

# Monocular rivalry exhibits three hallmarks of binocular rivalry

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## **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 and colour of the images. Second, we show that the distribution of dominance periods during monocular rivalry has a gamma shape and is stochastic. 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. 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.

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

We experience the visual world in astounding richness and detail, yet our knowledge of how these 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, In press) 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 (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 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. There are at least three general similarities between the two forms of rivalry that suggest

commonality. First, the basic phenomenology is similar in that both involve periods of alternating dominance. Second, 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). Third, the two forms of rivalry can influence each other, tending to synchronize 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 between the two rivalries. 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 alphabetic letters. Galton (1907) observed rivalry between pictures of different faces. Yet, with the possible exception of a study by Boutet and Chaudhuri (2001), 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, Logothetis, & Leopold, 2005). In Experiments 1 and 2, we show that monocular rivalry occurs between complex pictures of faces and houses.

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 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 independent.

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 (indicative of suppression of the whole eye) (e.g., Fox & McIntyre, 1967; Nguyen, Freeman, & Alais, 2003; Norman,

Norman, & Bilotta, 1999; 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 in abstract form (O'Shea, Alais, & Parker, 2005; O'Shea, Alais, & Parker, 2006; O'Shea & La Rooy, 2004).

## **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 deg. 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 to 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 one-minute trials, and asking them to track their perceptual alternations using key presses. We used images of faces and houses. Moreover, we explicitly compared monocular rivalry with binocular rivalry for identical stimuli over a range of stimulus sizes.

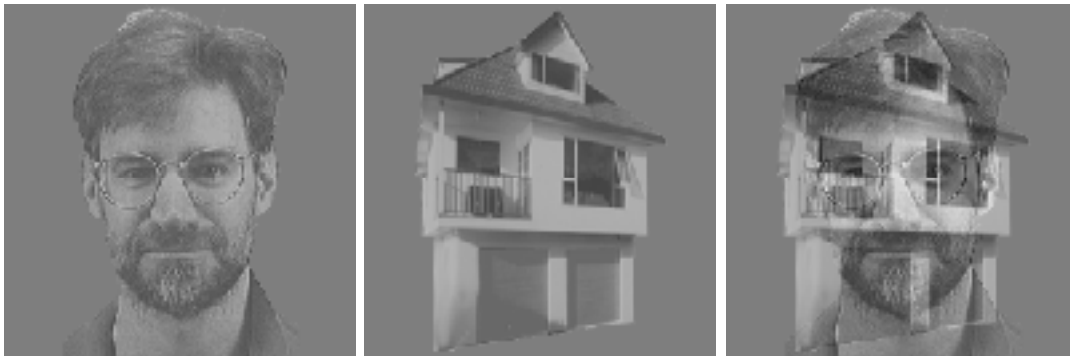
## **Method**

### *Observers*

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

### *Stimuli and Apparatus*

Stimuli were digitized photographs of ROS's face and part of his house on plain backgrounds as shown in Figure 1. Stimuli were 0.77, 1.54, 3.08, 6.16, and 12.32 degrees of visual angle square. They were surrounded by two bright vertical bars, each 0.5 deg wide, as tall as the stimulus, and separated from the edge of the stimulus by 0.5 deg. Stimuli were displayed on two identical Sony Trinitron colour monitors with a spatial resolution of 1152 x 870 pixels and a frame rate of 75 Hz. Each eye of the observer viewed only one monitor from a distance of 1 meter through a mirror stereoscope. The experiment was controlled by a Power Macintosh 8600 computer running specially written software (Handley, Bevin, & O'Shea, 2005).



**Figure 1.** The left and middle panels show the two images separately. The right panel shows the two images combined, as they would appear during a monocular-rivalry trial. Readers who can free fuse the left and centre images can experience binocular rivalry. Any reader can experience monocular rivalry by staring at the right image. After a short time, ten seconds or so, readers will notice fluctuations in the relative clarity of the two images.

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/sq m, and that of the vertical bars was 30 cd/sq m. Otherwise the screens were dark (0.2 cd/sq m). The standard deviation of the luminances in the two images was 2.45 cd/sq m for the face and 3.44 cd/sq m for the house.

