

FROM CONTOUR TO OBJECT-FACE RIVALRY: MULTIPLE NEURAL
MECHANISMS RESOLVE PERCEPTUAL AMBIGUITY

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INTRODUCTION

In constructing a representation of the visual world, the brain has to cope with the fact that any given two-dimensional retinal image could be the projection of countless object configurations in the three-dimensional world (Helmholtz, 1924). As we move about, or as the ambient illumination changes, the size, shape, intensity, and spectral quality of the images on the retina also change. To be useful, perception cannot simply represent the physical quality of images. Rather, it must take into account the context in which a stimulus appears.

Although in most situations this inherent ambiguity is resolved by the visual system, there are occasions when human vision alternates between different perceptions of a stimulus. Common examples of such bistable stimuli include figure-ground reversals (Rubin, 1915¹), transparent 3-dimensional objects (Necker, 1832; Wheatstone, 1838; Purves and Andrews, 1997) and binocular rivalry (Blake, 1989). Although fascinating in their own right, bistable stimuli offer a potentially fruitful paradigm for understanding how the brain routinely resolves ambiguity in the retinal image. This is because the physical nature of the stimulus does not change, therefore any shifts in awareness are presumably mirrored only by stages of visual processing that are tightly linked to a perceptual decision.

A number of recent reports using one particular paradigm, binocular rivalry, have provoked a lively debate over the stage in visual processing at which signals access perception (Andrews, 2001; Blake and Logothetis, 2002). Two general theories have emerged: One possibility is that visual information is suppressed by inhibitory

¹ Although the vase-face illusion is generally attributed to Rubin (1915), similar pictorial ambiguities were used in paintings by artists such as Pierre Crussaire in the 18th century (see Wade, chapter 2 this volume)

interactions prior to or at the stage of monocular confluence. In this concept, changes in perception would be mediated by shifts in the balance of suppression between neurons selective for one or other monocular image. Since these interactions must occur early in the visual pathway (e.g. the lateral geniculate nucleus or layer 4 of primary visual cortex), any changes in the activity of neurons in higher visual areas would be explained by a loss of input, equivalent perhaps to closing one eye. The alternative hypothesis is that rivalry reflects a competition between different stimulus representations. This would be comparable to the viewing of other bistable stimuli, such as the vase-face stimulus, and as such would be relevant to the resolution of ambiguity in normal viewing.

In this chapter, we argue that it is misleading to imagine that there is a single mechanism underlying binocular rivalry. Rather, it is likely that the neural events that underlie binocular rivalry (and other bistable stimuli) occur at multiple stages throughout the visual system (see also Freeman et al, chapter 3, and Ooi and He, chapter 7, this volume). *First*, we show that contour rivalry involves inhibitory or suppressive interactions between *binocular* neurons in primary visual cortex. *Second*, we suggest that the neural events that underlie contour rivalry can occur independently of binocular interactions for motion. *Finally*, we show that the neural events involved in resolving ambiguity in another bistable stimulus (the vase-face illusion) occur in visual areas within the temporal lobe.

THE SITE AND MECHANISM OF CONTOUR RIVALRY

The episodic perceptual suppression of one eye's image during binocular rivalry is a compelling phenomenon that should be reflected in the firing pattern of single neurons at

some stage in the visual system (Barlow 1972). The apparent ‘competition’ between the two eyes could be construed to imply that the interactions underlying rivalry occur at a stage where information about the eye of origin is still preserved. Indeed, most traditional models of binocular rivalry assume that this phenomenon is based on alternating dominance and suppression of the two eyes’ inputs into V1 (Blake, 1989; Lehky and Blake, 1991).

Here we describe the stimulus-dependence of interocular interactions in both the lateral geniculate nucleus (LGN) and striate cortex (V1) of normal cats, and evaluate the role that the suppressive behaviour seen in V1 may play in binocular rivalry. We recorded from single neurons in the LGN and V1 of anaesthetized cats that viewed dichoptically presented drifting gratings. These represent classic examples of stimuli evoking contour rivalry (Du Tour, 1760; Wheatstone, 1838; Lejeune, 1956²).

We recorded from 17 LGN cells in laminae A and A1, 12 X cells and 5 Y cells, all monocularly driven by conventional stimuli. To test for binocular interaction we employed a procedure which we found best reveals suppressive effects (Sengpiel and Blakemore, 1994): the receptive field in one (the dominant) eye was stimulated continuously with an optimal ‘conditioning’ grating and at intervals gratings of various orientations were presented to the other (non-dominant) eye. This stimulus paradigm mimics “flash suppression”: when one views a grating monocularly for a few seconds, and an orthogonal grating is then introduced to the other eye, the first grating will not be seen at all for some time (Wolfe 1984; see chapter 12, this volume). The advantage of

² Although Ptolemy (ca. 150) made the first reference to contour rivalry, Wheatstone was the first to systematically describe this phenomenon (Wade, 1998).

this paradigm is that one can safely predict the perceptual outcome without having tested it directly (which of course is not possible in anaesthetized animals).

In 7 LGN cells (including both X and Y cells; 41% of those tested) the binocular responses differed significantly from those through the dominant eye alone. In all these cases, the interaction was entirely inhibitory: we never saw significant augmentation of the response even when the stimuli were identical in the two eyes. More importantly, binocular inhibition was essentially independent of the orientation of the gratings shown to the non-dominant eye, such that it occurred even when the grating shown to the non-dominant eye was identical in orientation to that presented to the dominant eye. But since we know that in rivalry alternating suppression only occurs when the stimuli are dissimilar in the two eyes, and not when stimuli are fusible, it seems reasonable to exclude the possibility that the perceptual conflict is resolved at that level of monocular representation. This conclusion is supported by single-cell recording from macaque LGN (Lehky and Maunsell, 1996).

In layer 4 of cat V1 many of the cells are monocular, and also orientation selective. We therefore reasoned that they might be involved in the interactions that underlie contour rivalry. Of the five monocular neurons we studied, four showed significant interocular suppression. However, as in the LGN, there was no evidence of any orientation-selective suppression that one might expect to find if these cells were mediating rivalry and suppression occurred with both very similar (fusible) and dissimilar (rival) orientations present in the two eyes (see Fig. 1B).

Only binocularly driven neurons outside layer 4 exhibited effects that did seem to correlate with binocular contour rivalry (and fusion). In over 90% of binocular neurons,

we observed the expected facilitation of the dominant eye's response when the other eye was simultaneously stimulated with a grating of optimal orientation and optimal relative spatial phase. In perception, fusion of contours depends on the similarity of spatial frequency. For example, vertical gratings of slightly different spatial frequency in the two eyes are perceived as tilted in depth around the vertical axis, as expected from the geometry of actual rotated surfaces. But fusion and the perception of tilt break down at an interocular difference of about 0.4 octaves (Blakemore 1970). Concordant with these findings, we observed that dichoptic gratings of different spatial frequency, but identical orientation, demonstrate facilitation over a similarly narrow range of spatial frequency difference. Furthermore, a transition to suppression occurs when spatial frequency differs by more than 0.5 octaves between the two eyes (Fig. 2A; Sengpiel et al 1995b).

