

# Binocular rivalry: Spreading dominance through complex images

**Derek H. Arnold**

School of Psychology, The University of Queensland,  
Brisbane, Australia



**Bridie James**

School of Psychology, The University of Queensland,  
Brisbane, Australia



**Warrick Roseboom**

School of Psychology, The University of Queensland,  
Brisbane, Australia



When different images are presented to the two eyes, each can intermittently disappear, leaving the other to dominate perception. This is called binocular rivalry. When using radial gratings, focal contrast increments can trigger a traveling wave of perceptual dominance change, originating at the locus of the contrast increment and circling the stimulus. This has been linked to a sweep of activity through V1 that can be traced via fMRI. The dominance of more complex images, like human faces, has been linked to higher level processing structures characterized by more holistic object centered properties. We therefore decided to assess how dominance would spread through more complex images. Using Kanisza squares and human faces we found that dominance tended to spread gradually away from the locus of the contrast increment, often along real or illusory contours. We also found that perceptual dominance was slow to spread between facial regions encoded by different monocular channels. These data are consistent with low-level monocular mechanisms, like those found in V1, playing a determinant role in the spread of perceptual dominance through complex images during binocular rivalry.

Keywords: binocular rivalry, binocular vision, visual awareness

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## Introduction

Contemporary consensus holds that binocular rivalry (BR) is shaped by activity in multiple structures located at different levels of the human visual hierarchy (Blake & Logothetis, 2002; Haynes, Deichmann, & Rees, 2005; Lee & Blake, 1999; Tong & Engel, 2001; Watson, Pearson, & Clifford, 2004; Wunderlich, Schneider, & Kastner, 2005). Evidence for this includes findings from human brain imaging and monkey electrophysiology, which have implicated both high- (Leopold & Logothetis, 1996; Logothetis & Schall, 1989) and low- (Haynes et al., 2005; Polonsky, Blake, & Heeger, 2000; Tong & Engel, 2001; Wilson, Blake, & Lee, 2001) level structures as being integral to BR.

There is also behavioral evidence suggesting the involvement of multiple mechanisms. For instance, if simple conflicting images, like gratings, are too large they tend not to dominate perception exclusively. Instead, patches of both rival images are seen (Blake, O'Shea, & Mueller, 1992). More complex images, like human faces, are more resistant to such effects (Alais & Melcher, 2007).

One method that has proven informative in this context involves triggering a change of perceptual dominance via a sudden focal contrast increment within a suppressed radial

grating. The contrast increment instigates an almost instantaneous perceptual dominance change at the locus of the contrast increment (Knapen, van Ee, & Blake, 2007; Wilson et al., 2001; see also Blake, Westendorf, & Overton, 1980). Changes then sweep gradually away from the position of the contrast increment, often circling the stimulus. These perceptual changes have been linked to sweeps of activity that can be traced through V1 via fMRI (Lee, Blake, & Heeger, 2005, 2007; Wilson et al., 2001).

These data tie V1 activity to the spread of perceptual dominance through simple radial gratings. Thus far this method has only been employed using simple radial gratings. Given the physiological and behavioral evidence suggesting a link between perceptual dominance of more complex images and higher level brain structures, we decided to assess how triggered dominance changes would spread through these types of image.

## General methods

### Observers

Each of the experiments reported was completed by two of the authors and by three additional observers who were

naive as to the purpose of the study. All had normal, or corrected to normal, visual acuity.

## Apparatus

Visual stimuli were generated using Matlab software to drive a Cambridge Research Systems VSG2/3F stimulus generator and were displayed on a gamma-corrected 21" Samsung SyncMaster 1100p+ monitor (1024 × 768 resolution; 120-Hz refresh rate). All stimuli were viewed, from a distance of ~78 cm, through an individually adjusted mirror stereoscope. The display background was gray ( $x = 0.28$ ,  $y = 0.28$ ,  $Y = 86$ ). The observer's head was supported by a chin rest. Responses were recorded via a Cambridge Research Systems CB6 response box.