### *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.

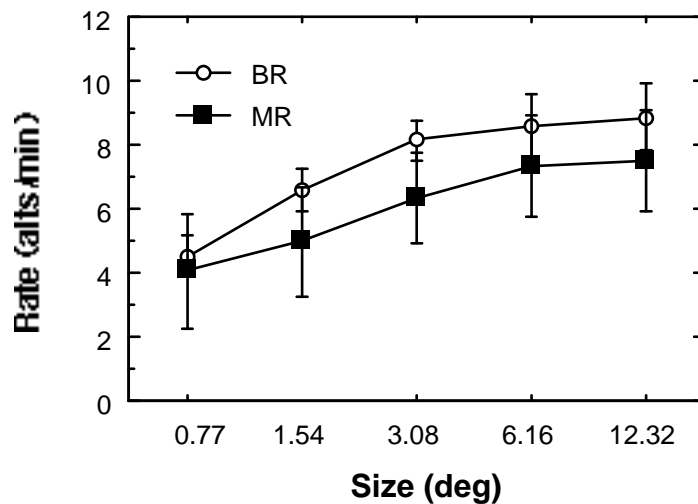
Each trial lasted for 60 seconds and was followed by an inter-trial interval of at least 45 seconds. Observers reported their perception of either the face or house by pressing the 'Z' or '?' keys respectively. They pressed a key whenever, and for as long as, a particular stimulus exceeded a criterion 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 twice as clear as the other, or was exclusively visible over at least two-thirds of the field.

### **Results and Discussion**

All observers readily tracked with key presses the fluctuations in 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 recently by Wilson, Blake, and Lee (2001). Observers also reported similar composites during monocular rivalry, although these were rarer than in binocular rivalry.

To quantify rivalry, we counted the number of times each key was pressed to obtain a *rate* measure of rivalry. We analysed this with a three-factor, within-subjects ANOVA (the factors were type of rivalry, size, and image reported). The only significant factor was size,  $F(4, 12) = 12.29, p < .001$ , such that rate increased with size of the images (see Figure 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, Sims, & Govan, 1997). Critically, there was no difference between monocular and binocular rivalry in the shape of the function relating size to rate. This was also true for each observer. For two observers, the overall rate of monocular rivalry was less than that of binocular rivalry, for one observer there was no difference, and for one observer the overall rate of monocular rivalry was greater than that of binocular rivalry. These differences probably arise from differences in the application of response criteria, but they nonetheless indicate a degree of consistency between monocular and binocular rivalry.



**Figure 2.** Plot of binocular-rivalry (binocular rivalry) and monocular-rivalry (monocular rivalry) rate (the number of episodes of dominance of each image per minute) against size of the images. The vertical bars show  $\pm 1$  standard error of the mean.

The increase in the rate of alternations with size for both sorts of rivalries is consistent with the idea that rivalry between complex stimuli involves higher level visual areas such as the inferotemporal cortex (Alais & Melcher, 2007; Sheinberg & Logothetis, 1997). Not only are neurons in these areas 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 and would therefore be preferentially activated by the larger rival stimuli (Gross, Bender, & Rocha-Miranda, 1969; Yoshor, Bosking, Ghose, & Maunsell, 2007).

A potentially important factor in this experiment is the change in spatial



frequency content that occurs when images are scaled up or down in size. In the case of pictures, increasing the image size lengthens the period of the spatial modulations, lowering the spatial frequency content of the images in direct proportion to the scale factor. This can be contrasted with grating stimuli, where a change in size would normally be achieved by keeping the spatial frequency constant and simply showing more cycles in the image. The image sizes used in Experiment 1 varied over a four-octave range. Since it has been shown that monocular rivalry is usually strongest at low spatial frequencies (Kitterle & Thomas, 1980; Mapperson & Lovegrove, 1984; O'Shea, 1998), the effect of increasing alternation rate with larger images shown in Figure 2 might be related to the lowering of spatial frequency. However, all these studies used grating stimuli, which contain a single spatial frequency, whereas our images are complex with a very broad spatial frequency spectrum. Increasing the size of broadband images extends the spatial spectrum at the lower end, but they remain broadband over a very large spatial range and this makes comparison with grating studies difficult.

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 Figure 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 rivalling images.