These binocular neurons exhibited interocular suppression selectively for stimuli that also cause binocular contour rivalry in humans. When the non-dominant eye was stimulated with a high-contrast grating oriented *orthogonal* to the optimal orientation being shown to the dominant eye, 56% of the binocular neurons showed statistically significant suppression, reducing the mean spike rate by between 15% and 90% of the monocular response through the dominant eye. The suppression with orthogonal stimulation did not vary convincingly with the spatial phase of the grating in the non-dominant eye.

Among all the cells that exhibited iso-orientation facilitation and cross-orientation suppression, the transition between the two occurred at between 5° and 70° from the peak, although for most it was between about 15° and 35°, with a mean of 22°. This value is in reasonable agreement with the finding that fusion gives way to binocular rivalry at

an interocular orientation difference of about 30° in human observers (Braddick 1979). Fig. 1A illustrates the orientation-dependence of interocular interactions for a representative complex cell recorded in layer 2/3; pooled results for 27 cortical cells are displayed in Fig. 1B. Cells with narrower orientation tuning tended to be suppressed at smaller interocular orientation differences and to have stronger suppression than did cells with broader orientation tuning.

A key characteristic of contour rivalry is that once a grating is perceptually suppressed, suppression persists despite changes in stimulus parameters, in particular orientation (Blake and Lema 1978). We found that the interocular suppression of binocular neurons in V1 caused by the presentation of rival contours was also independent of the parameters of the contours. For example, suppression could be elicited by a range of spatial frequencies to which the cell was not sensitive. When suppression was exerted by gratings with spatial frequencies that were too high to elicit an excitatory response from the cell in question, suppression became independent of orientation (Sengpiel et al., 1995b). Moreover, in strabismic cats, which lack the normal facilitation for binocularly matched stimuli, interocular suppression occurs with any stimulus orientation, even when the gratings shown to the two eyes have the same spatial frequency (Sengpiel et al 1994). This virtual absence of selectivity for orientation at the neuronal level resembles pathological suppression in strabismic humans (see Holopigian et al., 1988).

Finally, we examined the strength of interocular suppression in terms of its effect on neuronal contrast thresholds. In human rivalry, the contrast increment needed to break suppression and render the suppressed stimulus visible is about 0.3-0.5 log units (Fox &

Check 1966, 1968, Wales & Fox 1970). We found that in cat V1, contrast-response functions for an optimal grating in one eye are shifted to the right by an average 0.17 log units in the presence of an orthogonal grating in the other eye (Fig. 2B; Sengpiel et al. 1998).

These results demonstrate that interactions between binocular neurons in V1 may contribute toward the changes in perception during contour rivalry. However, in one important respect, interocular suppression falls short of what one would expect of a direct neural correlate of binocular rivalry: it does not exhibit any significant waxing and waning over time. When orthogonal gratings were presented to the two eyes for up to 30 seconds, suppression was generally strongest over the initial 1-3 sec, with slight recovery to a tonic level, which was then sustained over the remainder of the period of binocular stimulation. For most cells, spike trains from individual trials revealed no obvious variation of suppression over time, nor did the overall depth of suppression vary substantially from trial to trial. As our study was concerned with single-neuron responses, we did not examine whether synchronization of activity between groups of cells was affected by the nature of the stimuli or whether it varied in time with presentation of rival stimuli [see Fries et al., chapter 14, this volume].

What is the substrate of interocular suppression in V1? We hypothesize that it derives from a network of inhibitory connections between binocular neurons in neighbouring ocular dominance (OD) columns (Sengpiel and Blakemore 1994, 1996). We suggest that the response properties of binocular neurons in V1 can be explained by a combination of both suppressive and facilitative mechanisms. Thus, the binocular facilitation for matched stimuli, thought to underlie fusion and stereopsis, is

superimposed on non-selective inhibitory interaction between the two eyes. In that sense, binocular rivalry / interocular suppression may be the “default” outcome of binocular vision (see Blake and Camisa 1978).

A possible anatomical substrate for the excitatory and inhibitory binocular interactions postulated above is schematically illustrated in Fig. 3A. Thin lines symbolize excitatory, thick lines inhibitory connections. Excitatory intrinsic connections tend to be clustered (Rockland & Lund, 1982; Gilbert & Wiesel, 1983) and more frequently link regions of similar than dissimilar orientation preference (Ts'o et al 1986; Kisvárdy et al., 1997): they may mediate disparity-sensitive binocular facilitation. Connectivity between sites of oblique or orthogonal orientation preference is provided mainly by projections to inter-cluster regions (Kisvárdy et al., 1997). Long-range inhibitory connections are much more diffuse and more uniformly distributed across orientation and ocular dominance columns (Somogyi et al., 1983; Kisvárdy & Eysel, 1993).

One possible implementation of interocular suppression is reciprocal inhibition between cells dominated by the two eyes, lying in neighbouring OD columns. Since the majority of excitatory synapses on neurons in area 17 derive from closely neighbouring cells rather than from thalamic afferents (Kisvárdy et al., 1986; Douglas & Martin, 1991; Nicoll & Blakemore, 1993) the responses of cortical neurons are likely to depend crucially on 'amplification' of input from the thalamus operating through this local excitatory circuitry (Douglas et al., 1989; Douglas & Martin, 1991). Perhaps inhibitory interactions between adjacent OD columns, responsible for suppressive interocular interactions, modulate the gain of this local excitatory circuitry (Fig. 3B). The resultant

interocular suppression will be overcome by binocular facilitation when the images in the two eyes are sufficiently similar.

As adjacent ocular dominance columns tend to represent very similar regions of visual space, one would therefore predict that the “interocular suppression field” in one eye should be of similar location and extent as the classical, excitatory receptive field of a neuron in the other eye. We mapped suppression fields using small circular grating patches (Sengpiel et al 2001). We found that the suppression field of V1 neurons is generally centered on the same position in space and is slightly larger (by a factor of 1.3) than the minimum response field, measured through the same eye. These results are in agreement with the observation by Blake et al (1992) that the size of grating patches engaging in whole-stimulus rather than piecemeal rivalry is scaled with stimulus eccentricity in a way that reflects the cortical magnification factor in V1 (Hubel and Wiesel 1974). In other visual areas, where responses are less dependent on stimulus size and location, these findings might not have been expected.

