Independent Binocular Rivalry Processes for Motion and Form

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Summary

During binocular rivalry, conflicting monocular images undergo alternating suppression. This study explores rivalry suppression by probing visual sensitivity during rivalry with various probe stimuli. When two faces engage in rivalry, sensitivity to face probes is reduced 4-fold during suppression. Rivaling global motions also rivaled very deeply when probed with a global motion. However, in a surprising finding, sensitivity to face probes is completely unimpaired during global motion rivalry, and motion sensitivity is unimpaired during face rivalry. This suggests that rivalry suppression is localized to the neurons representing the image conflict, which means that probes of a different kind suffer no suppression. Sensibly, this would leave visual processes not involved in rivalry free to function normally.

Introduction

When two markedly dissimilar images are presented to each eye separately, an observer experiences alternations between one image and the other (Alais and Blake, 2005). This perceptual alternation, known as binocular rivalry, is of great interest to visual neuroscientists because despite two distinct images entering the visual system, only one of them reaches conscious perception. What becomes of the suppressed image in the visual system, and where the decision to make one of the images conscious is made, are examples of two challenging questions that arise from the phenomenon of binocular rivalry.

Two major theories of binocular rivalry have emerged, one proposing that rivalry is a low-level process, and the other proposing that it is a high-level process. According to the first theory, rivalry is an eye-based process, with the perceptual alternations experienced in binocular rivalry being due to a low-level process in which monocular visual channels engage in competition to determine which eye's input will determine perception (Blake, 1989). This theory is known as "eye rivalry," and is presumed to occur by default when binocular correspondence between the monocular inputs cannot be established (Blake and Boothroyd, 1985). In the second theory ("stimulus rivalry"), competition occurs at a higher level between stimulus representations so that it is the percepts of the rivaling stimuli that vie for conscious expression (Logothetis, 1998; Logothetis et al., 1996). Both theories of rivalry can claim to draw on considerable experimental support, and the emerging consensus is that rather than being mutually exclusive, both theories can coexist.

Eye rivalry is supported by functional imaging studies showing clear evidence for rivalry in V1 (Polonsky et al., 2000), even in the representation of the blind spot in V1, where input is exclusively monocular (Tong and Engel, 2001). Very recent neuroimaging work in the lateral geniculate nucleus, a structure prior to V1 where only monocular neurons are found, shows that neural activity during rivalry modulates with alternations in perceptual dominance (Haynes et al., 2005; Wunderlich et al., 2005). Psychophysical support for the low-level theory comes from a host of studies showing that rivalry suppression is not specific to the features engaged in rivalry, but acts indiscriminately on all features presented to the nondominant eye, as if the entire eye's input were suppressed (Blake and Fox, 1974; Blake et al., 1980; Wales and Fox, 1970).

Support for stimulus rivalry comes from a critical psychophysical experiment which swapped two flickering orthogonal gratings rapidly between the eyes (Logothetis et al., 1996). Because the eye-swapping rate was several times faster than typical perceptual alternations in rivalry, the eye rivalry theory clearly predicted that several orientation flips should have been visible while a given eye's view was dominant. However, Logothetis et al.'s data showed that stable percepts of one grating lasting several swap cycles were sometimes observed, despite the grating switching between the eyes. Reports that Gestalt-like organization principles can provoke interocular grouping (Alais et al., 2000; Kovacs et al., 1996) also imply a binocular locus for rivalry and therefore seem to be consistent with the stimulus rivalry theory. Functional imaging studies also provide support for stimulus rivalry by demonstrating rivalry in fully binocular cortical areas representing houses and faces (Tong et al., 1998).

However, these conclusions are not above dispute. It has recently been shown, for example, that the method of "flicker and swap" rivalry lacks the generality of traditional binocular rivalry, holding only for a limited parameter range (Lee and Blake, 1999). Moreover, when it does hold, there are periods corresponding to traditional eye rivalry as well as periods of stimulus rivalry. Thus, it appears that both kinds of rivalry can and do occur, so that eye and stimulus rivalry are not mutually exclusive, but instead represent different kinds of rivalry. The conclusions to be drawn from the studies showing interocular grouping during rivalry also need to be reconsidered since it has been demonstrated that low-level lateral interactions, perhaps in concert with feedback from higher levels selective for coherent objects, can bring about periods of figural completion in rivalry (Lee and Blake, 2004). This casts doubt over whether figural completion necessarily implies interocular grouping, and

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instead suggests that figural completion may be explicable in eye-based terms.

One of the distinguishing features of the stimulus rivalry theory is that rivalry occurs between the representations of the objects or features engaged in rivalry. Consequently, stimulus rivalry implies a more localized rivalry process, focused on the conflicting stimulus features, than the eye rivalry theory, which posits a broad-based and nonselective suppression of the nondominant eye. In stimulus rivalry, rivalry should be local to the network representing the conflicting stimuli. This leads to the prediction that representations of other stimuli or features not engaged in rivalry should remain unaffected by the rivalry process. In these experiments, we test this prediction by inducing rivalry between a pair of global motion stimuli or a pair of face stimuli (see Figure 1), and probing for sensitivity to either the same stimulus or the complementary stimulus. In the complementary conditions, face probes will be presented during motion rivalry, and motion probes during face rivalry.

Face and global motion stimuli were chosen to exploit one of the major processing divisions in visual cortex, the parallel pathways of the color/form and motion streams (DeYoe and Van Essen, 1988; Livingstone and Hubel, 1988). Processing of face stimuli is known to depend critically on a specialized extrastriate area in the form pathway called the fusiform face area (FFA; Grill-Spector et al., 2004; Kanwisher et al., 1997). The motion stimuli were random dot kinematograms undergoing global expansions or contractions. These types of global motion signals are not detected prior to the extrastriate medial superior temporal (MST) area in the motion pathway (Graziano et al., 1994; Tanaka et al., 1989) and were composed of limited lifetime dots so as to avoid form cues. Note that while these two kinds of stimuli will no doubt activate larger processing networks (with at least area V1 in common), they do depend critically on specialized cortical areas which reside in distinct processing pathways. Using these rival stimuli (i.e., rivaling faces) with a complementary probe (i.e., global motion), we should be able to determine whether rivalry is localized to the network processing faces or whether the whole eye's processing is attenuated during rivalry suppression (which would also compromise detection of the motion probe).

