binocular rivalry. For example, rivalry rate grows with orientation and spatial-frequency differences between the rivaling images (e.g., Atkinson et al., 1973; Campbell et al., 1973; O'Shea, 1998). It has been long known that binocular rivalry is difficult to control voluntarily (Breese, 1899); monocular rivalry is equally difficult to control voluntarily, both for gratings and for complex images (O'Shea, 2006). Moreover, the temporal limits over which rivalry will survive asynchronous flicker are similar for the two forms of rivalry, at around 350 ms (van Boxtel, Knapen, van Ee, & Erkelens, 2006). And as we pointed out earlier, alternations of one sort of rivalry in one region of the visual field synchronise with alternations of the other from an adjacent region (Andrews & Purves, 1997; Pearson & Clifford, 2005).

Although the conclusion that monocular rivalry shares common processes with binocular rivalry has appeal, there are alternative explanations of monocular rivalry that need to be considered, as well as certain notable differences between the two phenomena that must be addressed. One of the competing explanations of monocular rivalry is that it is not strictly a perceptual alternation but an epiphenomenon produced by a combination of eye movements and afterimages. This line of argument was proposed by Furchner and Ginsburg (1978), by Georgeson and Phillips (1980), and by Georgeson (1984). They maintained that in the case of two superimposed orthogonal gratings, for example, steady fixation would build up afterimages that would tend to cancel visibility of both. If an eye movement were made parallel to one of the gratings, with a magnitude of half the spatial period of the other grating, it would leave the visibility of the first grating impaired but superimpose the negative afterimage of the second grating onto its own real image, causing that grating suddenly to become visible, as if it had just appeared after an episode of suppression. According to this explanation, if eye movements were made randomly, they would produce random distributions of dominance times such as we observed in Experiment 3, and they would also produce the dependencies of monocular rivalry on orientation differences such that it would be most pronounced for orthogonal gratings (O'Shea, 1998).

We argue that eye movements and afterimages cannot be a complete explanation of monocular rivalry for at least four reasons. First, monocular rivalry occurs between afterimages themselves (Crassini & Broerse, 1982), which are fixed on the retina and therefore cannot combine with eye movements as required by the explanation. Second, observers report monocular-rivalry composites, patches of the visual field in which one image is seen and adjacent patches in which the other is seen (Sindermann & Lüddecke, 1972). Our observers also reported composites in all our experiments. Such composites would require eye movements that move the retina in different directions in different regions, which is quite impossible. Third, Bradley and Schor (1988) measured eye movements during monocular rivalry of gratings. They found some disappearances in monocular rivalry that did follow the predicted eye movements, but they also found a proportion of disappearances that followed an incorrect eye movement. Fourth, the explanation requires that the images be simple, repetitive stimuli such as grat-

ings, so that an afterimage can be displaced but still provide a matching overlay of the stimulus that generated it. Experiments 1 and 2 showed clearly that monocular rivalry is possible between complex images for which no eye movement can superimpose a matching afterimage.¹

Given the shortcomings of this alternative account of monocular rivalry, we conclude that monocular rivalry is indeed a genuine perceptual alternation, similar to binocular rivalry, and not an artefact of eye movements or afterimages. Nonetheless, despite the striking similarities between monocular and binocular rivalry, we elaborate below on three differences between the phenomena. We propose that these differences arise because binocular rivalry involves a distributed cortical network entailing both low-level and high-level processes (Blake & Logothetis, 2002; Freeman, Nguyen, & Alais, 2005; Nguyen et al., 2003) whereas monocular rivalry involves interactions only at higher levels. We agree with Maier et al. (2005) that monocular rivalry is likely to reflect a higher-level process because it involves global interpretations of the probable nature of the stimulus. Therefore, we propose that monocular and binocular rivalry share common high-level processing which can be characterised as interpretative processes (e.g., Alais, O'Shea, Mesana-Alais, & Wilson, 2000; Kovács, Papathomas, Yang, & Fehér, 1996). The key distinction, then, between the two types of rivalry is that binocular rivalry involves additional interocular interactions at early levels of the visual system.²