Altogether, our results support the hypothesis that contour rivalry arises from mutual inhibition between pools of neurons dominated by either the left or the right eye within retinotopically confined areas in V1. However, the proposed link between interocular suppression and the OD columnar architecture (see also Sengpiel et al 2001) should not be misinterpreted to imply that it is monocular neurons that interact. As we and others have shown, suppression during contour rivalry is much more likely to involve binocular rather than monocular cells in V1. However, it is not clear whether a similar neural mechanism is used to resolve rivalry for other aspects of vision.

INDEPENDENT RIVALRY FOR CONTOUR AND MOTION

Although binocular rivalry has been most commonly studied with orthogonal gratings (contour rivalry), it can also be elicited when the monocular images are distinguished by other attributes of vision, such as colour or motion. In this section, we review evidence that rivalry for different aspects of vision can involve independent visual processes. Specifically, we present data that shows a visual stimulus whose contours are rendered literally invisible through binocular rivalry can nevertheless contribute to the perception of movement.

A moving surface covered with stripes of a single orientation, viewed through a circular aperture, is usually seen as drifting in a direction orthogonal to the grating's orientation, whatever the actual direction of surface movement (Wallach, 1976). The ambiguity of a moving grating is resolved, however, if other features are added to the surface. A simple demonstration of such 'pattern' motion is provided by the superimposition of two drifting gratings, orthogonal to each other. While each grating presented alone would appear to move in its own 'component' direction, orthogonal to its contours, the two fuse together, forming a 'plaid' that drifts along an axis that usually corresponds to the vector average of the two components (Adelson and Movshon, 1982). Thus both gratings contribute to the direction of pattern motion, as well as to the perceived form of the stimulus.

To determine whether the system responsible for the awareness of movement could integrate component motion signals delivered separately to the two eyes, we presented human subjects with orthogonal moving gratings (4 deg diameter) that were viewed dichoptically. Even when the two gratings were identical in colour, spatial and

temporal frequency, they never fused to form a plaid, as they do when viewed through both eyes simultaneously. For periods of a few seconds at a time, totalling about half the entire one-minute viewing period, one or other of the two monocular gratings appeared to fill the entire field. During these epochs of apparently pure monocular perception, the grating almost always appeared to drift orthogonal to its orientation, just as it would if the other grating were not present at all.

Rarely, with these large fields, did direct and complete transitions occur between one eye's view and the other's. Usually, after a few seconds of apparently monocular perception, the grating broke up into a fluid mosaic consisting of contiguous patches of grating of the two different orientations (usually termed 'piecemeal rivalry'), the boundaries of which could shift slowly. Eventually the patchy mosaic was replaced for a few seconds by the other completely monocular view. In the fluid mosaic, which was seen for about half the entire viewing period, the individual patches were typically about one-third of the diameter of the entire patch (i.e. about 1 deg. or more across). Again, only one orientation was ever seen within each individual patch. Nevertheless, the entire mosaic usually appeared to move coherently, as if on a single surface, in the *pattern-motion* direction, appropriate to the combination of velocities of the two monocular gratings (see Fig. 4A).

One might imagine that, when the mosaic is seen during dichoptic viewing, the perceived direction is simply determined by integration of directional information from the visible single-grating patches, rather than through the integration of motion information from a grating whose orientation information is suppressed from perception (cf Alais et al., 1998). To test for this possibility, we used orthogonal grating patches that

were so small (<1 deg diameter), and presented for such a short time (1.5 s), that, on most trials, one orientation dominated completely over the entire area and for the whole period of exposure (Blake et al., 1992). The two gratings were always of oblique orientation and each could move in one of the two possible component directions. The orientations and directions were all randomized from trial to trial, producing four possible combinations (Andrews and Blakemore, 1999). Randomly interleaved with these conflicting presentations were non-rivalrous, control stimuli, in which the oblique grating patches shown to the two eyes were identical in orientation and direction of drift. With such small patches and brief presentations, the subjects were usually unaware of whether the stimulus was binocularly fused or rivalrous. They simply had the impression of a single, drifting grating.

For the non-rivalrous stimuli, as expected, subjects reported the grating moving in the appropriate component direction. For the rivalrous stimuli, whichever grating dominated consciousness also seemed to move orthogonal to its orientation (the expected component direction) on about 50% of trials. However, for fully half of the presentations, the single perceived grating appeared to drift in the direction of pattern motion predicted from the combination of movements in the two eyes, just as if the two gratings were actually superimposed (Andrews and Blakemore, 1999).

Evidence that the same mechanism underlies pattern motion in dichoptic and normal binocular viewing was apparent when the component gratings were made progressively more different from each other. We observed a similar decrease in the incidence of normal and dichoptic pattern motion when the difference in colour, direction of motion, contrast, velocity or spatial frequency between gratings was increased (Fig.

4B; Andrews and Blakemore, 2002). Moreover, as the stimulus properties of the gratings presented to the two eyes were made more different, there was a complementary increase in the amount of time that one grating or the other dominated perception over the whole patch (Fig. 4C). These results suggest that the dichoptic combination of moving gratings occurred in a similar manner to that observed in normal binocular vision (Adelson and Movshon, 1982; Stoner et al., 1990; Krauskopf and Farell, 1990).

This phenomenon, in which perceived movement is influenced by an apparently invisible grating, is compatible with other findings that show stimuli rendered invisible during binocular rivalry can nevertheless contribute either to the perception of apparent motion (Wiesenfelder and Blake, 1991), or to the motion after-effect (Lehmkuhle and Fox, 1975). Previous reports also suggest that, when stimuli of different colour are presented to the two eyes, chromatic rivalry can occur independently of binocular interaction between the shapes or movements of the targets (Creed, 1935; Carney et al., 1987). [see also chapter 5, this volume]

Can we draw any conclusions about the neural correlates of this phenomenon? Most neurons in primary visual cortex (V1) of monkey respond selectively to bars and gratings at particular orientations (Hubel and Wiesel, 1968). During contour rivalry, these neurons exhibit significant interocular suppression (see above). Direction-selective responses are also apparent in the activity of neurons in V1 (Hubel and Wiesel, 1968). However, these neurons only respond to component motion. When shown plaids moving in various directions, they fire only when one of the components has an orientation close to the optimum for the receptive field, as if they are blind to the other grating (Movshon et al., 1985). Clearly such activity cannot account for pattern motion perception.

Direction-selective neurons in V1 send signals, directly and indirectly, to the extrastriate area MT (Dubner and Zeki, 1971). A significant fraction of cells in MT are selective for pattern motion: they have the same preferred direction for drifting plaids as they do for single gratings (Movshon et al., 1985). Such cells, which presumably combine component motion signals from earlier stages of analysis (such as the local motion elements in piecemeal rivalry), appear to encode the perceived direction of pattern motion. Indeed, the activity of neurons in MT has been shown to covary with the changes in perceived direction of motion during binocular rivalry (Logothetis and Schall, 1989).