If binocular rivalry is indeed localized to the network of neurons and areas representing the conflicting stimuli, visual processing of other stimuli should not be impeded, provided they are represented by independent neural populations. Several findings hint that this may indeed be the case. For example, global motion requiring integration of motion components between the two eyes can still be perceived even though the differently colored components engage in color rivalry (Carney et al., 1987). It has also been found that motion signals (and temporal modulations) from a suppressed eye can still interact with those from the dominant eye to produce a dichoptic global motion (or temporal beat) percept (Andrews and Blakemore, 1999; Carlson and He, 2000). Earlier papers report related findings—that a figure can rival independently of its background (Creed, 1935)—and that stereopsis, which requires integration between the eyes, can still occur despite rivalry between the differently colored disparate contours (Treisman, 1962).
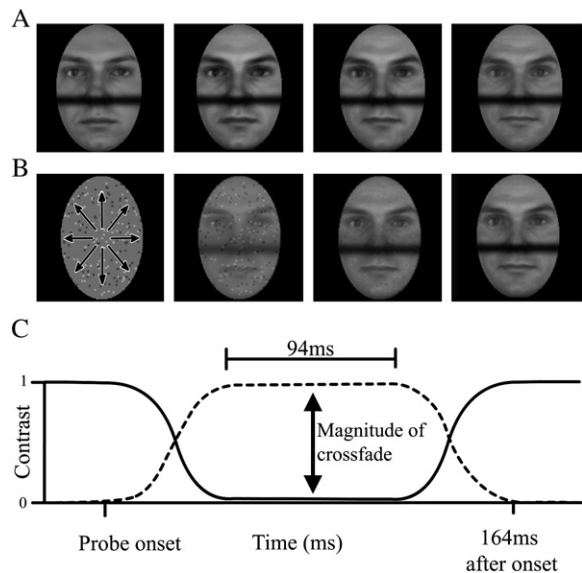

Figure 1. Examples of the Rival Stimuli and the Cross-Fade Method Used in These Experiments

(A) The first and last frames show two different faces, and the intermediate frames show a progressive cross-fade from one to the other. To minimize transients as the second (probe) face is cross-faded with the first, every frame has the same average luminance and RMS contrast, and the time course follows a Gaussian temporal profile. The dark stripes across the faces are bands where contrast was ramped down to zero. This was necessary because the probe faces were sometimes composed of the upper and lower halves of separate faces (see Experimental Procedures) and the dark band served to mask the joins. To avoid transients, the band was present on all faces.

(B) An example of a cross-fade between a face and an expanding motion. The two central frames show examples of a partial cross-fade: 30% face in frame 2, 60% face in frame 3.

(C) Probe stimuli were ramped on and off according to a smooth Gaussian cross-fade with a plateau period of 94 ms interposed between the ramps. Although the entire probe sequence took 164 ms, the effective probe duration (the portion bounded by the half-maximums of the on- and off-ramps) was 135 ms. The dependent variable in these experiments was a relative contrast threshold (the probe's contrast relative to the contrast of the rival stimuli) required to identify a face probe, or the proportion of coherent motion needed to discriminate the direction of the global motion rotation probe.

To test whether processing of other (i.e., nonrivaling) stimuli is impaired or not, we will use the probe method (Blake and Camisa, 1979; Blake and Fox, 1974; Fox and Check, 1972; Wales and Fox, 1970). This technique measures the depth of rivalry suppression by comparing sensitivities to brief probe stimuli presented during dominance and suppression. Generally, for simple stimuli such as gratings and contours, probe sensitivity is reduced during suppression to about 60% of the level measured during dominance (Makous and Sanders, 1978; Nguyen et al., 2003), although for higher-level stimuli such as global motions and complex forms sensitivity is reduced to about 25% of the dominance level (Nguyen et al., 2003). Thus, one prediction is that the rivaling faces and rivaling global motions used in the present experiments, whose processing networks include specialized extrastriate areas, should produce deep rivalry suppression. The more important prediction, however, is that suppression depth should depend critically on whether the probe stimulus activates the rivaling
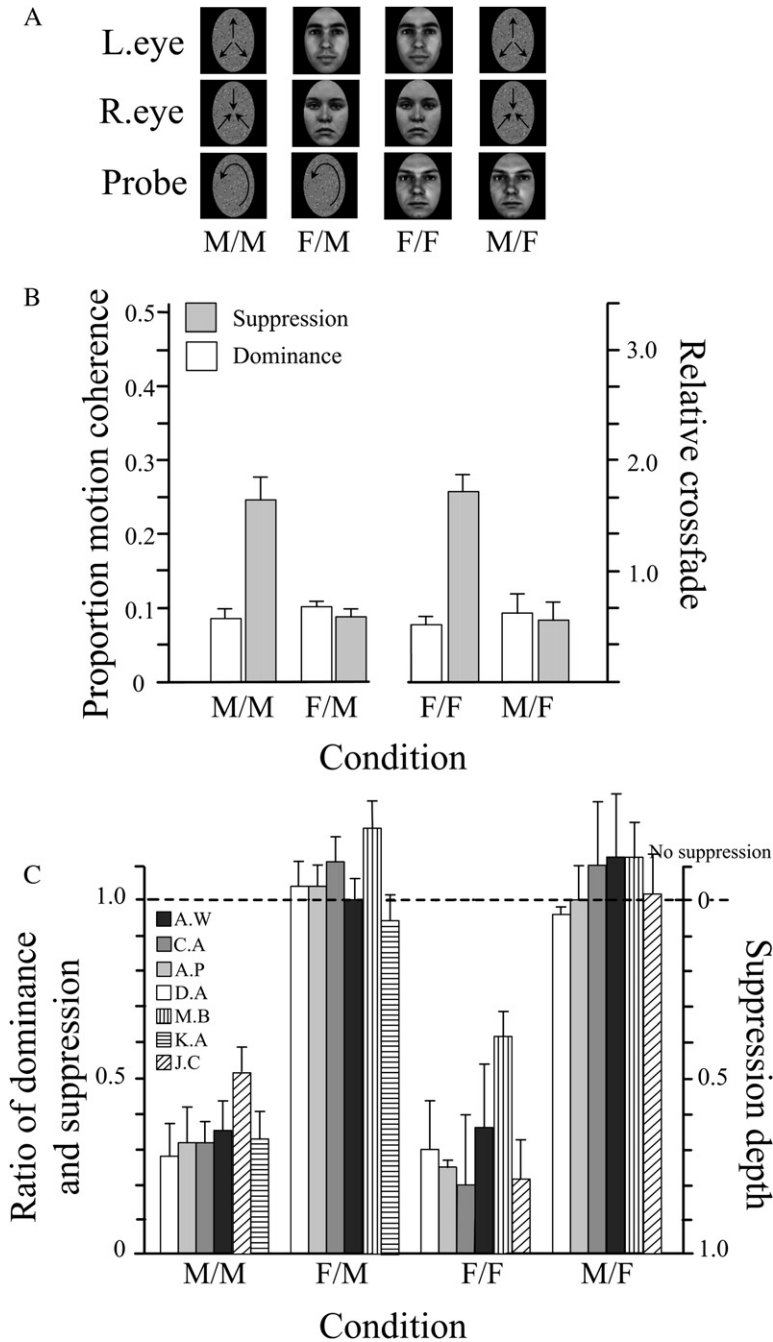
A

M/M   F/M   F/F   M/F

B

C

Figure 2. Stimuli and Results for Experiment 1

(A) The rival stimuli and test probes used for the four conditions of Experiment 1. The letter pairs at the foot of each column denote "motion" and "face." The first letter indicates the rival stimuli; the second letter, the probe stimulus.