The first difference between monocular and binocular rivalry was observed by Breese (1899) in his seminal study. He recorded that although binocular rivalry's episodes of dominance involved alternations in visibility, monocular rivalry was weaker and usually involved alternations in clarity. Consistent with this, we showed in Experiment 4 that the magnitude of suppression during monocular rivalry is much less than in binocular rivalry. We propose that the marked difference in suppression depth is due to the different extents of the monocular and binocular rivalry networks rather than to fundamentally different processes. A model similar to that by Wilson (2003) or by Nguyen et al. (2003) or Freeman (2005) could serve here. Specifically, the same inhibitory mechanisms exist at monocular and at binocular levels: these sum their effects in binocular rivalry, but the monocular part does not participate in monocular rivalry, weakening the suppression. The idea of additive suppression components is consistent with recent findings that exclusive visibility during rivalry increases as more dimensions of stimulus conflict are combined (Knapen et al., 2007).

An important consequence of the notion that monocular rivalry involves neural interactions common to the high-level part of the binocular rivalry network is that monocular rivalry should resemble other higher-level rivalries. Here, we review only one: *stimulus rivalry*, or *flicker-and-swap rivalry*. Devised by Logothetis, Leopold, and Sheinberg (1996), stimulus rivalry occurs when two rival images are swapped between the eyes at around 1.5 Hz, while also flickering on and off at around 18 Hz. The key observation is that observers report episodes of stable visibility of one of the images

that endure for long enough to incorporate several interocular stimulus swaps. Each swap, however, is noticeable as a pulse of some sort during a single episode of visibility, showing a similar phenomenal absence of complete suppression in this sort of rivalry as in monocular rivalry. Logothetis et al. proposed that rivalry process acts on representations of images at a high level of the visual system where eye-of-origin information (a low-level property) has been discarded. Recent corroborative evidence for this comes from Pearson, Tadin, and Blake (2007) who showed that transcranial magnetic stimulation of V1 disrupts conventional binocular rivalry but has no effect on flicker-and-swap rivalry.

We argue that with eye-of-origin information removed, flicker-and-swap rivalry should be very similar to monocular rivalry. Supporting this, we recently found that suppression depth in this form of rivalry is also shallow (Bhardwaj, O'Shea, Alais, & Parker, 2008), similar to that of monocular rivalry. There are at least three other similarities between monocular rivalry and flicker-and-swap rivalry phenomena that support our proposal. 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 and monocular rivalry share some interesting parametric similarities. Both are enhanced at low contrast (Lee & Blake, 1999) and by making the images different colours (Bonneh, Sagi, & Karni, 2001; Logothetis et al., 1996). Moreover, Knapen et al. (2007) found that exclusive visibility in monocular rivalry is similar to that from flicker-and-swap rivalry over a range of colour differences. These similarities between monocular rivalry and flicker-and-swap rivalry are, of course, consistent with our overall conclusion that all forms of rivalry involve a similar, high-level mechanism. Indeed, Pearson and Clifford (2005) showed that all three types of rivalry, monocular, binocular, and flicker-and-swap, synchronise their alternations when all are presented together in adjacent regions of the visual field.

The second major difference between monocular and binocular rivalry, and the hardest to reconcile, is that they are affected oppositely by contrast (O'Shea and Wishart, 2007). Binocular rivalry alternation rate increases with increasing contrast of the rival images whereas monocular rivalry alternation rate decreases with increasing contrast. Evidence from imaging and transcranial magnetic stimulation support the claim that early visual processes are critical in eliciting binocular rivalry (Lee & Blake, 2002; Pearson et al., 2007; Polonsky, Blake, Braun, & Heeger, 2000). Because early visual responses depend strongly on the level of stimulus contrast, exhibiting a graded monotonic response to contrast, it makes sense that binocular rivalry would be strongly modulated by contrast. Specifically, because increases in stimulus contrast would increase the V1 response to the rival stimuli, it is as expected that binocular rivalry should be more vigorous at high contrast.