NEURAL CORRELATES OF PERCEPTUAL AMBIGUITY

The spontaneous alternation in perception that occurs when different images are presented to the two eyes (binocular rivalry) has many features in common with that experienced when viewing other ambiguous stimuli (Logothetis et al., 1996; Andrews and Purves, 1997). A number of reports have suggested that activity in relatively 'high' areas of visual cortex correlates with changes in perception that occur during binocular rivalry in both monkeys (Leopold and Logothetis, 1996; Sheinberg and Logothetis, 1997) and humans (Tong et al., 1998). However, recent evidence suggests that the simple rivalry between contours of different orientation depends on inhibitory or suppressive interactions occurring in primary visual cortex (Polonsky et al., 2000; Tong and Engel, 2001), as previously suggested by Sengpiel and Blakemore (1994; see above). Interestingly, modulations of BOLD signals from V1 also correlate with rivalry state when the rival targets are more complex (Lee and Blake, 2002).

This recent controversy suggests that the mechanism underlying rivalry might be quite different, in nature and location, from that causing shifts in the perception of other ambiguous figures. In a recent study, we investigated human cortical activity while subjects were viewing the vase-face illusion, where different stimulus interpretations (faces and vase) were clearly competing (Andrews et al., 2002).

We took advantage of the fact that inanimate objects and faces are known to be analysed in different areas of extrastriate visual cortex. Using fMRI, we localised regions of visual cortex selective for unambiguous faces in the fusiform gyrus and the superior temporal sulcus (Kanwisher et al., 1997). Object-selective areas were localised in the parahippocampal gyrus (Epstein and Kanwisher, 1998) and the lateral occipital lobe (LOC) (Malach et al., 1995). However, the selectivity of neural responses to these different classes of stimuli does not in itself demonstrate that the conscious perception of a face or an object is made explicit in these visual areas. It could be that this activity represents a divergence of processing before the level at which percepts arise. Indeed, it is also possible that explicit representations of faces and objects cannot be localised to particular areas in the brain, but are widely distributed (Haxby et al., 2001).

To determine whether the perception of faces and objects is made explicit in these areas, in the sense that activity correlates with conscious perception regardless of the physical stimulus, we monitored activity when subjects viewed the ambiguous vase-face stimulus. We hypothesized that a cortical area that makes 'explicit' in its activity the interpretation of a face would show more activity for a perceptual transition from vase to face than for a shift from face to vase. Conversely, areas directly involved in or leading to the awareness of inanimate objects ought to display an opposite pattern of activity. We

further posited that, if an area is involved in a specific aspect of visual awareness, the trial-by-trial variation in activity should correlate with the subjects' perceptual responses.

Since the frequency of spontaneous perceptual change was too rapid to be followed by the underlying BOLD response, we devised the procedure of adding local contrast gradients to emboss the edges of the ambiguous stimulus (Fig. 5A), and thus prolong perception of either the vase or the face after a perceptual transition. The activity of face-selective voxels in the fusiform gyrus did indeed discriminate between the alternative perceptions of the stimulus in this paradigm (Fig. 5B). Greater activity was detected following *vase-to-faces* transitions than during *faces-to-vase* changes.

These results are consistent with an earlier fMRI study of binocular rivalry in which complex objects (houses) and faces were presented independently to the two eyes and changes in perception from *house-to-face* were associated with increased activity in the fusiform gyrus (Tong et al., 1998). However, the authors also reported that changes from *face-to-house* resulted in a decrease in MR signal, while we did not find a systematic decrease following perceptual switches to the non-preferred (*vase*) percept. Kleinschmidt et al. (1998) also report only increases in activity in the fusiform gyrus during changes in perception when subjects viewed the vase-face stimulus, although they did not discriminate the direction of perceptual changes. This leads us to speculate that the competitive interactions underlying binocular rivalry between complex figures might, in some circumstances, employ a different mechanism to that involved in the interpretation of conventional ambiguous figures (cf. Andrews, 2001).

Activity in voxels in the superior temporal sulcus that were selective for unambiguous faces were not statistically significant predictors for the two perceptual

interpretations of the vase-face image (Fig. 5B). One explanation for why this area is able to distinguish between photographs of faces and objects, but is not able to discriminate between the vase and faces in the ambiguous stimulus is the paucity of explicit detail in the latter. It is possible that areas in the superior temporal sulcus are more concerned with the details of facial structure, such as eye gaze, expression and lip movement (Perrett et al., 1985; Hasselmo et al., 1989; Calvert et al., 1997; Haxby et al., 2000). Consistent with these findings, lesions to the superior temporal sulcus in non-human primates do not impair face recognition (Heywood and Cowey, 1992).

Areas selective for unambiguous inanimate objects were similarly unable to discriminate the direction of perceptual change when viewing the vase-face stimulus (Fig. 5B). Perceptual transitions to the preferred percept (*faces-to-vase*) did not produce more activity than shifts to the non-preferred percept (*vase-to-faces*) in either the parahippocampal gyrus or the lateral occipital lobe. Again, the most parsimonious explanation for this result is that the vase representation is a less salient percept than the photographs of objects that were used to define this area.

The observation that activity in the fusiform gyrus was selective for the different conscious interpretations of the vase-face stimulus when prolonged by embossing does not alone imply that the perception of a face is made explicit in this area. It could be, for example, that this activity simply reflects differential responsiveness to the relatively unambiguous embossed image, rather than to the initial spontaneous switch to perception of faces (see also Hasson et al., 2001). To control for the change in the stimulus, we compared activity in the fusiform gyrus when the sequence of stimuli was identical, but perception was different (Fig. 6A). We found that even when the physical stimulation

remained the same, more activity was recorded in the fusiform gyrus when a *vase-to-faces* transition preceded the presentation of an embossed face compared to when a *faces-to-vase* switch was initially reported (Fig. 6B). Moreover, using an analysis of choice probability (Britten et al., 1996), we found that the face-selective area in the fusiform gyrus was statistically predictive of the subjects' responses on a trial-by-trial basis (Fig. 6C). The implication is that activity in the fusiform gyrus could make a decision that leads directly to the perception of a face.

Our results are consistent with other studies that have shown the responses of regions within the temporal lobe are modulated by selective attention to faces (O'Craven et al., 1999) or when a degraded image of a face becomes recognizable after the subject views a photographic version of the same image (Dolan et al., 1997). More generally, it could be that this area is involved directly in the awareness of a broader range of specialized object categories (Tarr and Gauthier, 2000). Together these results strongly suggest that activity in the fusiform gyrus 'face area' reflects the perceived rather than merely the retinal stimulus.