## Experiment 1

### Methods

Stimuli consisted of groups of 4 gray pacman-like elements (see [Figures 1a](#) and [1b](#)) subtending 1.1 degrees of visual angle (dva) at the retina and centered 1.1 dva from the center of the visible display. These were presented to the observer's non-dominant eyes, determined

via a simple pointing task prior to the experiment. Elements were arranged to form an illusory Kanizsa (1979) square or were rotated to form a non-Kanizsa configuration (see [Figures 1a](#) and [1b](#)).

Four square patches of white noise (diameter subtending 1.1 dva, element sizes subtending 0.15 dva) were presented to the dominant eye. The positions of the noise patches corresponded with that of the four stimulus elements shown to the non-dominant eye. Both the noise patches and stimulus elements were surrounded by white rings (diameter 4.17 dva, line width 0.15 dva), which served as fusion locks during the experiment. To aid convergence, we provided a small white ( $x = 0.28$ ,  $y = 0.28$ ,  $Y = 86$ ) fixation point (diameter subtending 0.15 dva) in the middle of the stimuli presented to each eye.

On each trial observers were instructed to wait, if necessary, until no part of any of the four stimulus elements were visible. They pressed a button when this was achieved. In test runs of trials, this triggered a contrast increment (from 0.05 to 0.17 Michelson contrast relative to background) of one of the four stimulus elements. Other elements remained unchanged (Michelson contrast 0.05). The position of the cued element in test runs of trials was determined at random on a trial-by-trial basis. In control runs of trials, there was no contrast increment, allowing us to estimate times for spontaneous recovery from suppression.

After observers had reported that stimulus elements were invisible, they pressed one of 4 buttons to mark the

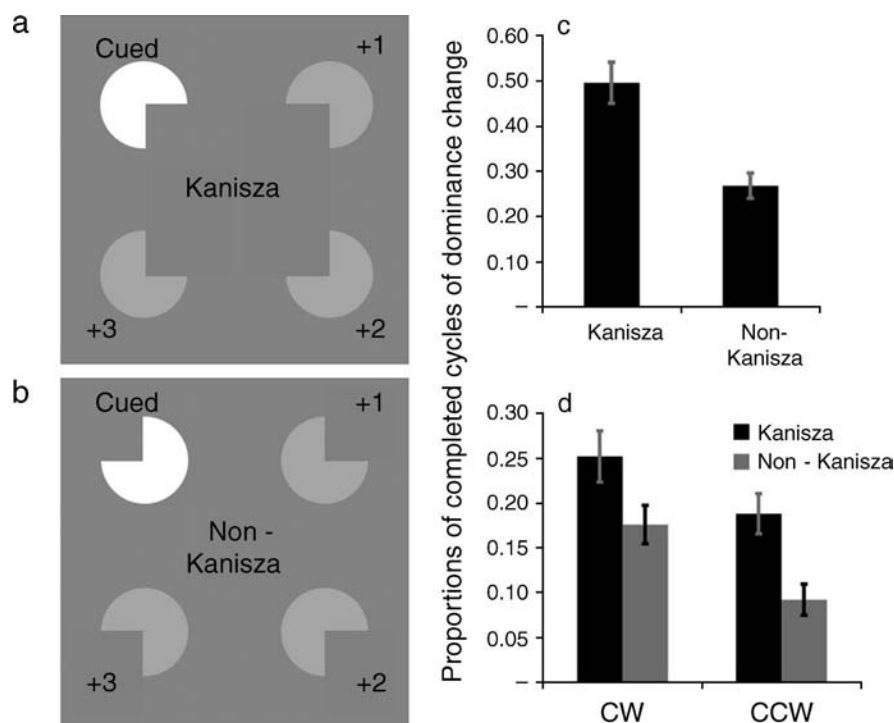


Figure 1. (a, b) Depictions of stimuli from [Experiment 1](#). (c) Bar plot showing proportions of completed dominance cycles, beginning at the cued element and circling clockwise or counterclockwise around the stimulus. Error bars show  $\pm 1$  SEM. (d) As in (c), but data are shown separately for clockwise (CW) and counterclockwise cycles (CCW).

first instance that any part of each noise mask had begun to fade from view. We took these times as estimates of perceptual dominance change at that location. Each trial persisted until observers had reported that all four noise masks had begun to fade from view, or until 10 s had elapsed since the observer had reported that all elements were suppressed from view.