What is less obvious is why monocular rivalry would be more vigorous at low contrast. One reason may be that the global interpretative processes implied by Maier et al.'s (2005) work on monocular rivalry, and more generally by Leopold and Logothetis's (1999) review, may be less stable at low contrast. That is, reduced signal-to-noise ratios and stochastic fluctuations would add considerable uncertainty to whether a monocular-rivalry stimulus should be interpreted as one or two objects, and possibly to the depth ordering if two objects were signalled. To take Maier et al.'s (2005) real-world example, the bottom of a pond might be visible transparently even though the water's surface may reflect the image of a tree. In this case, with both aspects of the visual scene imaged at the same retinal location, high contrast would facilitate a transparency interpretation and the correct depth order

¹ The same explanation could also apply to binocular rivalry of gratings. Indeed, van Dam and van Ee (2006) found that saccades changing fixation from one luminance to the opposite luminance (e.g., from a bright bar to a dark bar) were more likely to be followed by a binocular-rivalry alternation to that grating than saccades changing fixation from one luminance to the same luminance (e.g., from a dark bar to a dark bar). This is not to say that binocular rivalry is an epiphenomenon of eye movements and afterimages. There is an abundance of evidence similar to that for monocular rivalry, including binocular rivalry with afterimages, binocular rivalry with complex images, and visibility of composites of the two rival stimuli, showing that eye movements and afterimages are not necessary for binocular rivalry.

² Although the term "monocular rivalry" suggests a low-level process, it is simply because it has been misleadingly labelled, prompting Maier et al. (2005) to propose that monocular rivalry would be more appropriately called "pattern rivalry".

because both images would be reliably signalled with little ambiguity. Low contrast, however, would render the problem more difficult as both interpretations would be potentially valid but the correct transparency and order relationship would be hard to make with poorly visible cues. Under these conditions, an interpretative process with bistable behaviour appears to assume more prominence and perceptual alternations result.

The lack of vigorous monocular rivalry at high contrast may be because there are robust cues for interpreting the image as stable, such as the visibility of the intersections of contours. It may also be because high-level neurons tend to be contrast invariant. That is, their contrast-response functions are much steeper initially with a longer saturated plateau (e.g., Sclar, Maunsell, & Lennie, 1990). A magnetic resonance imaging study (Avidan et al., 2002) showed steeper contrast-response functions in human subjects 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 monocular 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 interpretative process would be least stable.

The third major difference between monocular and binocular rivalry is that they are potentially affected oppositely by disparity. Knapen et al. (2007) have shown that monocular rivalry increases as two monocular-rivalry gratings are given different disparities to make them appear to be at different depths. Shimojo and Nakayama (1994) and have shown that binocular rivalry decreases by adding disparities. Knapen et al. argued from their results that monocular rivalry and binocular rivalry are nevertheless similar, in that the strength of rivalry is determined by the difference between two stimuli in their component features: adding disparity to monocular-rivalry stimuli increases their difference whereas adding disparity to binocular-rivalry stimuli decreases the amount of interocular conflict between them. Knapen et al.'s approach, although from a different direction to ours, comes to a similar conclusion: that monocular rivalry and binocular rivalry are similar processes aimed at resolving ambiguity in visual inputs.

15. Conclusion

In summary, we have shown several qualitative and quantitative similarities between monocular and binocular rivalry. Both occur between complex images, both are similarly affected by the images' size and colour, both involve fluctuations in image visibility that are random and sequentially independent, and both involve suppression of visual sensitivity to the non-dominant image. We propose that both sorts of rivalry are mediated by a common high-level mechanism for resolving ambiguity (Alais, O'Shea, Mesana-Alais, & Wilson, 2000; Kovács et al., 1996; Leopold & Logothetis, 1999; Maier et al., 2005), although this process cannot be the primary driver in the case of binocular rivalry, which must be initiated by mutually inhibitory interactions between neurons retaining eye-of-origin information in early cortex. This high-level process for ambiguity resolution probably exerts a modulatory influence on binocular rivalry, exerting its influence via feedback for such things as coordinating local rivalry processes into coherently rivalling global images (Alais & Melcher, 2007), whereas it is more likely to be the primary driver of monocular rivalry.