CONCLUSION

Results from three lines of investigation lead us to believe that there is no single mechanism underlying binocular rivalry (and the perception of other ambiguous stimuli). Intuitively, the visual system must first determine whether the images in the two eyes should fuse or rival. Given the parallel nature of visual processing (Felleman and Van Essen, 1991), we suggest that the level at which competitive interactions occur will vary with the submodality of vision that is explicit in different bistable stimuli. Second, if

having determined that the images are incompatible, the visual system must then have a mechanism to suppress one monocular image and render the other image dominant. It is quite conceivable that this process occurs independently of the process that is involved in registering whether the two images are compatible (see Blake, 2001).

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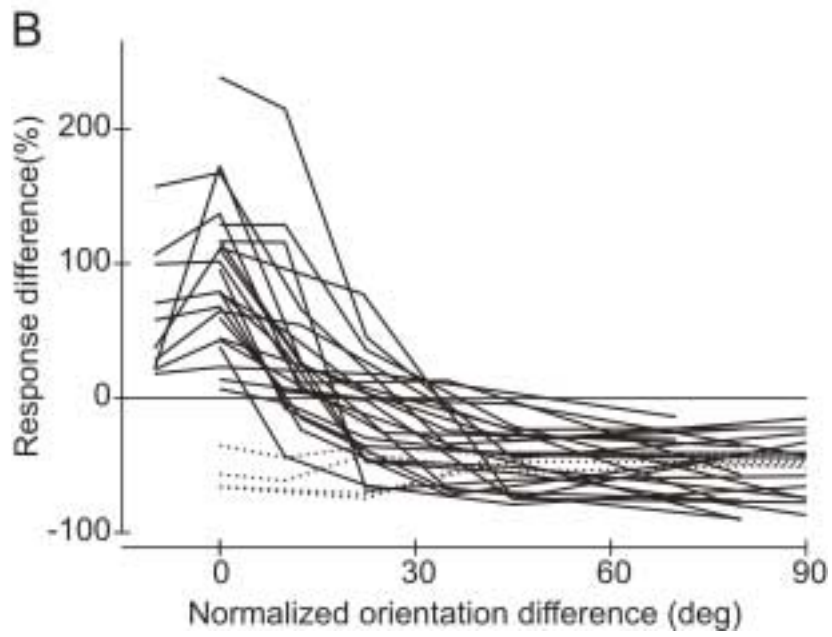
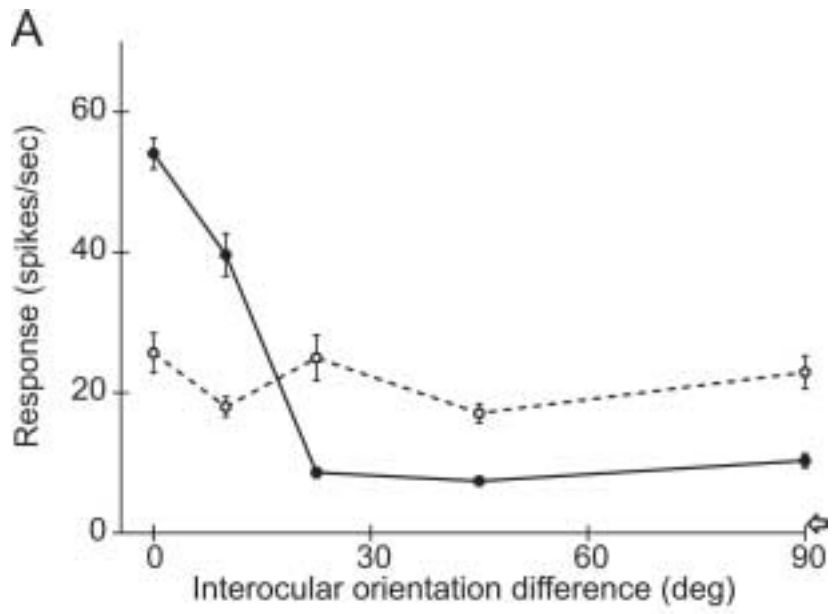


Figure 1 Orientation dependence of binocular interactions in an individual complex cell (**A**) and for 27 cortical neurons (**B**), modified from Sengpiel et al 1995a. **A**: Results of the binocular stimulation protocol for a layer 2/3 complex cell. A 'conditioning' grating of optimal orientation and direction of drift was presented continuously to the dominant, ipsilateral eye and gratings of various orientations were shown intermittently to the contralateral eye. Filled circles plot mean responses (\pm SEM) during binocular stimulation against the difference in orientation of the gratings in the two eyes, while unfilled circles show the mean responses during the immediately preceding periods of monocular stimulation. The arrow indicates the mean level of spontaneous discharge **B**: Binocular interaction functions for 27 cortical cells, plotting the difference between binocular and monocular responses as a function of the interocular difference in orientation. These functions show the range of variability in the depth of suppression and in the threshold interocular orientation difference for the transition between facilitation and suppression. All tuning curves with maximum facilitation at an orientation difference other than zero have been shifted to peak at zero. Included are the four monocular units recorded in layer 4 (data plotted as dotted lines), where suppression was essentially independent of interocular difference in orientation.