Test runs of trials consisted of 25 presentations with elements arranged to form each of the two stimulus configurations. Each observer completed 2 test runs of trials. For each observer, this provided 50 estimates of the dynamics of perceptual dominance change following focal contrast increments for each stimulus configuration. Control runs of trials contained 25 trials wherein there was no focal contrast increment. Each observer completed two control run of trials.

## Results

For test runs of trials, on each trial we coded the four stimulus locations as cued (where the focal contrast increment occurred), +1, +2, and +3. The latter refer to element locations rotated clockwise from the cued element. As the position of the cued element was randomized from trial to trial, these positions were relative, not fixed. From each of these trials, we were able to extract estimates of the delay, post-cued element contrast increment, at which dominance changes began to occur at each of the 4 stimulus locations. We also recorded the order of dominance change across these four locations.

In [Figure 1c](#), we have depicted the proportion of trials, during test runs of trials, in which dominance changes began at the cued location and then cycled, in order, clockwise or counterclockwise around the stimulus. We refer to these as completed cycles of dominance change. Trials in which the order of dominance change was inconsistent with a cycle around the stimulus, or in which any element did not emerge from suppression during the 10-s stimulus presentation, were inconsistent with a completed cycle.

These data reveal two things. First, the cued element shaped the order in which elements emerged from suppression. Consider that there are two orders of dominance change consistent with a completed cycle (cued, +1, +2 then +3, and cued, +3, +2 then +1). Given that there are 4 stimulus elements, these orders could be expected to occur on 0.08 of trials if the order of emergence from suppression were at chance. Instead, the proportion of completed cycles for both the Kanisza ( $0.50 \pm 0.05$ , see [Figure 1c](#)) and non-Kanisza ( $0.27 \pm 0.03$ , see [Figure 1c](#)) configurations exceeded this value (Kanisza single sample  $t_4 = 9.09$ ,  $p = 0.001$ ; non-Kanisza single sample  $t_4 = 6.71$ ,  $p = 0.003$ ). From this, we can conclude that the cued element impacted on the order in which elements emerged from suppression.

The second thing these data reveal is that completed cycles of dominance change only happened at a level that can be considered above chance for the Kanisza configuration. To appreciate this, we must consider that the cued element almost invariably emerged from suppression first (on 99.4% of all trials). Given this limitation, there are only 6 possible subsequent orders in which the remaining 3 elements could emerge from suppression, so the chance level for a completed cycle subsequent to the emergence of the cued element is 33%. While the percentage of completed cycles for the Kanisza configuration exceeded this (single sample  $t_4 = 3.63$ ,  $p = 0.02$ ), the percentage for the non-Kanisza configuration did not ( $t_4 = -2.21$ ,  $p = 0.09$ ).

In [Figure 1d](#), we have depicted proportions of completed clockwise and counterclockwise cycles of dominance change during test runs of trials. As the reader will note, more clockwise cycles were observed. We would not like to place a great emphasis on this observation, as we cannot exclude the possibility that this was indicative of some form of response bias, although we think that this is unlikely. One reason for our skepticism is that the position of the cued element was determined at random on a trial-by-trial basis. A bias toward reporting a clockwise rotation would thus necessitate a remapping of motor responses on each trial. However, at this point we cannot provide any firm conclusions on this trend, but note that it would be interesting to compare these results with past behavioral and brain imaging data sets.

Average dominance change delays, post-cued element contrast increment, for each element in each stimulus configuration during test runs of trials, are depicted in [Figure 2](#). The first thing to note is that although we have only contrasted data from trials in which complete cycles of dominance change were observed, the spread of dominance away from the cued element was still faster through our Kanisza than our non-Kanisza configuration. This is evident from the significant linear interactions between element position and stimulus configuration (CW cycles: repeated measures  $F_{1,4} = 182$ ,  $p < 0.001$ ; CCW cycles: repeated  $F_{1,4} = 186$ ,  $p < 0.001$ ).