Acknowledgments

We are grateful to Frank Tong for allowing us to use his stimuli for Experiment 2, to Janine Mendola for helpful discussion, and to Urte Roeber for help with figures.

References

- Alais, D., & Blake, R. (Eds.). (2005). *Binocular rivalry*. Boston: MIT Press.
- Alais, D., & Melcher, D. (2007). Strength and coherence of binocular rivalry depends on shared stimulus complexity. *Vision Research*, 47, 269–279.
- Alais, D., O'Shea, R. P., Mesana-Alais, C., & Wilson, I. G. (2000). On binocular alternation. *Perception*, 29, 1437–1445.
- Andrews, T. J., & Purves, D. (1997). Similarities in normal and binocularly rivalrous viewing. *Proceedings of the National Academy of Sciences of the United States of America*, 94, 9905–9908.
- Atkinson, J., Fiorentini, A., Campbell, F. W., & Maffei, L. (1973). The dependence of monocular rivalry on spatial frequency. *Perception*, 2, 127–133.
- 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.
- Beloff, H., & Beloff, J. (1959). Unconscious self-evaluation using a stereoscope. *Journal of Abnormal & Social Psychology*, 59, 275–278.
- Bhardwaj, R., O'Shea, R. P., Alais, D., & Parker, A. (2008). Probing visual consciousness: Rivalry between eyes and images. *Journal of Vision*, 8(11,2), 1–13.
- Blake, R., & Camisa, J. (1979). On the inhibitory nature of binocular rivalry suppression. *Journal of Experimental Psychology: Human Perception and Performance*, 5, 315–323.
- Blake, R., & Fox, R. (1974). Binocular rivalry suppression: Insensitive to spatial frequency and orientation change. *Vision Research*, 14, 687–692.
- Blake, R., Fox, R., & Westendorf, D. (1974). Visual size constancy occurs after binocular rivalry. *Vision Research*, 14, 585–586.
- Blake, R., & Logothetis, N. (2002). Visual competition. *Nature Reviews Neuroscience*, 3, 1–12.
- Blake, R., & O'Shea, R. P. (2009). Binocular rivalry. In L. R. Squire (Ed.), *Encyclopedia of Neuroscience* (Vol. 2, pp. 179–187). Oxford: Academic Press.
- Bonneh, Y., Sagi, D., & Karni, A. (2001). A transition between eye and object rivalry determined by stimulus coherence. *Vision Research*, 41, 981–989.
- Bonneh, Y. S., Cooperman, A., & Sagi, D. (2001). Motion-induced blindness in normal observers. *Nature*, 411, 798–801.
- Boutet, I., & Chaudhuri, A. (2001). Multistability of overlapped face stimuli is dependent upon orientation. *Perception*, 30, 743–753.
- Bradley, A., & Schor, C. (1988). The role of eye movements and masking in monocular rivalry. *Vision Research*, 28, 1129–1137.
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10, 433–436.
- Brascamp, J. W., van Ee, R., Pestman, W. R., & van den Berg, A. V. (2005). Distributions of alternation rates in various forms of bistable perception. *Journal of Vision*, 5, 287–298.