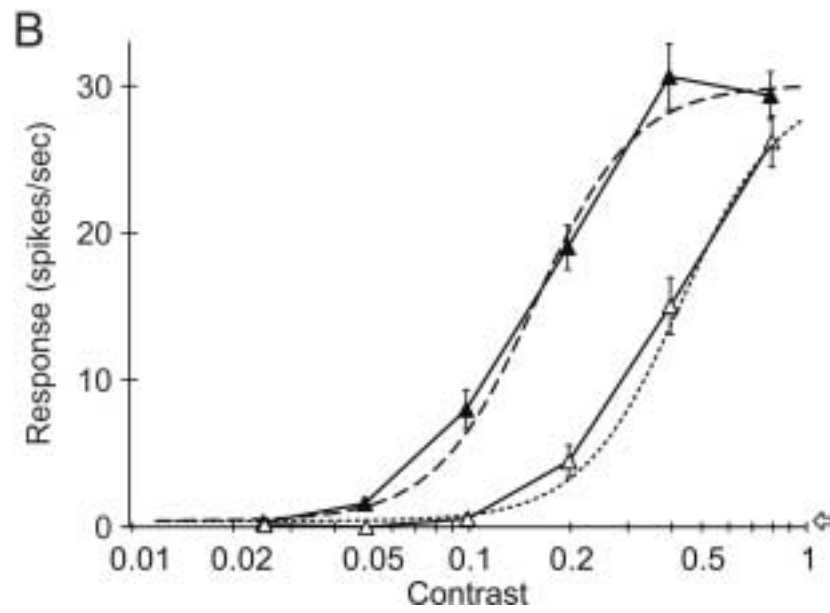
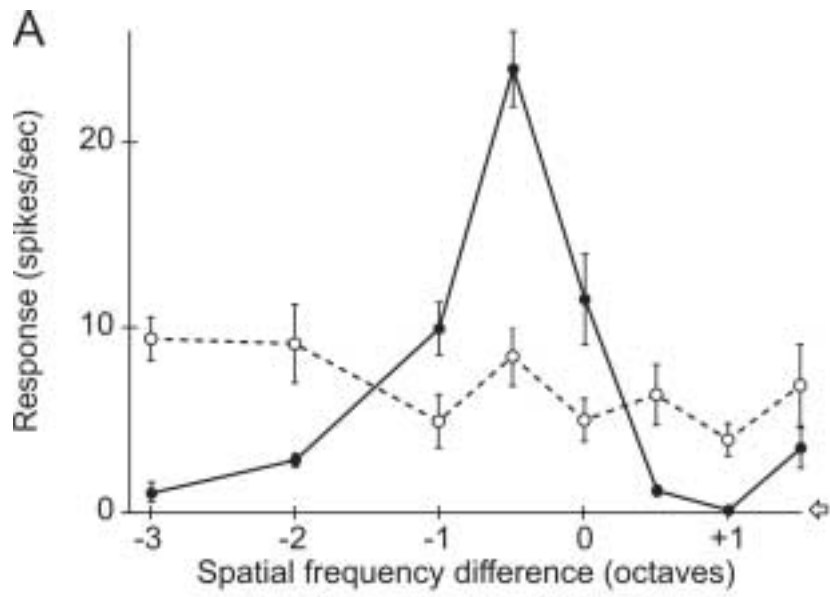


Figure 2 Spatial frequency dependence of binocular interactions (**A**) and effect of interocular suppression on the contrast-response function (**B**). **A**: Binocular responses of a layer 5 complex cell as a function of the spatial frequency presented to the non-dominant eye (modified from Sengpiel et al 1995b). The dominant eye was stimulated continuously with a grating of optimum orientation and spatial frequency (1.13 c/deg) while a grating of the same orientation but varied in spatial frequency was presented intermittently to the non-dominant eye. Filled circles plot mean responses (\pm SEM) during binocular stimulation against the difference in spatial frequency of the gratings in the two eyes, while unfilled circles show the mean responses during the immediately preceding periods of monocular stimulation. The abscissa is plotted in octaves relative to the spatial frequency of the grating shown to the dominant eye. The arrow represents the mean spontaneous discharge. **B**: Effects of interocular suppression on the contrast-response function of a layer 2/3 complex cell (modified from Sengpiel et al 1998). Mean responses (\pm SEM) are plotted against effective Michelson contrast of the (optimally oriented) test grating in the dominant eye, in the presence and absence, respectively, of a grating of the orthogonal orientation placed in the corresponding region in the non-dominant eye (contrast, 0.9). Contrast-response data obtained under the control, unsuppressed condition were fitted by a hyperbolic ratio function,

$$R = R_{\max} \cdot c^n / (c_{50}^n + c^n) + b,$$

where R_{\max} is the maximum attainable response, c_{50} the contrast that elicits the half-maximal response, and b the cell's spontaneous activity. Filled triangles plot unsuppressed responses; the dashed line represents the best fit ($R_{\max} = 29.69$ spikes/sec, $c_{50} = 0.16$, $n = 2.93$). Open triangles show suppressed responses; the dotted line

represents the best fit under the assumption that R_{\max} and n are unaffected ($c_{50} = 0.43$).

This corresponds to a threshold elevation by 0.43 log units.