In [Figure 2](#), we have also depicted average dominance change delays during control runs of trials, wherein there was no focal contrast increment (thick shaded horizontal bars). These data provide estimates of spontaneous recovery from suppression for Kanisza and non-Kanisza stimulus elements. The average spontaneous recovery time for Kanisza elements was  $5.9 (\pm 0.7)$  s, whereas for non-Kanisza elements it was  $7.1 (\pm 0.6)$  ms. These times were slower relative to the last elements to emerge from suppression during completed cycles of dominance change during test runs of trials (see [Figure 2](#)). This was true for both Kanisza (last Kanisza  $3.8 \pm 0.2$  s, paired samples  $t_4 = 3.11$ ,  $p = 0.036$ ) and non-Kanisza (last non-Kanisza  $5.0 \pm 0.3$  s, paired samples  $t_4 = 3.10$ ,  $p = 0.036$ ) configurations.

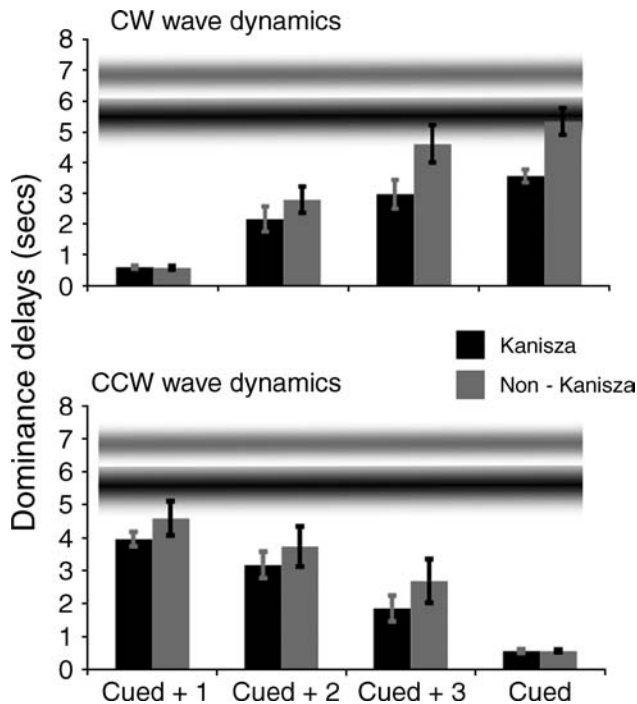


Figure 2. Bar plots showing average delays, post-focal contrast increment, for dominance changes at each of four element positions during completed cycles of dominance change. Data relate to completed clockwise (CW) and counterclockwise (CCW) cycles of dominance change for the Kanizsa and non-Kanizsa configurations. Error bars show  $\pm 1$  SEM between estimates for each of the 5 participants. Thick horizontal bars depict data from trials with no focal contrast increment, black for Kanizsa and gray for non-Kanizsa. These are centered on average delays and the shading depicts  $\pm 1$  SEM.

To facilitate comparison with existing data sets, we can estimate the propagation speed of dominance changes through our Kanizsa configuration during completed cycles of dominance change. The average delay between successive elements emerging from suppression was 1.26 s ( $\pm 0.16$  s). The Kanizsa square elements were separated by 1.5 dva and the eccentricity of the real and illusory contours linking elements was 0.93 dva. At this eccentricity, we can estimate that 1 dva will equate to  $\sim 1.2$  cm across the cortical surface (Horton & Hoyt, 1991). Thus the cortical propagation speed would be  $\sim 1.4$  cm/s.

## Discussion

In [Experiment 1](#), we used sets of four elements, arranged to form illusory Kanizsa squares or a non-Kanizsa configuration. At the start of each trial these were suppressed from awareness. In test runs of trials we found that, following a contrast increment of one of the four suppressed elements, an almost instantaneous dominance change was triggered for the cued element. For the Kanizsa configuration, dominance changes then tended

to cycle, clockwise or counterclockwise, around the stimulus. For the non-Kanizsa configuration, this was not true. Instead, following the emergence of the cued element from suppression, non-cued elements emerged from suppression in a random order.