(B) Left-hand panel: Thresholds for discriminating rotation of a global motion probe in dominance and suppression phases of rivalry (averaged over six observers; error bars indicate one standard error). When rivalry was between two global motions (motion/motion), motion probe sensitivity was reduced 3-fold during rivalry suppression. However, when the rival stimuli were faces (face/motion), thresholds for the same motion probe showed no dependence on whether face rivalry was in a dominance or suppression phase. Right-hand panel: Thresholds for the same observers for identity discrimination of the face probe. Relative cross-fade refers to the probe's contrast relative to the contrast of the rival stimuli. When face rivalry was probed with a face (face/face), probe sensitivity was reduced about 4-fold during rivalry suppression. However, when the rival stimuli differed in kind from the probe stimulus (motion/face), thresholds for the same face probe showed no dependence on the state of motion rivalry.

(C) Ratio of dominance-to-suppression thresholds for each observer (left axis), with suppression depth plotted on the right axis. A ratio of 1 would indicate identical performance in suppression and dominance conditions and therefore corresponds to a suppression depth of zero. Suppression depth is approximately zero for both conditions where the probe was of a different kind from the rival stimuli. Error bars indicate one standard deviation.

neurons. Specifically, if two faces are engaged in rivalry, sensitivity to a global motion probe should remain unaffected by whether the probed eye happens to be dominant or suppressed (i.e., there should be zero suppression depth). Similarly, if two global motions are engaged in rivalry, sensitivity to a face probe should remain the same during dominance and suppression. The reason in both cases is that rivalry should be localized to the neurons representing the rivaling stimuli, leaving the probe stimulus to be detected by a population not involved in binocular rivalry, as in normal viewing. Conversely, if the probe is a face stimulus and the rivaling stimuli are also faces, then probe sensitivity should be greatly reduced if it is presented during suppression,

and similarly for a motion probe presented during motion rivalry. These predictions are tested below.

Results and Discussion

Figure 2A illustrates the rival stimuli and probes for the four conditions. Note that subjects triggered the probe presentation themselves when (depending on the condition) the eye to be probed was completely dominant or completely suppressed (see Experimental Procedures). The design was a 2 × 2 factorial combining rivalry type (rivaling faces versus rivaling motions) and probe type (motion probe versus face probe). Thresholds for detection of the motion probes during rivalry are presented in

the left-hand panel of Figure 2B, and those for face probes are shown in the right-hand panel. For the motion probes (Figure 2B, left) thresholds were defined as the level of motion coherence required to judge whether the probe stimulus rotated clockwise (CW) or counter-clockwise (CCW). For the first pair of columns in Figure 2B, both the probe (CW or CCW rotation) and the rival stimuli (expansion versus contraction) were global motions ("motion/motion" condition). Thresholds for the monocular motion probe (plotted here as the average of six observers) were higher when it was triggered during suppression (dark column) than when it was triggered during dominance (light column). Reduced sensitivity for probes presented to the suppressed eye is typical in studies using the probe technique, and this is generally interpreted in terms of eye rivalry: if the probed eye is subject to suppression, then detection thresholds must be higher in that eye. Here, thresholds for discriminating direction of rotation are roughly three to four times greater in suppression than in dominance, in agreement with an earlier probe study that used spiral motion as a global motion probe (Nguyen et al., 2003).

The second pair of columns in the left panel of Figure 2B shows the threshold for the same motion probe presented when the rival stimuli were faces ("face/motion" condition). Regardless of whether the probe was presented during dominance (light columns) or suppression (dark columns), sensitivity to the motion probe was equally as good, and motion probe sensitivity in both cases was equivalent to that obtained during dominance in the motion/motion condition. Thus, even though the observer experiences a subjective blindness in the eye receiving the suppressed face, sensitivity to the global motion probe was not affected.

A similar pattern of results was found for face probe thresholds (Figure 2B, right). The face probes were monocular faces that were morphed (using a cross-fade technique: see Figure 1A and Experimental Procedures) with the rivaling face present in the probed eye. The observer's task was to make a binary choice: whether the probe face was one drawn from a previously learned set or whether it was a composite face (made of upper and lower halves of different faces in the previously learned set). The extent of the cross-fade—in effect, the contrast of the probe relative to the contrast of the rival faces—was varied from trial to trial (Figure 1A) using an adaptive staircase procedure to find the level of probe contrast required for observers to recognize whether or the probe face was one drawn from a previously learned set or was a composite.

The first pair of columns in the right panel of Figure 2B shows thresholds obtained when both the probe and the rivaling stimuli were faces ("face/face" condition). Thresholds were higher when the probe was triggered during suppression (dark columns) than when triggered during dominance (light columns). As in the motion/motion condition, suppression thresholds were about 4-fold higher than dominance thresholds, a ratio that agrees with other recent studies of sensitivities to high-level form probes (Nguyen et al., 2003). However, face probe measurements obtained when the rival stimuli were motions ("motion/face" condition) show that thresholds during suppression (dark columns) were

not any higher than those measured during dominance (light columns). Thus, as was observed when the rival stimuli were motions, there is no loss of probe sensitivity in the apparently suppressed eye provided the probe and rival stimuli differ in kind. (An interesting side issue that may occur to some readers is that detecting the face probe against a face background was no harder than detecting the face probe against a motion background [dominance thresholds in each condition are very similar]. We explored this apparent lack of face masking in a supplementary experiment and conclude that it is due to the lag in switching from motion to face processing in the motion/face condition within a brief probe period of 140 ms [see Supplemental Data].)