## **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 study 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 used grating stimuli and found that colour affected monocular but not binocular rivalry (Kitterle & Thomas, 1980). In Experiment 2, we also examine the role of colour on

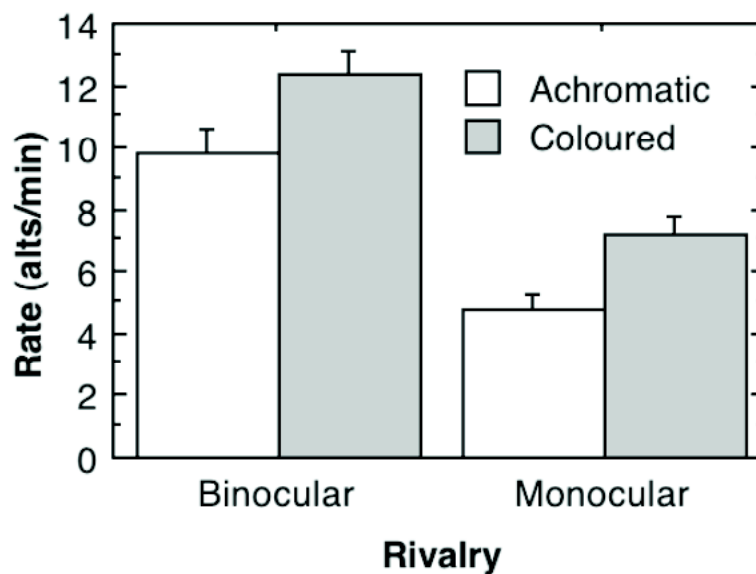
binocular and monocular rivalry but extend it to include complex broadband images.

### 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, Nakayama, Vaughan, and Kanwisher (1998) was used, and one of the male observers from Experiment 1 did not participate. All stimuli were 6.16 deg square; Pixel luminances in Tong et al.'s face and house had standard deviations of 3.22 cd/sq m and 4.98 cd/sq m 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.

### Results and Discussion

Again we analysed rivalry rate with a four-factor, within-subjects ANOVA (the factors were type of rivalry, colour, stimulus set, and image reported). The only significant factor was colour,  $F(1, 2) = 19.87$ ,  $p < .05$ , such that the alternation rate was greater with coloured images than with achromatic images (see Figure 3). All observers showed this pattern of results. The difference between the rates for monocular and binocular rivalry was not significant,  $F(1, 2) = 5.19$ ,  $p > .15$ , despite the appearance of Figure 3. This is because two observers had greater rates for binocular than for monocular rivalry whereas one (ROS) did not. This difference probably arises from differences in response criteria.



**Figure 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  $\pm 1$  standard error of the mean.

Figure 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,  $F = 0.03$ ). 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, as high binocular rivalry rates would leave little capacity to be further enhanced by colour.

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 colour differences 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, as 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.

### **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.

## **Method**

### **Observers**

Two of the authors acted as observers, ROS and AP. AP was 25.99 years old. Both observers have normal vision.

### **Apparatus**

The computer controlling this experiment was a Macintosh G4, running MatLab 5.2 scripts that used the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Stimuli were displayed on a 19-inch XYZ monitor showing 1024 x 768 pixels at a 75 Hz vertical refresh rate. Stimuli were shown one on each side of the screen and viewed via a mirror stereoscope at a viewing distance of 1999 cm.

### **Visual Stimuli**

Stimuli were two orthogonal square-wave gratings, one red (CIE???) and the other green (CIE???), 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  $4.6^\circ$ . Gratings had a mean luminance of 19.99 cd/sq m; the background had a luminance of 19.99 cd/sq m. 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.

### **Procedure**

For both binocular and monocular rivalry, the observer's task was similar to that in Experiment 1: to track episodes of perceptual dominance of one and the other stimuli by pressing keys on the computer keyboard. There were x trials lasting 5 minutes for each viewing condition. Viewing condition was alternated for each observer over trials; each observer started with a different condition [if true!].

### **Results and Discussion**

We analysed the records of rivalry in two ways. First, we plotted distributions of dominance times to which we fitted Gamma functions. Specifically, we divided each

dominance duration by the mean for that observer and that condition, we constructed the distribution, and we fit Gamma functions using a weighted least-squares algorithm. 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.

Figure 4 shows the distributions of dominance times separately for monocular and binocular rivalry for each observer. All four plots exhibit the classic Gamma distribution shape, rather like a positively skewed normal distribution; the smooth curves show the best fitting Gamma distribution function. The parameters of all four fits are remarkably similar, showing that monocular and binocular rivalry exhibit globally similar alternation dynamics. This is especially true for ROS, although for AP there was an over-representation of long dominance durations in monocular rivalry relative to binocular rivalry that is not well captured by the best-fitting Gamma distribution.

**Figure 4.** Distribution of dominance times for two observers for binocular rivalry (top row) and for monocular rivalry (bottom row). The continuous plot shows that best-fitting Gamma distribution fitted to the data. The dominance durations were binned into 150 ms intervals and were normalised to the mean duration.