A comparison of data obtained in test and control runs of trials is informative. The latter provide estimates of spontaneous recovery from suppression. Elements arranged to form Kanizsa squares spontaneously recovered from suppression *sooner* than did elements arranged to form non-Kanizas (see [Figure 2](#)). This effect may have been driven by mutual contrast facilitation along collinear contours, present in the Kanizsa configuration but not in the non-Kanizsa (Das & Gilbert, 1995; Field, Hayes, & Hess, 1993). However, these spontaneous recoveries were slower relative to the last elements to emerge from suppression during completed cycles of dominance change through corresponding configurations in test trials.

Our data are reminiscent of previous studies involving radial gratings. One of the most interesting observations from these experiments has been that dominance changes tend to spread along image contours (Maruya & Blake, 2009; Wilson et al., 2001), possibly driven by reciprocal interconnections that subserve contrast facilitation (Das & Gilbert, 1995; Field et al., 1993). Here too dominance changes appear to have spread along contours, thereby causing more frequent cycles of dominance change for the Kanizsa configuration, wherein the corners of the configuration are linked by contours, over the non-Kanizsa configuration. However, in our Kanizsa configuration some extent of each contour is illusory, implied rather than physical.

We were also able to estimate the speed at which dominance changes spread through our Kanizsa configuration during completed cycles of dominance change ( $\sim 1.2$  cm across the cortical surface). These data reveal that, while dominance changes tended to propagate around the stimulus, the propagation speed was slower than the traveling waves of dominance change observed in radial gratings ( $\sim 2.24$  cm/s, see Wilson et al., 2001). This may indicate that the propagation of dominance changes through these different stimuli is driven by distinct processes. Alternatively, it may simply show that a common mechanism brings about a more gradual propagation of dominance change along illusory contours.

Collinear contours were physically more proximate in our Kanizsa configuration than in the non-Kanizsa. In addition, non-collinear contours lay in-between collinear contours in the non-Kanizsa configuration but not in the Kanizsa. Given the propagation of signals along collinear contours (Das & Gilbert, 1995; Field et al., 1993), the combination of these factors probably contributed to the effectiveness of our Kanizsa configuration. This prompts a reasonable question; can any of our effects be attributed to a spread of dominance change along illusory contours?

Some recent complimentary evidence supports the efficacy of illusory contours (Maruya & Blake, 2009). In

this study triggered interocular suppression only spread across a discontinuity, or gap, if that discontinuity seemed to arise because of an occlusion. Thus suppression only spread across a gap when stimulus elements on either side of the gap were linked by an assumed, *unseen*, image contour. In our experiment, triggered dominance changes spread more rapidly and systematically through our Kanizsa configuration, wherein stimulus elements are linked by unseen illusory contours. We suggest this convergence of evidence points to the efficacy of illusory contours in spreading triggered dominance changes and interocular suppression (Maruya & Blake, 2009).

While some evidence links the perceptual experience of complex forms, like illusory Kanizsa squares, to V1 activity (Lee & Nguyen, 2001), other evidence has linked them to higher level structures (Mendola, Dale, Fischl, Liu, & Tootell, 1999). Given that such structures display more global response properties than do lower level structures, one might have expected dominance changes to spread more rapidly through these complex forms than they do within more simple forms, like radial gratings. One might even have expected to see some form of rapid perceptual pop-out of the entire stimulus configuration once its form became evident. One reason why this might not have occurred is that the global form of a Kanizsa square does not become evident until at least 3 of the 4 stimulus elements are visible. Until then, the illusory form is ambiguous. For example, it is equally probable that two elements on either side of the stimulus could be indicative of a square or of a rectangle. This degree of ambiguity could be eliminated by using more common, symmetrical, complex forms, like human faces.

## Experiment 2

### Methods

Details concerning [Experiment 2](#) are similar to those described for [Experiment 1](#), with the following exceptions.

We used an image depicting a female human face (width 4 dva, height 5.26 dva). We split this into 6 sections, segregated by gray lines ( $x = 0.28$ ,  $y = 0.28$ ,  $Y = 43$ ) subtending 0.15 dva in width (see [Figure 3](#)). We refer to each of the 6 sectors as the left eye (LE), upper nose (UN), right eye (RE), left cheek (LC), lower nose (LN), and right cheek (RC).