- Breese, B. B. (1899). On inhibition. *Psychological Monographs*, 3, 1–65.
- Breese, B. B. (1909). Binocular rivalry. *Psychological Review*, 16, 410–415.
- Campbell, F. W., Gillsky, A. S., Howell, E. R., Riggs, L. A., & Atkinson, J. (1973). The dependence of monocular rivalry on orientation. *Perception*, 2, 123–125.
- Campbell, F. W., & Howell, E. R. (1972). Monocular alternation: A method for the investigation of pattern vision. *Journal of Physiology*, 225, 19P–21P.
- Chalmers, D. (1995). Facing up to the problem of consciousness. *Journal of Consciousness Studies*, 2, 200–219.
- Crassini, B., & Broerse, J. (1982). Monocular rivalry occurs without eye movements. *Vision Research*, 22, 203–204.
- Crick, F., & Koch, C. (1995). Are we aware of neural activity in primary visual cortex? *Nature*, 375, 121–123.
- Einhäuser, W., Stout, J., Koch, C., & Carter, O. (2008). Pupil dilation reflects perceptual selection and predicts subsequent stability in perceptual rivalry. *PNAS*, 105, 1704–1709.
- Engel, E. (1956). The role of content in binocular resolution. *American Journal of Psychology*, 69, 87–91.
- Field, D. J. (1994). Scale-invariance and self-similar 'wavelet' transforms: An analysis of natural scenes and mammalian visual scenes. In M. Farge, J. C. R. Hunt, & J. C. Vassilicos (Eds.), *Wavelets, fractals, and fourier transforms* (pp. 151–193). Oxford: Clarendon Press.
- Fox, R., & Check, R. (1972). Independence between binocular rivalry suppression duration and magnitude of suppression. *Journal of Experimental Psychology*, 93, 283–289.
- Fox, R., & Herrmann, J. (1967). Stochastic properties of binocular rivalry alterations. *Perception & Psychophysics*, 2, 432–436.
- Fox, R., & McIntyre, C. (1967). Suppression during binocular fusion of complex targets. *Psychonomic Science*, 8, 143–144.
- Freeman, A. W., Nguyen, V. A., & Alais, D. (2005). The nature and depth of binocular rivalry suppression. In R. Blake & D. Alais (Eds.), *Binocular rivalry* (pp. 47–62). Cambridge, MA: MIT Press.
- Freeman, A. W. (2005). Multistage model for binocular rivalry. *Journal of Neurophysiology*, 94, 4412–4420.
- Furchner, C. S., & Ginsburg, A. P. (1978). "Monocular rivalry" of a complex waveform. *Vision Research*, 18, 1641–1648.
- Galton, F. (1907). *Inquiries into human faculty and its development*. London: Dent.
- Georgeson, M. A. (1984). Eye movements, afterimages and monocular rivalry. *Vision Research*, 24, 1311–1319.
- Georgeson, M. A., & Phillips, R. (1980). Angular selectivity of monocular rivalry: Experiment and computer simulation. *Vision Research*, 20, 1007–1013.
- Gross, C. G., Bender, D. B., & Rocha-Miranda, C. E. (1969). Visual receptive fields of neurons in inferotemporal cortex of the monkey. *Science*, 166, 1303–1306.