Figure 5 shows the autocorrelation analyses for binocular and monocular rivalry. The correlation is arbitrarily 1.0 when there is no lag. Similar to binocular rivalry (Levelt, 1968), that there no tendency for a given dominance duration to be related to the previous dominance duration, or to dominance durations several phases earlier.. Overall, for all of the four autocorrelation analyses, none of the correlations at any phase lag (from 1 to 12) were statistically significant.

**Figure 5.** Results of the autocorrelation analysis for two observers for binocular rivalry (top row) and for monocular rivalry (bottom row). Apart from the arbitrarily perfect autocorrelation when the signal was not lagged, there were no statistically significant deviations from zero. 95% confidence intervals around the correlation at each non-zero lag included a correlation of zero.

#### **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), although for higher-level stimuli such as faces and complex global motions and forms, sensitivity is reduced to about 30% of the dominance level (Alais & Melcher, 2007; Alais & Parker, 2006).

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 rivalling 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. We used red and green orthogonal gratings oriented  $\pm 45^\circ$  to vertical and we briefly and smoothly pulsed the luminance 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.

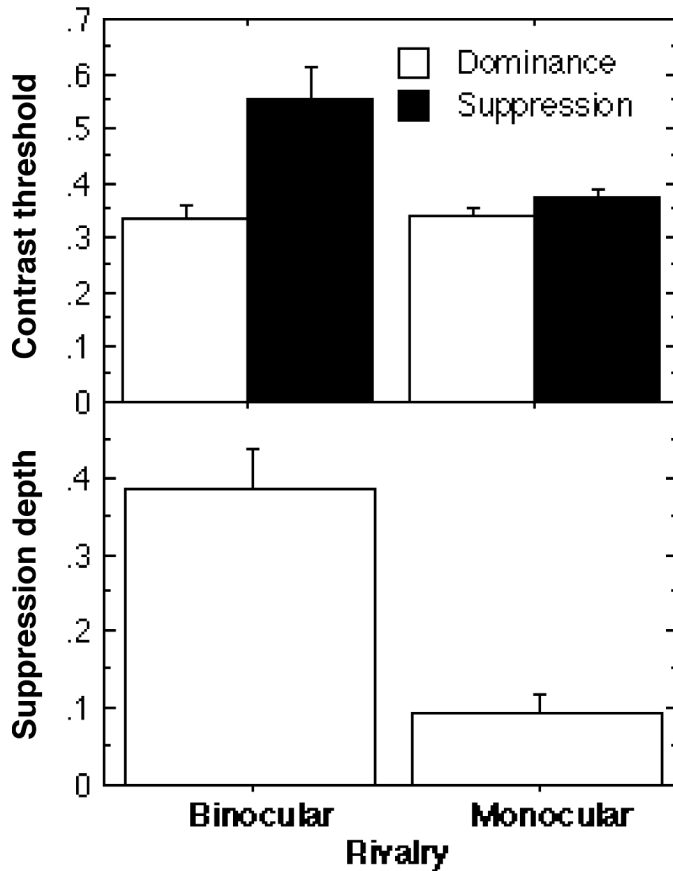
#### **Method**

The Method was similar to that of Experiment 3 with the following exceptions. Two new observers volunteered for the experiment for a total of four, one of us (DA), an experienced observer aged 29.99, and JT, an inexperienced observer naive to the purposes of the experiment aged 19.99. All observers had normal vision. Instead of tracking monocular or binocular rivalry observers pressed a key either whenever the red or the green grating was dominant. 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 1999 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 counterbalanced over sessions and over observers.

### **Results and Discussion**

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 Figure 6. Suppression depths are shown in the lower panel of Figure 6. Suppression depth is calculated by subtracting from unity the ratio of the dominance threshold to the suppression threshold. A suppression depth of zero, complete absence of suppression, would occur if suppression and dominance thresholds were equal. Suppression depths approach unity, complete 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., 1999; Wales & Fox, 1970); the lower panel of Figure 6 shows that the suppression depth we measured for binocular rivalry is consistent with this value. By contrast, suppression depth for monocular rivalry is much weaker at around 0.10. Although this value is significantly greater than zero,  $t(3) = 4.67, p < .05$ , it is several times shallower than suppression depth for binocular rivalry.



**Figure 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 are expressed as suppression depth. Error bars show 1 standard error of the mean.