In the monocular condition, the sectored image of the female face was presented to the observer's non-dominant eyes and 6 patches of white noise, matched in size and position relative to the face sections, were shown to the observer's dominant eye. In the dichoptic condition, the outer 4 face sections and the central 2 noise patches were shown to the dominant eye and the other sections to the

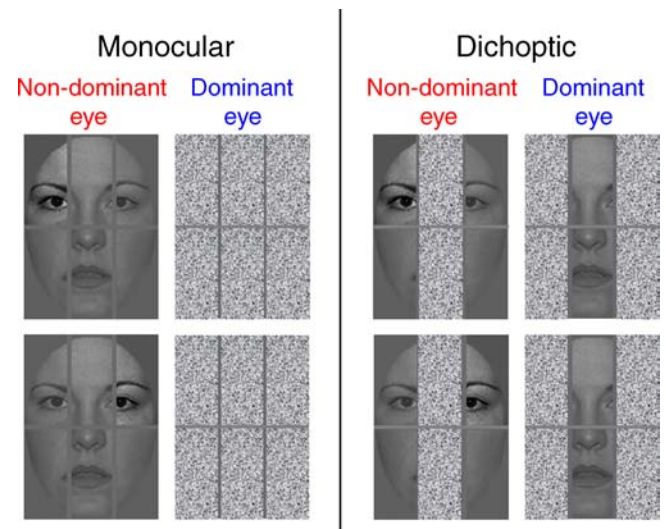


Figure 3. Depiction of stimuli used in [Experiment 2](#). Monocular and dichoptic conditions are shown.

non-dominant eye (see [Figure 3](#)). Stimuli in both eyes were surrounded by a red rectangle (height 6.2 dva, width 4.9 dva, line width 0.15 dva), which served as a fusion lock during the experiment. To aid convergence, we presented a small red fixation point (diameter subtending 0.15 dva) in the middle of the stimuli shown to each eye. In separate runs of trials, observers viewed configurations wherein facial regions were presented in an upright configuration (as depicted in [Figure 3](#)) or in an inverted configuration.

At the start of each presentation, observers were instructed to wait, if necessary, until no part of the face was visible and to then press a button. This triggered a contrast increment in either the LE or RE, taking the face from a Michelson contrast of 0.46 to 1.0. Observers then pressed one of 6 response buttons to indicate the first moment that each section of noise began to fade from view.

### Results

The symmetry of the human face allows us to summarize our data according to cued and non-cued facial sides. We did this by averaging, for each observer, data from the cued eye, upper nose, and the opposite eye across trials in which the left and right eyes were cued. These data, averaged across observers, are depicted in [Figure 4](#).

For both the MONO and DICH conditions in the upright facial configuration, perceptual dominance of the cued eye began to emerge almost immediately after its contrast was enhanced. In the MONO condition, perceptual dominance then spread gradually across the upper facial regions, reaching the other eye after  $\sim 2.5$  s. In the DICH

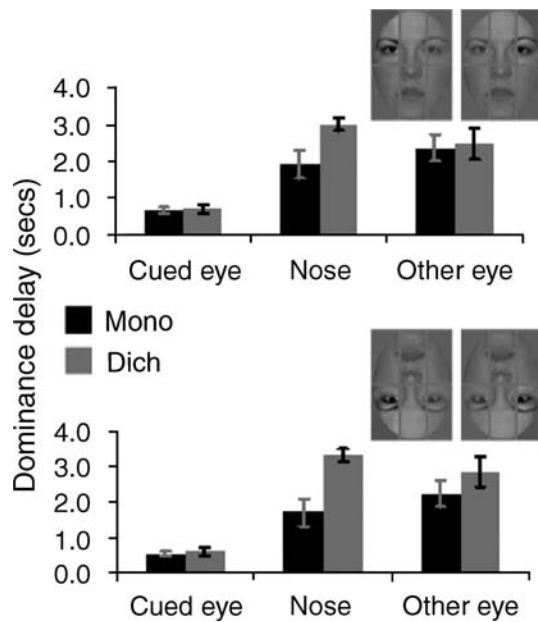


Figure 4. Bar plots depicting delays, post-contrast increments, at which perceptual dominance began to change in different facial regions. The plot above depicts data for upright faces, the plot below depicts data for inverted faces. Error bars show  $\pm 1$  SEM.