To quantify the depth of suppression, probe thresholds are usually expressed as a ratio. Figure 2C shows the ratio of dominance-to-suppression thresholds (left axis) and the corresponding amount of suppression depth (right axis). A ratio of 1.0 would indicate no suppression depth, although typical ratios would be around 0.6 to 0.7 (i.e., 30%–40% suppression depth) for probe studies using low-level stimuli such as gratings (Makous and Sanders, 1978; Nguyen et al., 2001). In line with a recent study (Nguyen et al., 2003) showing that suppression depth is far deeper for complex stimuli, dominance-to-suppression ratios are low at about 0.25 for the face/face and motion/motion conditions, corresponding to 75% suppression depth. Remarkably, however, here we find that when the probe stimulus was of a different kind from the rivaling stimuli, there was no loss of sensitivity at all during suppression; the dominance-to-suppression threshold ratios were close to 1.0 for all observers, indicating a complete absence of suppression. Results from a two-way ANOVA on the dominance-to-suppression ratios show no main effect of rivalry type ($F_{1,5} = 0.334$; $p = 0.589$) or of probe type ($F_{1,5} = 0.223$; $p = 0.657$), but a very strong interaction ($F_{1,5} = 437.611$; $p < 0.0001$). This confirms what is clear from the graph: the suppression of a probe depends upon the kind of rivaling stimuli. Together, these findings suggest that rivalry suppression is limited to the cortical area representing the conflicting stimuli and does not entail wholesale suppression of one or the other eye.

The data in Figure 2 show that face recognition and global motion processing do not interact during binocular rivalry, as probes differing in kind from the rival stimuli show no reduction in sensitivity. Consistent with this, it is known that critical cortical areas in the neural networks underlying face recognition and global motion are located in separate visual processing pathways (Graziano et al., 1994; Grill-Spector et al., 2004; Kanwisher et al., 1997; Tanaka et al., 1989). However, the independence of motion sensitivity during face rivalry (and face sensitivity during motion rivalry) prompts the question of whether faces and global motion could ever engage in rivalry. To test this, we produced a mixed pair of rival stimuli combining both kinds of stimuli: a face presented to one eye and a global expansion or contraction to the other. We found that cross-pairing the stimuli did indeed produce binocular rivalry, and we proceeded to measure rivalry suppression depth for the cross-paired stimuli by probing for sensitivity to face and motion probes. For motion probes and face probes (see Figure 3B), thresholds during dominance were lower
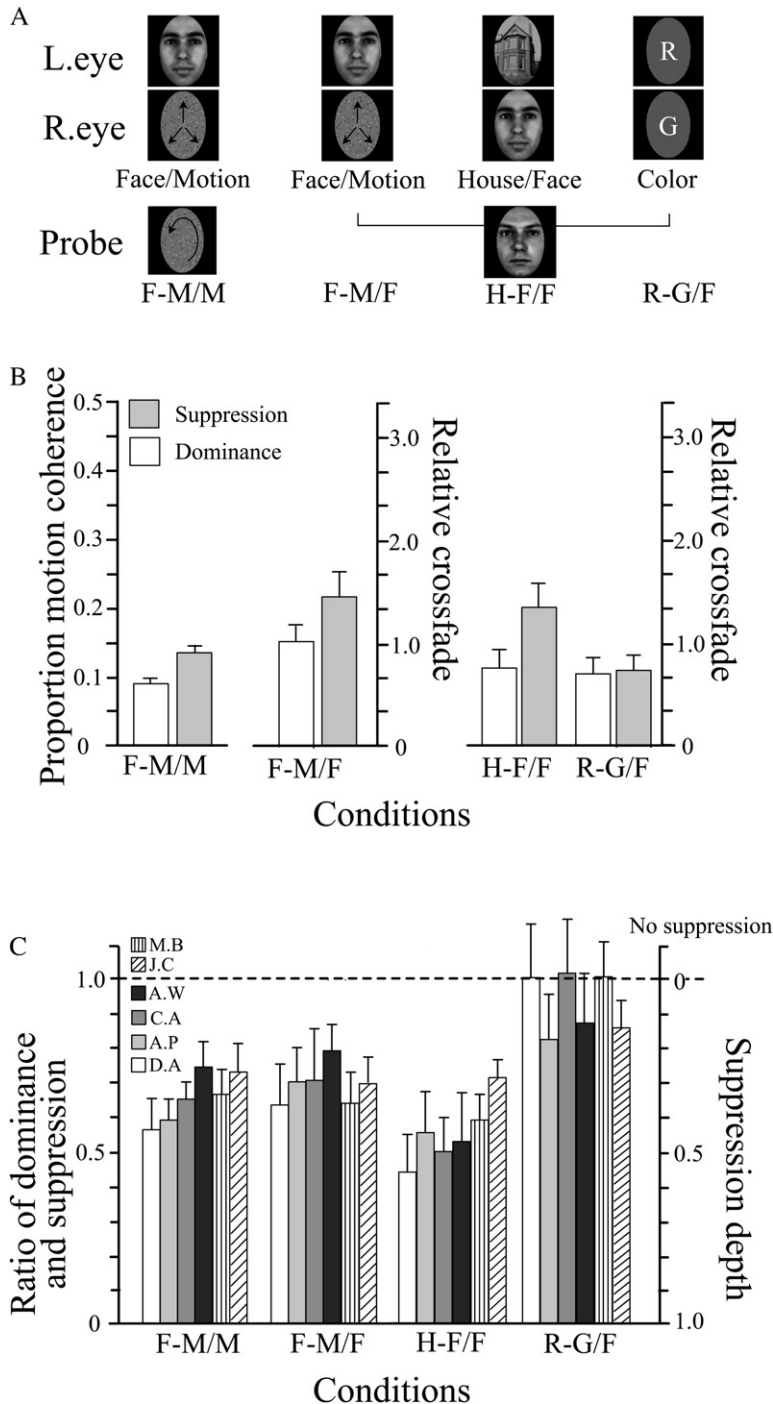
Figure 3. Stimuli and Results for Experiment 2

(A) Rival stimuli and test probes used for the four conditions of Experiment 2.

(B) Dominance and suppression thresholds averaged over observers for the four conditions shown in (A). Relative cross-fade refers to the probe's contrast relative to the contrast of the rival stimuli. Error bars indicate one standard error.

(C) Dominance-to-suppression ratios and suppression depth for the four conditions of Experiment 2. In the cross-paired conditions (form and motion rivaling), suppression depth was very similar for both conditions irrespective of whether the probe was a face or a global motion (not significantly different: see text) and quite shallow. Previously, when not cross-paired, faces and global motions were deeply suppressed (see Figure 2C). In the face/house pairing, suppression was slightly deeper than in the cross-paired conditions, but not significantly (see text). There was no suppression depth when the face probe was used in uniform color rivalry, showing that our use of color-tinted faces did not contribute to the deep suppression we reported in the face-face condition of Experiment 1 (see Fig 2C). The only statistical differences between any of the groups are that the color-tinted condition is significantly different from each of the other three groups (see text). Error bars indicate one standard deviation.

than those measured during suppression, but by much less than was observed in Figure 2B for face/face and motion/motion pairs. The threshold values were roughly equivalent whether the face was presented to the left eye and motion to the right (with right eye probed, as shown in Figure 3A) or whether the right eye was probed with the rival stimuli reversed (motion left eye, face right eye), and Figure 3B shows the means of these counterbalanced orders. As shown in Figure 3C, the dominance-to-suppression ratios for these two cross-paired conditions were very similar at 66% and 69%, respectively. This corresponds to a rather shallow suppression, although it is

similar in magnitude to values obtained in probe studies using low-level stimuli such as gratings (Makous and Sanders, 1978; Nguyen et al., 2001, 2003).