- Handley, M., Bevin, M., & O'Shea, R. P. (2005). *User guide for the ocular dominance experiment 2.21*. Dunedin: Department of Psychology, University of Otago.
- Hollins, M., & Leung, E. H. L. (1978). The influence of colour on binocular rivalry. In C. Armington, J. Krauskopf, & B. Wooten (Eds.), *Visual psychophysics and physiology. A volume dedicated to Lorrin Riggs* (pp. 181–190). New York: Academic Press.
- Kang, M.-S., & Blake, R. (2006). How to enhance the incidence of stimulus rivalry. *Journal of Vision*, 6(6), 46a [Abstract].
- Kitterle, F., & Thomas, J. (1980). The effects of spatial frequency, orientation, and colour upon binocular rivalry and monocular pattern alternation. *Bulletin of the Psychonomic Society*, 16, 405–407.
- Knapen, T., Kanai, R., Brascamp, J., van Boxtel, J., & van Ee, R. (2007). Distance in feature space determines exclusivity in visual rivalry. *Vision Research*, 47, 3269–3275.
- Kovács, I., Papathomas, T. V., Yang, M., & Fehér, Á. (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.
- Lee, S.-H., & Blake, R. (2002). V1 activity is reduced during binocular rivalry. *Journal of Vision*, 2, 618–626.
- Lee, S. H., & Blake, R. (1999). Rival ideas about binocular rivalry. *Vision Research*, 39, 1447–1454.
- Leopold, D. A., & Logothetis, N. K. (1999). Multistable phenomena: Changing views in perception. *Trends in Cognitive Sciences*, 3(7), 254–264.
- Levelt, W. J. M. (1967). Note on the distribution of dominance times in binocular rivalry. *British Journal of Psychology*, 58, 143–145.
- Levelt, W. J. M. (1968). *On binocular rivalry*. The Hague, Netherlands: Mouton.
- Logothetis, N. K., Leopold, D. A., & Sheinberg, D. L. (1996). What is rivaling during binocular rivalry? *Nature*, 380, 621–624.
- Lumer, E. D., Friston, K. J., & Rees, G. (1998). Neural correlates of perceptual rivalry in the human brain. *Science*, 280, 1930–1934.
- Maier, A., Logothetis, N. K., & Leopold, D. A. (2005). Global competition dictates local suppression in pattern rivalry. *Journal of Vision*, 5, 668–677.
- Mapperson, B., & Lovegrove, W. (1984). The dependence of monocular rivalry on spatial frequency: Some interaction variables. *Perception*, 13, 141–151.
- Meng, M., & Tong, F. (2004). Can attention selectively bias bistable perception? Differences between binocular rivalry and ambiguous figures. *Journal of Vision*, 4, 539–551.
- Necker, L. A. (1832). Observations on some remarkable optical phenomena seen in Switzerland; and on an optical phenomenon which occurs on viewing a figure of a crystal or geometrical solid. *The London and Edinburgh Philosophical Magazine and Journal of Science*, 1(5), 329–337.
- Nguyen, V. A., Freeman, A. W., & Alais, D. (2003). Increasing depth of binocular rivalry suppression along two visual pathways. *Vision Research*, 43, 2003–2008.
- Norman, H. F., Norman, J. F., & Bilotta, J. (2000). The temporal course of suppression during binocular rivalry. *Perception*, 29, 831–841.
- O'Shea, R. P. (1998). Effects of orientation and spatial frequency on monocular and binocular rivalry. In N. Kasabov, R. Kozma, K. Ko, R. O'Shea, G. Coghill, & T. Gedeon (Eds.), *Progress in connectionist-based information systems: Proceedings of the 1997 international conference on neural information processing and intelligent information systems* (pp. 67–70). Singapore: Springer Verlag.
- O'Shea, R. P. (2006). Control of binocular rivalry and of pattern alternation. *Australian Journal of Psychology*, 58(Suppl.), 87 [Abstract].
- O'Shea, R. P., Alais, D., & Parker, A. (2005). The depth of monocular-rivalry suppression. *Australian Journal of Psychology*, 57(Suppl.), 66 [Abstract].
- O'Shea, R. P., Alais, D., & Parker, A. (2006). The depth of suppression during monocular rivalry and binocular rivalry. *Perception*, 35(Suppl.), 9 [Abstract].
- O'Shea, R. P., & La Rooy, D. J. (2004). Monocular and binocular rivalry with complex images. *Australian Journal of Psychology*, 56(Suppl.), 130 [Abstract].