condition, perceptual dominance of the other eye began to emerge after an equivalent delay, but dominance of the intervening upper nose section was delayed, only emerging after  $\sim 3$  s. This represents a clear cost when facial image sections are located in a different monocular channel relative to the focal contrast increment. This brought about a significant interaction between facial region and presentation condition ( $F_{5,2} = 4.309$ ,  $p = 0.023$ ).

Data for the inverted facial configuration was qualitatively very similar. Dominance took  $\sim 2.18$  s to spread to the opposite eye in the MONO condition compared to  $\sim 2.5$  s for upright faces and  $\sim 2.71$  s in the DICH condition ( $\sim 2.5$  s for upright faces). The later condition was also marked by the same temporal cost for dominance to spread to a different monocular channel, with dominance of the upper nose in the DICH condition only emerging after  $\sim 3.24$  s ( $\sim 3$  s for upright faces). There was therefore a significant interaction between facial region and presentation condition for inverted faces ( $F_{5,2} = 4.932$ ,  $p = 0.014$ ).

## General discussion

Our data show that focal contrast increments trigger dominance changes that spread through complex images in a qualitatively similar fashion to the traveling waves of dominance change observed in simple radial gratings

(Knapen et al., 2007; Lee et al., 2005, 2007; Wilson et al., 2001). Data from Experiment 1 suggests that such changes tend to spread along image contours. Thus dominance changes are slower to spread around stimulus elements that are not joined via illusory contours. Data from Experiment 2 shows a clear cost, in terms of delayed dominance changes, for facial sections encoded by a different monocular channel relative to the cued facial region. This was true for both upright and inverted facial configurations.

There are striking similarities between these data and that obtained with simple gratings. Recently it has been shown that triggered dominance changes in grating stimuli tend to propagate along monocular channels (Kang, Heeger, & Blake, 2009). We have now observed the same pattern with human faces. This reinforces the importance of monocular channels in the context of binocular rivalry, even when rivalry involves complex images like the human face.

One possible criticism of our data is that we segregated the human face into distinct regions. The progression of dominance changes might have been perturbed as a result. We accept this obvious criticism on the basis that segregating our stimuli would have disrupted the natural contours of the human face. We believe that dominance changes usually propagate along image contours (see Kang et al., 2009; Wilson et al., 2001), thus this manipulation probably somewhat disrupted the spread of perceptual dominance change.

While we split our facial stimuli into regions, these images still clearly represented human faces. This was apparent to all observers as soon as either eye became perceptually dominant. Presumably activity in high-level structures of the human visual system was, at least in part, responsible for this recognition (Kanwisher, McDermott, & Chun, 1997). However, despite the global characteristics of activity at these levels of processing, this link does not appear to have facilitated the spread of perceptual dominance through our stimuli over that which has previously been reported for simple radial gratings (Knapen et al., 2007; Lee et al., 2005, 2007; Wilson et al., 2001). Rather, there was a clear cost when a part of the facial image was located in the opposite eye relative to the cued facial section (see Figure 4). These traits are more characteristic of activity in the primary visual cortex than they are with activity in higher level brain structures.

We do not believe these observations are in conflict with the extensive behavioral (Alais & Melcher, 2007; Dorrenhaus, 1975; Logothetis, Leopold, & Sheinberg, 1996) and physiological (Leopold & Logothetis, 1996; Logothetis & Schall, 1989) evidences pointing to the importance of higher level brain structures in binocular rivalry. We take our data to suggest that the role of these structures is more likely to be in their ability to modulate activity in lower level structures, rather than in their being directly responsible for determining perceptual dominance. For instance, higher level brain structures may

increase the probability of facial images being seen as a coherent whole, rather than becoming perceptually fragmented (Alais & Melcher, 2007), because of a feedback process that modulates activity in monocular channels (also see Watson et al., 2004). The propagation of triggered dominance changes may therefore depend on the dynamics of processing interactions at monocular processing stages, while the probability of perceptual dominance could still be shaped by higher level analyses.