It has been suggested that the amount of suppression depth is indicative of how far along the visual pathways the rivalry process occurs since suppression deepens for more complex global stimuli (Nguyen et al., 2003). For this reason, it appears that rivalry between the cross-paired stimuli occurs at a lower level than rivalry between motion/motion or face/face pairs, possibly because the motion and form processing pathways are divergent at stages beyond V1 (Livingstone and Hubel,

1988). In this view, deep suppression would require two stimuli that are complex and of the same kind (such as two global motions or two faces) so that they would be processed within the same pathway. To test the generality of this suggestion, we measured suppression depth for rivalry between a face and a house. Both of these stimuli are detected beyond V1 in the ventral object-processing pathway and would therefore be expected to rival quite deeply. The first pair of columns in the right-hand panel of Figure 3B shows detection thresholds for face probes during "face/house" rivalry, with the dominance-to-suppression ratio shown in Figure 3C. While the ratio in the face/house condition (averaging 56%) was lower than those for the two cross-paired conditions (66% and 69%), it was not significantly lower than either (Bonferroni-corrected t tests; for both tests, p > 0.05) and was not nearly as low as was observed for motion/motion or face/face rivalry in Experiment 1 (35% and 33%, respectively). As discussed below in the Conclusions subsection, this may be due to a lack of coordinated feedback in the face/house condition.

We ran a control condition to check that the deep suppression reported for the face/face condition was not due to the fact that the face stimuli were tinted red and green. We simply rivaled uniform red and green patches and measured suppression with a monochrome green (or red) face probe that was cross-faded onto the green (or red) color patch. Sensitivity to the face probe did not depend on whether red or green probes were used, and the mean of both counterbalanced orders are shown (second pair of columns in the right panel of Figure 3B). Importantly, probe sensitivities were equivalent whether tested during dominance or suppression, showing that the deep suppression in our original face/face condition was not due to any extra suppressive effects due to rivalry between the colors of the faces, since face sensitivity was unaffected by the state of color rivalry. Indeed, following a one-way ANOVA comparing the four conditions in Figure 3, Bonferroni-corrected t tests showed that the only statistical differences between any of the groups are that the color-tinted condition is significantly different from the other three groups (for all three tests, p < .001). It is also noteworthy that subjects never observed independent rivalry between the colors and the faces in the original face/face condition—each color remained bound to its corresponding face.

Finally, to complement the suppression depth data for the various conditions described above, we measured a rivalry coherence index, a measure that quantifies the extent to which rivaling alternations tend to occur in a globally coherent way or in a piecemeal manner. Rival stimuli that tend to alternate exclusively (either the left-eye or right-eye stimulus is seen in its entirety) have a high rivalry coherence index. Piecemeal rivalry (low coherence index) is one of the hallmarks of low-level rivalry and is thought to be due to the small size of early receptive fields (Blake et al., 1992). In contrast, higher-level stimuli such as faces, cars, and houses tend to rival coherently (even when up to 12 degrees in diameter; Alais and Melcher, 2006), reflecting the larger receptive field sizes in the cortical areas representing these objects. Figure 4 plots rivalry coherence (percentage of exclusive dominance over a 200 s viewing period averaged over four observers) for all of the rivalry conditions tested

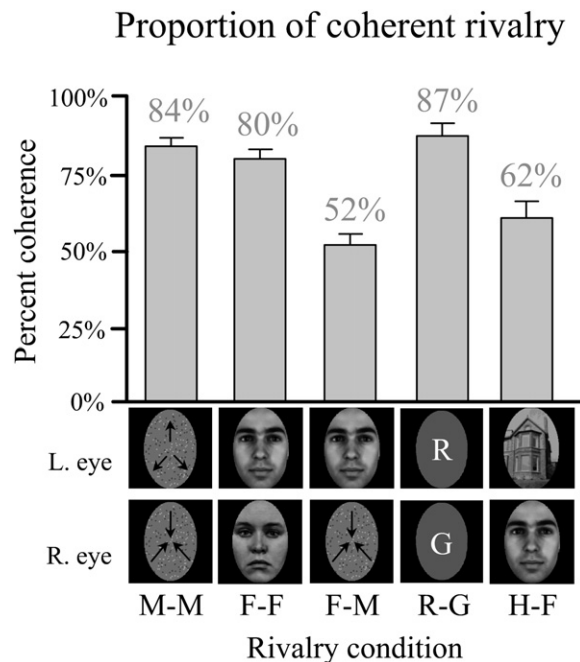## Proportion of coherent rivalry

Figure 4. Stimuli and Results for Experiment 3

Rivalry coherence measurements for the five different rivalry stimuli used in Experiments 1 and 2 (averaged over observers; error bars indicate one standard error). Rivalry coherence indicates the proportion of time that one or the other stimulus was visible in its entirety. The complement remaining represents the incidence of piecemeal rivalry. Rivalry between a pair of faces or between a pair of global motions produced high coherence, probably reflecting a role for feedback from large receptive fields in extrastriate areas such as FFA and MST, which are essential in global motion and face processing networks. The cross-paired (face/motion) condition produced the least rivalry, significantly less than the average for face/face and motion/motion. The face/house pair also rivaled less coherently than the motion/motion and face/face conditions (see Conclusions in main text).

above. It can be seen that despite the large size of the stimuli (7.5° × 5°), rivalry tended to be very coherent for the conditions that paired complex stimuli of the same kind (face/face, motion/motion). Rivalry coherence was lowest for the mixed face/motion pair, being significantly lower than the average of the face/face and motion/motion conditions ($t_9 = 7.6$; $p < 0.001$), and also lower than the house/face condition ($t_9 = 5.3$; $p < 0.001$).