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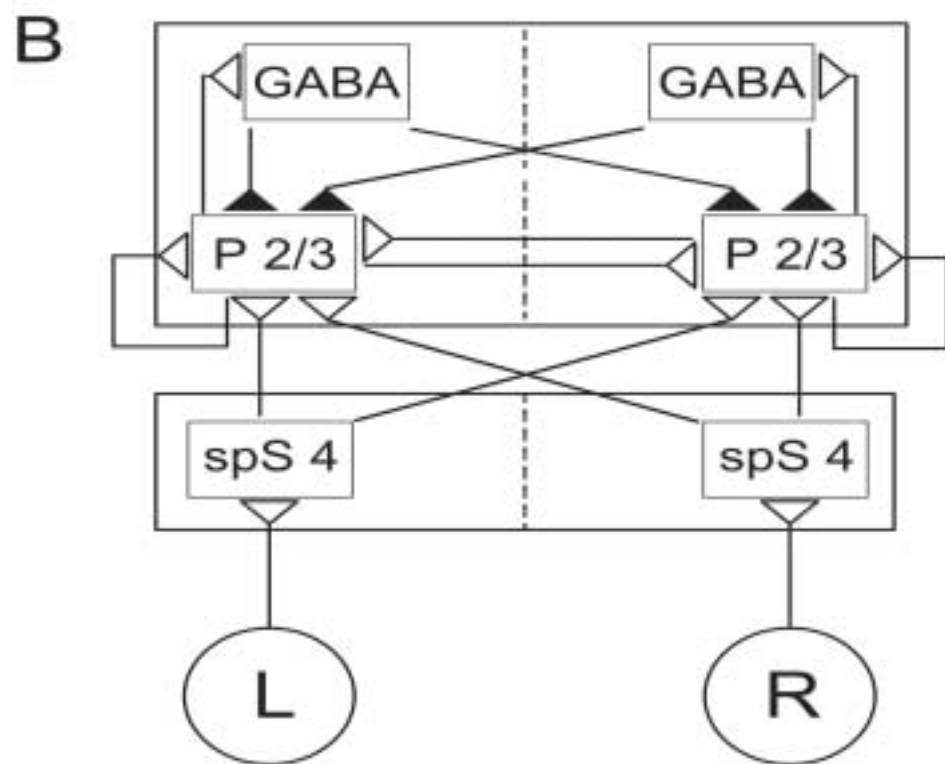
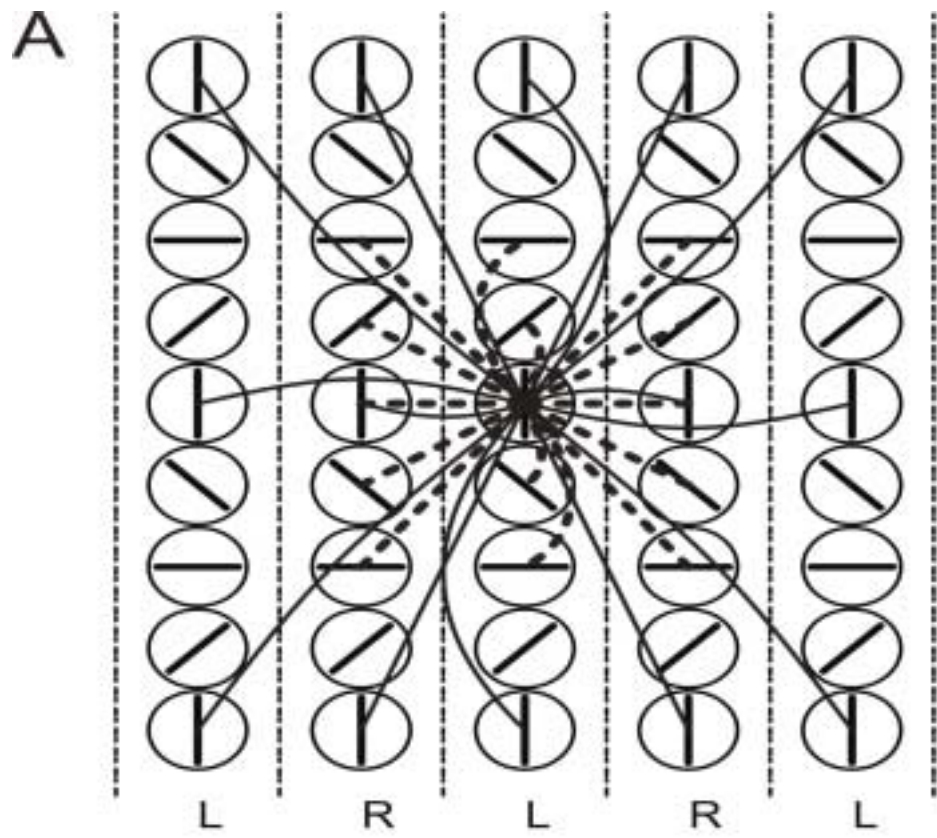
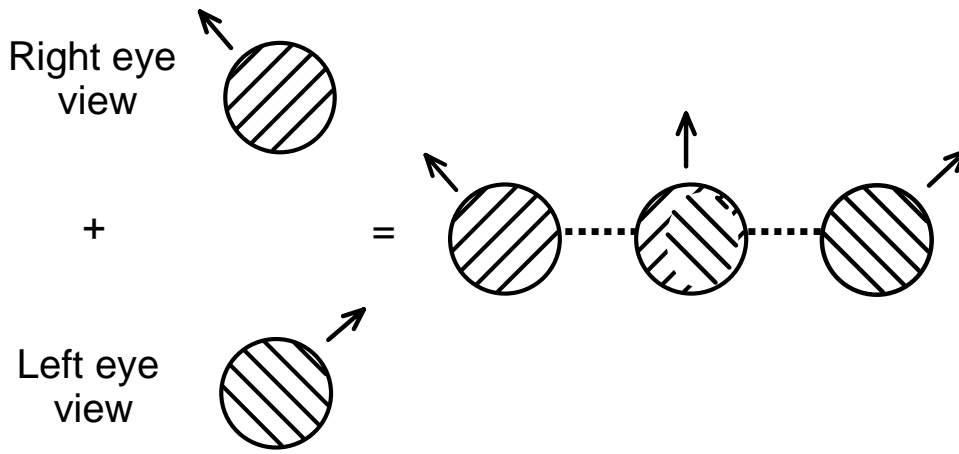
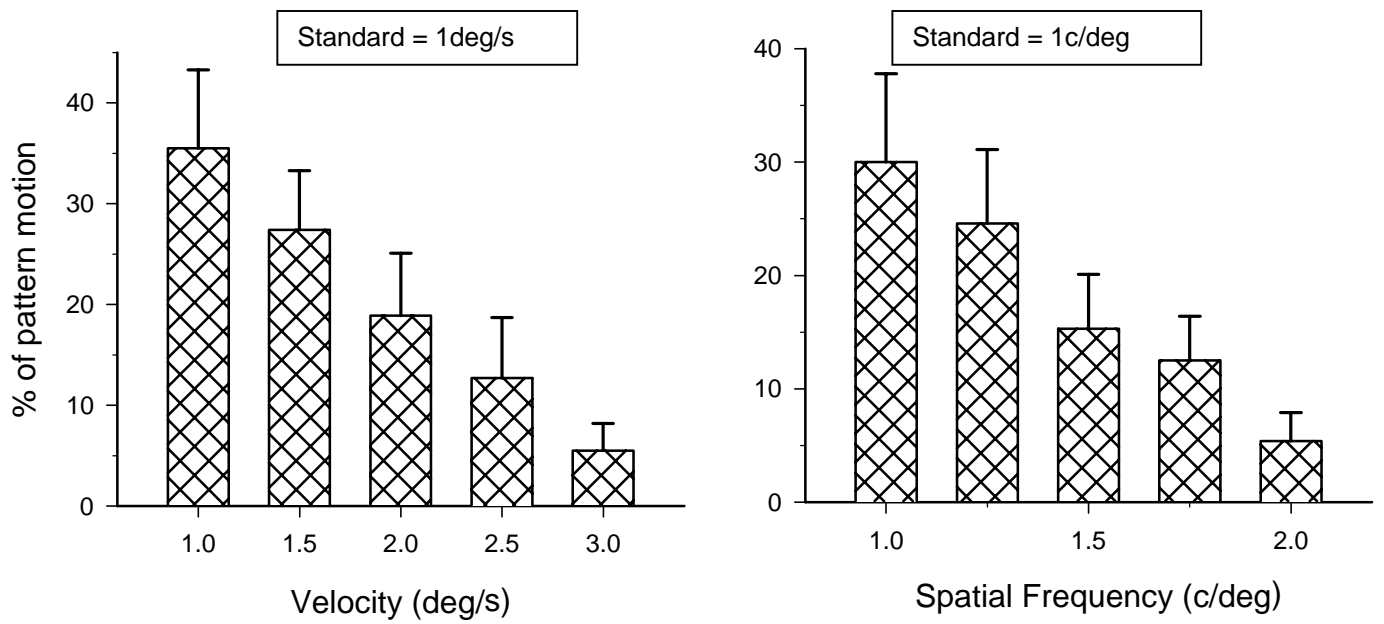


Figure 3 Schematic diagrams of intrinsic horizontal connections (**A**) and of within- and between-columns signal processing (**B**) that might underlie binocular interaction in cat V1. **A**: Surface view of orientation and ocular dominance domains with horizontal connections (modified from Sengpiel & Blakemore 1996). Parallel slabs or “columns” marked “L” and “R” represent left-eye and right-eye OD columns, respectively. Columns of cells with similar orientation preference are depicted as circles with an oriented line inside. Thin lines represent excitatory projections, which selectively connect neurons of similar orientation preference, respectively, within and between neighbouring OD columns, while thick dashed lines show widespread non-selective inhibitory connections. **B**: Diagram of a cortical microcircuitry in V1 that could generate binocular responses of the type that we observed. Circles marked 'L' and 'R' represent left- and right-eye inputs to spiny stellate cells in layer 4 of V1 ('spS 4'). Layer 2/3 pyramidal cells are indicated as 'P 2/3', GABA-ergic interneurons as 'GABA'. Open and filled triangles represent excitatory and inhibitory synapses, respectively. Vertical dashed lines separate cells with predominantly left-eye excitatory input from those with predominantly right-eye input.