- O'Shea, R. P., Sims, A. J. H., & Govan, D. G. (1997). The effect of spatial frequency and field size on the spread of exclusive visibility in binocular rivalry. *Vision Research*, 37, 175–183.
- O'Shea, R. P., & Wishart, B. (2007). Contrast enhances binocular rivalry and retards monocular rivalry. *Australian Journal of Psychology*, 59(Suppl.), 51–52 [Abstract].
- Papathomas, T. V., Kovács, I., Fehér, Á., & Julesz, B. (1999). Visual dilemmas: Competition between the eyes and between percepts in binocular rivalry. In Z. Pylyshyn & E. LePore (Eds.), *What is cognitive science?* (pp 263–294). Malden MA: Basil Blackwell.
- Pearson, J., & Clifford, C. W. G. (2005). When your brain decides what you see: Grouping across monocular, binocular, and stimulus rivalry. *Psychological Science*, 16, 516–519.
- Pearson, J., Tadin, D., & Blake, R. (2007). The effects of transcranial magnetic stimulation on visual rivalry. *Journal of Vision*, 7, 1–11.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10, 437–442.
- 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.
- Rauschecker, J. P., Campbell, F. W., & Atkinson, J. (1973). Colour opponent neurones in the human visual system. *Nature*, 245, 42–43.
- Rubin, E. (1915). *Visuell Wahrgenommene Figuren*. Copenhagen: Gyldenalske Boghandel.
- Rubin, N. (2003). Binocular rivalry and perceptual multi-stability. *Trends in Neurosciences*, 26, 289–291.
- Ruderman, D. L., & Bialek, W. (1994). Statistics of natural images: Scaling in the woods. *Physical Review Letters*, 73, 814–817.
- Sclar, G., Maunsell, J. H. R., & Lennie, P. (1990). Coding of image contrast in central visual pathways of the macaque monkey. *Vision Research*, 30, 1–10.
- 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.
- Shimojo, S., & Nakayama, K. (1994). Interocularly unpaired zones escape local binocular matching. *Vision Research*, 34, 1875–1881.
- Sindermann, F., & Lüddecke, H. (1972). Monocular analogues to binocular contour rivalry. *Vision Research*, 12, 763–772.
- Thomas, J. (1978). Binocular rivalry: The effects of orientation and pattern color arrangement. *Perception & Psychophysics*, 23, 360–362.
- Tong, F., Nakayama, K., Vaughan, J. T., & Kanwisher, N. (1998). Binocular rivalry and visual awareness in human extrastriate cortex. *Neuron*, 21, 753–759.
- van Boxtel, J. J., Knapen, T., van Ee, R., & Erkelens, C. J. (2006). Exploring the parameter space of stimulus rivalry. *Perception*, 35(Suppl.), 32.
- van Boxtel, J. J. A., van Ee, R., & Erkelens, C. J. (2007). Dichoptic masking and binocular rivalry share common perceptual dynamics. *Journal of Vision*, 7(14, 3), 1–11.
- van Dam, L. C. J., & van Ee, R. (2006). Retinal image shifts, but not eye movements per se, cause alternations in awareness during binocular rivalry. *Journal of Vision*, 6, 1172–1179.
- Wade, N. J. (1975). Monocular and binocular rivalry between contours. *Perception*, 4, 85–95.
- Wade, N. J. (1996). Descriptions of visual phenomena from Aristotle to Wheatstone. *Perception*, 25, 1137–1175.
- Wales, R., & Fox, R. (1970). Increment detection thresholds during binocular rivalry suppression. *Perception & Psychophysics*, 8, 90–94.
- Wallach, H., & O'Connell, D. N. (1953). The kinetic depth effect. *Journal of Experimental Psychology*, 45, 205–217.
- Watson, A. B., & Pelli, D. G. (1983). QUEST: A Bayesian adaptive psychometric method. *Perception & Psychophysics*, 33, 113–120.
- Wheatstone, C. (1838). Contributions to the physiology of vision—Part the first. On some remarkable, and hitherto unobserved, phenomena of binocular vision. *Philosophical Transactions of the Royal Society of London*, 128, 371–394.
- 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.
- Wilson, H. R., Blake, R., & Lee, S. H. (2001). Dynamics of traveling waves in visual perception. *Nature*, 412, 907–910.
- Wilson, H. R., Krupa, B., & Wilkinson, F. (2000). Dynamics of perceptual oscillations in form vision. *Nature Neuroscience*, 3, 170–176.
- Yoshor, D., Bosking, W. H., Ghose, G. M., & Maunsell, J. H. (2007). Receptive fields in human visual cortex mapped with surface electrodes. *Cerebral Cortex*, 17, 2293–2302.