Conclusions

The aim of these experiments was to test whether rivalry suppression is a local process involving the neurons representing the conflicting images, or whether it is a large-scale process entailing alternating suppression of a whole eye. The main conclusion to be drawn is that rivalry appears to involve processes localized to the neurons representing the stimulus inputs, since rivalry suppression reduced probe sensitivity only when the probe was of the same kind as the rivaling stimuli. When the probe differed in kind from the two rivaling stimuli, probe discrimination was completely unhindered by rivalry suppression. During face rivalry, for example, sensitivity to motion probes was unaffected whether the motion probe was presented to the dominant eye or to the suppressed one. Conversely, during

motion rivalry, sensitivity to a face stimulus was independent of whether the probed eye was dominant or suppressed. Thus, while an observer's subjective experience is of being temporarily blinded in their suppressed eye (in that they can no longer perceive the rival stimulus in that eye), their vision is in fact completely unimpaired for stimuli which differ in kind from those engaged in rivalry. Rivalry, therefore, appears to be restricted to the neural populations dedicated to representing the particular rival stimuli, with neurons processing features or attributes not related to the rival stimuli continuing to function normally.

The finding that sensitivity to motion during form rivalry (and to form during motion rivalry) is independent of whether the probe is presented to the dominant or suppressed eye would seem to argue against the eye rivalry hypothesis. This hypothesis posits a broad, nonselective suppression and would therefore predict that sensitivity to any kind of probe should be reduced if presented during suppression, and this clearly was not observed. However, the overall pattern of data does not necessarily support stimulus rivalry either. While stimulus rivalry would posit an inhibition that is selective for the rivaling stimuli, the data from the "cross-paired" conditions provide a challenge to it. While the face/face condition found that faces are deeply suppressed when probed with a face, the face/motion condition showed this is not always the case: suppression depth for faces was shallow when the face rivaled with a global motion stimulus. (Note that although detecting face probes and motion probes are different tasks, the cross-paired conditions can be compared as each condition has its own control. For a given condition, performance during suppression is always normalized to performance during dominance. The data therefore represent a standardized quantity—suppression depth—defined without reference to other, possibly nonequivalent, conditions and so can be compared across conditions.) Moreover, rivalry alternations in the face/motion condition were much more piecemeal. Since piecemeal rivalry and shallow suppression depth are thought to be hallmarks of low-level rivalry, this is difficult to explain in terms of stimulus rivalry. Being a higher-level process, stimulus rivalry should instead exhibit deep suppression and coherent alternations.

We propose that these data are best explained in terms of a rivalry process that is initiated early and which is primarily driven by early competition, but which can be coordinated and deepened by feedback from higher areas that process global stimulus attributes (Alais and Blake, 1998). Supporting the primacy of early processes in rivalry is the fact that rivalry is triggered by the failure of binocular fusion (an early cortical process). Recent psychophysical findings also support this proposal. For example, Carlson and He (2004) placed a matching fine-scale grid over two dichoptic drifting gratings. Without the grid, the gratings engaged in robust rivalry (as expected); however, they failed to rival when the grid was added. They reasoned that fine-scale binocular fusion of the images was made possible by the grid, and that therefore rivalry failed to initiate. In the absence of rivalry, the component motions in each eye were simply integrated into a dichoptic plaid by a global motion mechanism downstream of V1. Plaid motion is known

to be detected in area MT, but not in V1, although MT does feed back strongly to V1. Their findings therefore support the idea that rivalry is initiated early (when fusion fails), but that global conflicts alone are not sufficient to provoke rivalry when fusion conditions exist.

A similar conclusion was drawn in another recent study (Watson et al., 2004). These authors dichoptically presented global, point-light-walker stimuli walking in opposite directions and found that this produced robust binocular rivalry. However, intermixing the stimulus elements between the eyes, such that each eye received a mixture of the two rival stimuli, effectively eliminated binocular rivalry. Since neurons in the extrastriate areas thought to underlie detection of biological motion stimuli are binocular (Oram and Perrett, 1994), interocular mixing should not have prevented rivalry if indeed it were initiated at this level (since two globally coherent walkers were still present). As with the Carlson and He (2004) study, this indicates that conflict at this global level was not sufficient to provoke rivalry. Clearly though, once initiated (in the nonintermixed dichoptic condition), these biological motion areas were able to feed back to an earlier rivalry process and coordinate rivalry oscillations in a globally coherent manner since alternating coherent walkers were perceived about 50% of the time in extended observation. The point to be taken from both studies is that global processes appear unable to induce rivalry themselves and are instead limited to exerting modulatory influences once rivalry is initiated, providing a global frame of reference for organization of local rivalry processes.

It is known that feedback from extrastriate areas to primary visual cortex is widespread, and it probably occurs regardless of whether viewing conditions give rise to normal fused vision or to rivalrous vision. One of the functions of feedback is to provide large-scale organization for the fine-scale topography of V1. Because feedback from global processes endows spatial organization on V1, this should result in greater coherence in rivalry alternations (that is, less piecemeal rivalry) when two global stimuli rival. This can be seen in the data of Figure 4, where the highest rivalry coherence was obtained (apart from the uniform color patches) between opposed global motions and between two similar faces. Interestingly, coherence was significantly less for rivalry between the house and face, even though both these stimuli activate global object processing areas (Aguirre et al., 1998; Kanwisher et al., 1997; Tong et al., 1998) which feed back and globally organize activity at earlier levels where receptive fields are small (Salin and Bullier, 1995). This is probably due to these two rival stimuli differing greatly in their distributions of orientation and spatial frequency energy, which would elicit rivalry in many local zones where the stimuli conflict. Thus, this condition pits early local rivalry processes against global feedback and suggests that the low-level processes initiating rivalry have primacy over the modulatory role of global feedback.

The primacy of local over global processes is exactly what would be expected in this condition. Since rivalry processes are local and stochastic, using large stimuli (as we did) inevitably leads to piecemeal rivalry—a chaotic process in which roughly half of the zones are in a dominance state and half are in suppression at any one moment. Since the set of dominance zones would

be an ever-changing sample of approximately half of the rivalry zones in the image, any organizational role of global feedback would be impeded because images would seldom reach the extrastriate areas involved in house and face perception in coherent form. It would be like trying to complete a jigsaw puzzle with a constantly changing subset of pieces. In contrast, the greater incidence of global rivalry in the face/face condition probably stems from the fact that these stimuli were much more congruent in local stimulus energy and therefore did not elicit such a dense patchwork of piecemeal rivalry. This would allow global organizational feedback to play a greater role.

These experiments also shed light on another question: whether rivalry can occur between motion stimuli. Since motion is often confounded with form (e.g., as in a drifting grating), it is not clear from existing investigations of rivalry between motion stimuli whether rivalry was really instigated by motion conflict. Indeed, it has been specifically argued that examples of motion rivalry in the literature are actually due to form conflict (He et al., 2005). The motion stimuli used in the present study have minimal form cues because they were defined by spatially random dot patterns with short lifetimes that were unlikely to provide effective activation for form processes, and yet they still elicited vigorous binocular rivalry, which produced deep suppression. More critically, however, we can conclude that rivalry must have occurred within the motion system because sensitivity to form probes was not reduced when presented to a suppressed eye. Clearly, if form processes were also activated by our motion rivalry stimulus, some loss of sensitivity to a form probe would have been expected. Instead, form sensitivity was completely independent of the state of motion rivalry. This finding is also consistent with data indicating that contour rivalry can occur independently of global motion integration (Andrews and Blakemore, 1999).