### 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 Experiment 3, we illustrated the similar temporal dynamics of the two sorts of rivalry, showing that both exhibit a gamma distribution of dominance durations 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. These similarities between monocular and binocular rivalry are consistent with the idea



that the their underlying processes involve common neural mechanisms (cf. Leopold & Logothetis, 1999; O'Shea, 1998; Papatomas, Kovács, Fehér, & Julesz, 1999).

Although the conclusion that monocular and binocular rivalry share common processes has appeal, there are alternative explanations that need to be considered and certain notable differences between the two phenomena 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 has been 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 will build up afterimages that would tend to cancel visibility of both. If an eye movement were made in the direction 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. However, 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 theory. 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 & Lüddeke, 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, the explanation requires that the images be simple, repetitive stimuli such as gratings, 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.

Although there are striking similarities between monocular and binocular rivalry, there are two notable differences. We tentatively propose that these differences arise because binocular rivalry involves interactions at early levels of the visual system and monocular rivalry involves interactions at high levels of the visual system. Although the name of the phenomenon suggests a low-level process it is simply because it is misleadingly labelled, prompting Maier et al. (2005) to propose that monocular rivalry would be more appropriately called “pattern rivalry”. More importantly, Maier et al. argue that because monocular rivalry is not a result of local processing conflict it is more likely to be due to a higher-level process involving global interpretation of the probable nature of the stimulus.

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. If the same suppressive mechanism were to underlie both types of rivalry, its gain would need to be reduced during monocular compared with binocular rivalry and the reasons why this would be so are not clear.

If, however, monocular rivalry involves similar neural interactions to binocular rivalry at a higher level, we might expect it to resemble such higher-level rivalries. Intriguingly, although suppression depth in monocular rivalry is very shallow, it is similar in magnitude to suppression measurements that we recently made (O’Shea, Bhardwaj, Alais, & Parker, 2007) for a higher-level form of binocular rivalry known as *stimulus rivalry*, or *flicker-and-swap rivalry*. Invented 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 which endure for long enough to incorporate several interocular stimulus swaps. Logothetis et al. explained this in terms of rivalry process acting 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.

If flicker-and-swap rivalry occurs at a high level of the visual system, we can ask whether monocular rivalry also occurs at a similar level. Apart from the similarities in the level of suppression depth, there are three other similarities between the phenomena. 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.

The second major difference between monocular and binocular rivalry is that they are affected oppositely by contrast (O'Shea & Wishart, In press). 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. However, if monocular rivalry is a high-level process as we have argued, then there is no reason why it should become more vigorous with contrast because responses of high-level neurons tend towards contrast invariance. That is, their contrast-response functions are much steeper initially with a longer saturated plateau. Sclar, Maunsell, and Lennie (1990) compared contrast-response functions from macaque lateral geniculate, primary visual cortex, and middle temporal visual area (MT) and found they steepened along these successive stages of processing. 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, Vp, V4/V8 and LO/pFs. Because of this tendency towards contrast invariance, there is no reason to expect that a high-level monocular rivalry process should behave more vigorously at high contrast.

What is less obvious is why monocular rivalry would be more vigorous at *low* contrast. One reason that may explain this is that the global interpretative processes implied by Maier et al.'s (2005) work on monocular rivalry, and more generally by Leopold and Logothetis (1999), may be less stable at low contrast. That is, as a consequence of reduced signal and because of noise and stochastic fluctuations, there would be considerable uncertainty as to whether a monocular rivalry stimulus should be interpreted as one or two objects. To take a real-world example shown in Maier et al. (2005), the bottom of a pond might be visible transparently even though the surface of the pond may reflect the image of a tree. In this case, both aspects of the visual scene are imaged at the same retinal location. High contrast would facilitate an interpretation such as transparency because both images would be reliably signaled with little ambiguity. Low contrast, however, would render the scene hard to interpret as both interpretations would be potentially valid but the distinction hard to make with poorly visible and unreliable stimuli. Under these conditions, an interpretative process with bistable behaviour appears to assume more prominence and perceptual alternations result. At high contrast, presumably, image interpretations can be made far more definitively and bistability is less likely to be observed.

### **Conclusion**

In summary, we have shown 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 partially mediated by a common high-level mechanism for resolving ambiguity (Leopold & Logothetis, 1999; Maier et al., 2005), although this process cannot be the primary driver 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, whereas it is more likely to be the primary driver of monocular rivalry.

## **Figure legends**

Figure 1:

Figure 2

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