Our data add to the considerable body of research concerning the spread of perceptual dominance changes during binocular rivalry. In radial gratings, this process can trigger a rapid sweep of perceptual dominance change, originating and finishing at the site of the contrast increment (Lee et al., 2005, 2007; Wilson et al., 2001). Our data show that somewhat analogous situations can be observed in complex images. There are, however, important differences. For instance, the spread of triggered dominance changes in our Kanisza stimuli was slower than the traveling waves of dominance change in radial gratings (Wilson et al., 2001). In addition, in radial gratings the spread of triggered dominance changes can be disrupted by stimulus gaps, whereas here dominance changes seem to spread across gaps, possibly propagating slowly along illusory contours (see Maruya & Blake, 2009).

What are we to make of these differences? It is possible that the propagation of triggered dominance changes through radial gratings is driven by distinct processes relative to those responsible for the spread of dominance change in our complex stimuli. Our data might instead be related to processes previously identified as contributing to perceptual grouping (Alais & Blake, 1999; Alais & Melcher, 2007; Dorrenhaus, 1975). For instance, collinear contours are more likely to group during binocular rivalry, fading in and out of awareness in unison, than are orthogonal contours (Alais & Blake, 1999).

However, we suspect these differences are more quantitative than qualitative. Ultimately, we attribute the spread of dominance change to the spread of signal strength changes (Levelt, 1968). Some manipulations, like enhancing the contrast of a stimulus region joined to another region encoded within a common monocular channel (Lee et al., 2005, 2007; Wilson et al., 2001), might induce rapid spreads of signal strength change within a monocular channel. Other manipulations might achieve the same outcome but less efficiently. The presence of feedback within the human visual system dictates that the efficacy of apparently high-level manipulations might rely on monocular levels of processing (see Watson et al., 2004).

We have previously pointed out that many of the characteristics that contribute to signal strength vary with distance in depth from fixation (Arnold, Grove, & Wallis, 2007; Arnold, Law, & Wallis, 2008; also see Fahle, 1982). Perceptual suppression during binocular rivalry could therefore be driven by a functional adaptation that

facilitates visibility in cluttered environments, ensuring that the focal point is experienced rather than more proximate occlusions that can obstruct just one eye (Arnold et al., 2007, see also Changizi & Shimojo, 2008). These observations are consistent with recent data showing that images that conform to a  $1/f$  amplitude spectra are more likely to dominate perception during binocular rivalry than are images that do not conform to this distribution (Baker & Graf, 2009). Focused images typically conform to this distribution, blurred images do not.

To support our perspective, we have previously shown that perceptual dominance can *seamlessly* track the stronger of two images as the conflicting images switch between the eyes (Arnold et al., 2007, 2008). Equally importantly, we have shown that perceptual dominance changes can be driven at the same rate as the alternation of relative focus for images fixed in each eye. Thus perceptual dominance tracks the stronger signal, regardless of whether that signal relates to a single image as it swaps between monocular channels or to discrepant images persistently encoded by different monocular channels.

Our previous data therefore showed that there can be no temporal cost, in terms of perception, when a stronger signal switches between monocular channels (Arnold et al., 2007, 2008). However, here we have shown a clear cost, in terms of the spread of perceptual dominance, when signals relating to a single complex form must spread *between* monocular channels. Taken together, these data suggest that perceptual dominance during binocular rivalry is usually resolved in favor of the monocular channel with the highest instantaneous signal strength.

## Conclusions

We have found that, during binocular rivalry, triggered dominance changes tend to spread through complex images in much the same way as they sweep through simple images. Specifically, dominance changes tend to propagate along image contours and are slow to spread to regions encoded by a different monocular channel. These data are consistent with low-level processing structures, like V1, playing a determinant role in the spread of perceptual dominance through complex images during binocular rivalry.

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Corresponding author: Derek H. Arnold.

Email: darnold@psy.uq.edu.au.

Address: School of Psychology, The University of Queensland, St Lucia, QLD, 4072, Australia.

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