In summary, the main conclusion is that binocular rivalry suppression is at least a partially localized process. Global motion rivalry does not entail suppression of face probes, and face rivalry does not entail suppression of global motion probes. Although this is not strictly compatible with the broad and nonselective suppression posited by eye rivalry, it is not compatible either with the conception of rivalry as a high-level process between competing percepts since global processes appear to exert an organizing and coordinating influence on local rivalry processes without overriding the primacy of local rivalry processes. Our results are therefore consistent with other recent findings indicating that global processes do not have a primary causative role in determining rivalry (Carlson and He, 2004; Lee and Blake, 2004; Watson et al., 2004). Thus, low-level processes retain a central role in initiating rivalry and in regulating rivalry alternations (since neurons that are monocular or strongly ocularly biased are only found in early visual cortex), but they are modulated by higher-level processes through feedback (Carlson and He, 2004; Watson et al., 2004). This arrangement allows global factors to influence rivalry, which is useful given the small extent and narrow tuning of V1 neurons, without requiring that the rivalry process actually occurs at those higher levels.

Experimental Procedures

Participants
Four naive observers and both authors served as subjects in all conditions. All had normal stereo acuity and normal or corrected visual acuity.

Rivalry Stimuli
As shown in Figure 2A, the form stimuli used to induce rivalry were two faces matched in average luminance and RMS contrast and subtending approximately 7.5 × 5 degrees visual angle from the viewing distance of 57 cm. To simplify the task of identifying when one face was completely dominant in the face/face condition, one face was tinted red and the other green. (Using monochromatic stimuli was necessary as it was otherwise difficult to determine when one face was wholly dominant—a condition for presenting the probes. Note that a control experiment ruled out any influence of color on face rivalry [Figure 3], and that the colors and faces remained bound and never rivaled independently.) The motion stimuli used to induce rivalry were monochromatic dynamic random dot arrays composed of 150 dots moving with 100% coherence. The dots had a two-frame lifetime, so that after each displacement they were randomly repositioned. The left eye was presented with expanding motion and the right eye with contracting motion (Figure 2A). Individual dots were three pixels in diameter; half were brighter than the average luminance background and half were lighter. Each dot moved at a rate of two pixels per frame, or approximately 6.5°/s. All stimuli were presented using an Apple G4 computer running Matlab software with the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997).

Probe Stimuli
The motion probe was a rotating random dot motion composed of 100 dots with the same size, displacement, and contrast (32% Weber contrast) as the rivaling motions. The face probe was either one of three faces that subjects learned to identity with >95% accuracy prior to the experiment on speeded tests that used the same temporal profile as the probe stimuli, or were composites of these faces combining the upper half of one of the three faces with the lower half of another. Using composite faces forced subjects to make global face identity discriminations instead of focus on distinguishing local features. All faces had a dark band across the middle where luminance was ramped down to zero. This served to mask the joins between different halves when composite faces were used (see Figure 1). Probe faces were tinted the same color as the face they were cross-faded with. The probe was always presented to the right eye and, importantly, regardless of which probe stimulus was combined with which rival stimulus, the mean luminance and RMS contrast of the right eye's stimulus was kept constant at every moment of the cross-fade.

Design and Procedure
In Experiment 1, four conditions were tested in a 2 × 2 design combining two types of rival stimuli (face/face and motion/motion) with two types of probe stimulus (face probe and motion probe) to measure suppression depth. In Experiment 2, the rival stimuli were combined into a face/motion pair, and were probed separately with a face and a motion probe. The two rival stimuli were presented on the left and right halves of a Digital 20" CRT monitor (1024 × 768 pixels, 85 Hz). Subjects viewed them through a mirror stereoscope and aligned them by adjusting the orientation of the mirrors. Stable fusion was assisted by surrounding the elliptical stimulus window with a black square (see Figure 1).

A trial started with the presentation of the rival stimuli to induce binocular rivalry. In Experiment 1 this was either a face/face or a motion/motion pair. The subject waited for the right eye's stimulus to be completely dominant (or completely suppressed, depending on the condition) and then triggered a brief monocular probe stimulus presented to the right eye. After the key press to trigger the probe, there was a brief pause of 106 ms before the probe stimulus was ramped on (see next paragraph), which served to desynchronize the motor action from the presentation of the visual probe. In Experiment 2, when the face and motion stimuli were cross-paired in rivalry, the eye of presentation for the face and motion stimuli was

counterbalanced across subjects. For two of the naive subjects, the face was presented to the left eye and the motion to the right (as shown in Figure 3A), and for the other two naive subjects, the presentation was reversed (motion left, face right). Both authors were tested in both orders. Sensitivities to face and motion probes were equivalent for both configurations of cross-paired rival stimuli (see Figure 3C), and the data in Figure 2B are means of the pooled data.

For all conditions the probe stimulus was combined with the rival stimulus by smoothly introducing and removing it using a Gaussian temporal profile (Figure 1) and a cross-fading technique that kept the probed eye's stimulus constant in RMS contrast and average luminance at all times. The temporal profile of the probe followed a Gaussian on-ramp that smoothly reached a maximum and then remained at maximum for an eight-frame plateau period (94 ms) before returning to zero probe contrast via a Gaussian off-ramp. The entire probe sequence took 164 ms, although we define the effective probe duration as the plateau period plus the portion of the Gaussian on-/off-ramps that are above half-maximum. Defined this way, the effective probe duration is 136 ms. Following presentation of the probe, there was a further 94 ms in which only the rival stimuli were visible; then the screen went blank and subjects indicated their responses. Depending on the subject's response, task difficulty was varied from trial to trial using the adaptive Quest procedure (Watson and Pelli, 1983), either by altering the extent of the face probe's cross-fade (its maximum contrast relative to the rival stimulus) or by altering the level of motion coherence of the motion probe, to obtain 75% correct discrimination of the probe stimulus.

For motion probes, the subject's task was to identify whether the probe rotated CW or CCW. For face probes, the task was to identify whether the probe was one of the previously learned faces or was a composite of two of the learned faces. Each condition was tested in separate blocks. In a given session, two Quests consisting of 25 trials each were randomly interleaved. Observers completed three sessions for each condition, the data from all six Quests were pooled, and a single psychometric function was fitted to the global data set from which the threshold was obtained. Where individual data is shown, 1000 iterations of a bootstrapping procedure were used to generate estimates of variance from which individual error bars were calculated.

Supplemental Data
The Supplemental Data for this article can be found online at http://www.neuron.org/cgi/content/full/52/5/911/DC1/.

References

Aguirre, G.K., Zarahn, E., and D'Esposito, M. (1998). An area within human ventral cortex sensitive to "building" stimuli: evidence and implications. Neuron *21*, 373–383.

Alais, D., and Blake, R. (1998). Interactions between global motion and local binocular rivalry. Vision Res. *38*, 637–644.

D. Alais and R. Blake, eds. (2005). Binocular Rivalry (Cambridge, MA: MIT Press).

Alais, D., and Melcher, D. (2006). The strength and coherence of binocular rivalry depends on shared stimulus complexity. Vision Res., in press.

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

Andrews, T.J., and Blakemore, C. (1999). Form and motion have independent access to consciousness. Nat. Neurosci. *2*, 405–406.

Blake, R. (1989). A neural theory of binocular rivalry. Psychol. Rev. *96*, 145–167.

Blake, R., and Boothroyd, K. (1985). The precedence of binocular fusion over binocular rivalry. Percept. Psychophys. *37*, 114–124.

Blake, R., and Camisa, J. (1979). On the inhibitory nature of binocular rivalry suppression. J. Exp. Psychol. Hum. Percept. Perform. *5*, 315–323.

Blake, R., and Fox, R. (1974). Binocular rivalry suppression: insensitive to spatial frequency and orientation change. Vision Res. *14*, 687–692.

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

Blake, R., O'Shea, R.P., and Mueller, T.J. (1992). Spatial zones of binocular rivalry in central and peripheral vision. Vis. Neurosci. *8*, 469–478.

Brainard, D.H. (1997). The psychophysics toolbox. Spat. Vis. *10*, 433–436.

Carlson, T.A., and He, S. (2000). Visible binocular beats from invisible monocular stimuli during binocular rivalry. Curr. Biol. *10*, 1055–1058.

Carlson, T.A., and He, S. (2004). Competing global representations fail to initiate binocular rivalry. Neuron *43*, 907–914.

Carney, T., Shadlen, M., and Switkes, E. (1987). Parallel processing of motion and colour information. Nature *328*, 647–649.

Creed, R.S. (1935). Observations on binocular fusion and rivalry. J. Physiol. *84*, 381–392.

DeYoe, E.A., and Van Essen, D.C. (1988). Concurrent processing streams in monkey visual cortex. Trends Neurosci. *11*, 219–226.

Fox, R., and Check, R. (1972). Independence between binocular rivalry suppression duration and magnitude of suppression. J. Exp. Psychol. *93*, 283–289.

Graziano, M.S., Andersen, R.A., and Snowden, R.J. (1994). Tuning of MST neurons to spiral motions. J. Neurosci. *14*, 54–67.

Grill-Spector, K., Knouf, N., and Kanwisher, N. (2004). The fusiform face area subserves face perception, not generic within-category identification. Nat. Neurosci. *7*, 555–562.

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

He, S., Carlson, T.A., and Chen, X. (2005). Parallel pathways and temporal dynamics in binocular rivalry. In Binocular Rivalry, D. Alais and R. Blake, eds. (Cambridge, MA: MIT Press), pp. 81–100.

Kanwisher, N., McDermott, J., and Chun, M.M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. J. Neurosci. *17*, 4302–4311.

Kovacs, I., Papathomas, T.V., Yang, M., and Feher, A. (1996). When the brain changes its mind: interocular grouping during binocular rivalry. Proc. Natl. Acad. Sci. USA *93*, 15508–15511.

Lee, S.H., and Blake, R. (1999). Rival ideas about binocular rivalry. Vision Res. *39*, 1447–1454.

Lee, S.H., and Blake, R. (2004). A fresh look at interocular grouping during binocular rivalry. Vision Res. *44*, 983–991.

Livingstone, M., and Hubel, D. (1988). Segregation of form, color, movement, and depth: anatomy, physiology, and perception. Science *240*, 740–749.

Logothetis, N.K. (1998). Single units and conscious vision. Philos. Trans. R. Soc. Lond. B Biol. Sci. *353*, 1801–1818.

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

Makous, W., and Sanders, R.K. (1978). Suppression interactions between fused patterns. In Visual Psychophysics and Physiology, A.C. Armington, J. Krauskopf, and B.R. Wooten, eds. (New York: Academic Press).

Nguyen, V.A., Freeman, A.W., and Wenderoth, P. (2001). The depth and selectivity of suppression in binocular rivalry. Percept. Psychophys. *63*, 348–360.

Nguyen, V.A., Freeman, A.W., and Alais, D. (2003). Increasing depth of binocular rivalry suppression along two visual pathways. Vision Res. *43*, 2003–2008.

Oram, M.W., and Perrett, D.I. (1994). Responses of anterior superior temporal polysensory neurons to "biological motion" stimuli. J. Cogn. Neurosci. *6*, 99–116.

Pelli, D.G. (1997). The VideoToolbox software for visual psychophysics: transforming numbers into movies. Spat. Vis. *10*, 437–442.

Polonsky, A., Blake, R., Braun, J., and Heeger, D.J. (2000). Neuronal activity in human primary visual cortex correlates with perception during binocular rivalry. Nat. Neurosci. *3*, 1153–1159.

Salin, P.A., and Bullier, J. (1995). Corticocortical connections in the visual system: structure and function. Physiol. Rev. *75*, 107–154.

Tanaka, K., Fukada, Y., and Saito, H.A. (1989). Underlying mechanisms of the response specificity of expansion/contraction and rotation cells in the dorsal part of the medial superior temporal area of the macaque monkey. J. Neurophysiol. *62*, 642–656.

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

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

Treisman, A. (1962). Binocular rivalry and stereoscopic depth perception. Q. J. Exp. Psychol. *14*, 23–37.

Wales, R., and Fox, R. (1970). Increment detection thresholds during binocular rivalry suppression. Percept. Psychophys. *8*, 90–94.

Watson, A.B., and Pelli, D.G. (1983). QUEST: a Bayesian adaptive psychometric method. Percept. Psychophys. *33*, 113–120.

Watson, T.L., Pearson, J., and Clifford, C.W. (2004). Perceptual grouping of biological motion promotes binocular rivalry. Curr. Biol. *14*, 1670–1674.

Wunderlich, K., Schneider, K.A., and Kastner, S. (2005). Neural correlates of binocular rivalry in the human lateral geniculate nucleus. Nat. Neurosci. *8*, 1595–1602.