A)



B)



C)

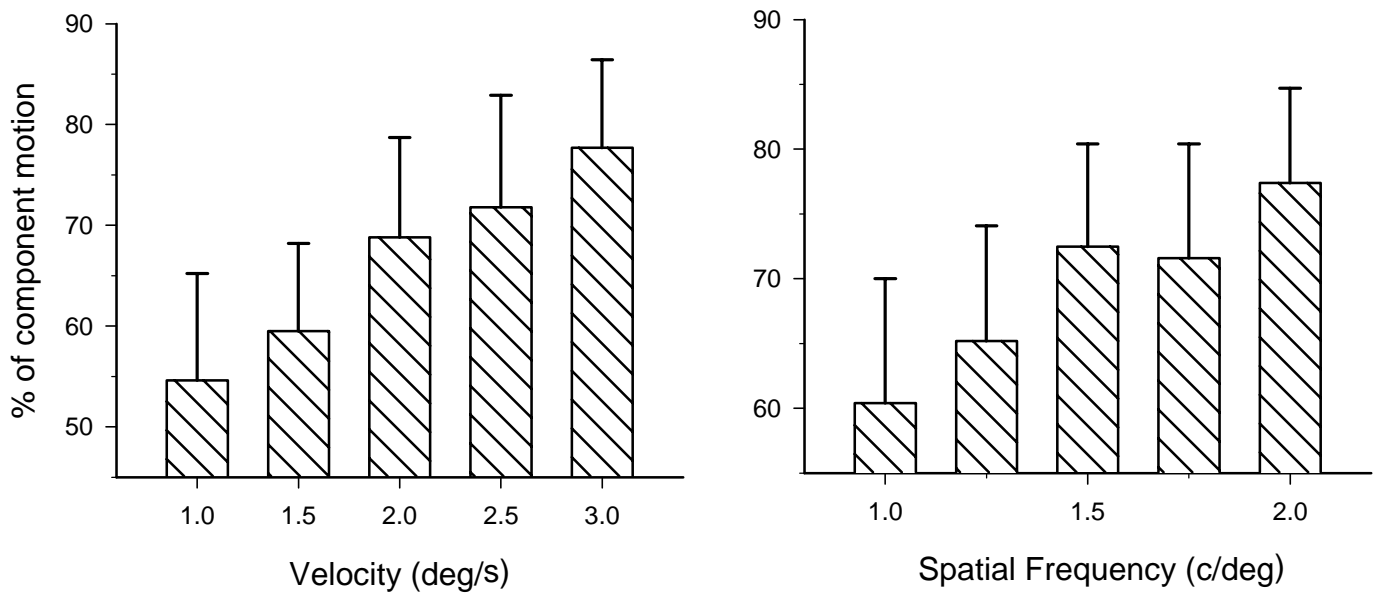
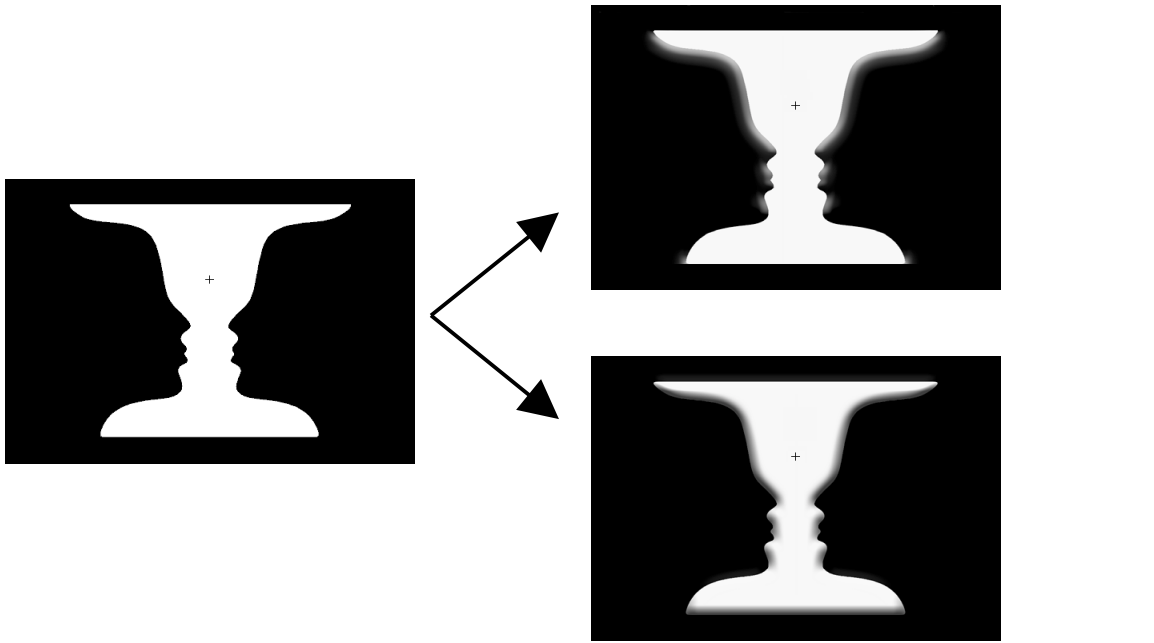


Figure 4 Integration of motion information during contour rivalry (modified from Andrews and Blakemore, 2002). A) During the transitions between exclusive dominance of one grating to dominance by the other, a fluid mosaic of contiguous patches of the two gratings is often seen. The grating patches within this mosaic are usually seen to move together, in the direction of pattern motion. Thus, the motion signals in the two eyes are combined, while orientation signals continued to rival. B) The grating in one eye (the Standard) was kept unaltered, while the grating presented to the other eye was gradually changed. The proportion of dichoptic pattern motion decreased as the gratings were made more different from each other in velocity or spatial frequency. C) In contrast, the periods of exclusive perceptual dominance increased in duration as the stimulus characteristics of the two gratings were made more dissimilar. The columns represent the mean from four observers. Error bars show 1 SEM.

A



B

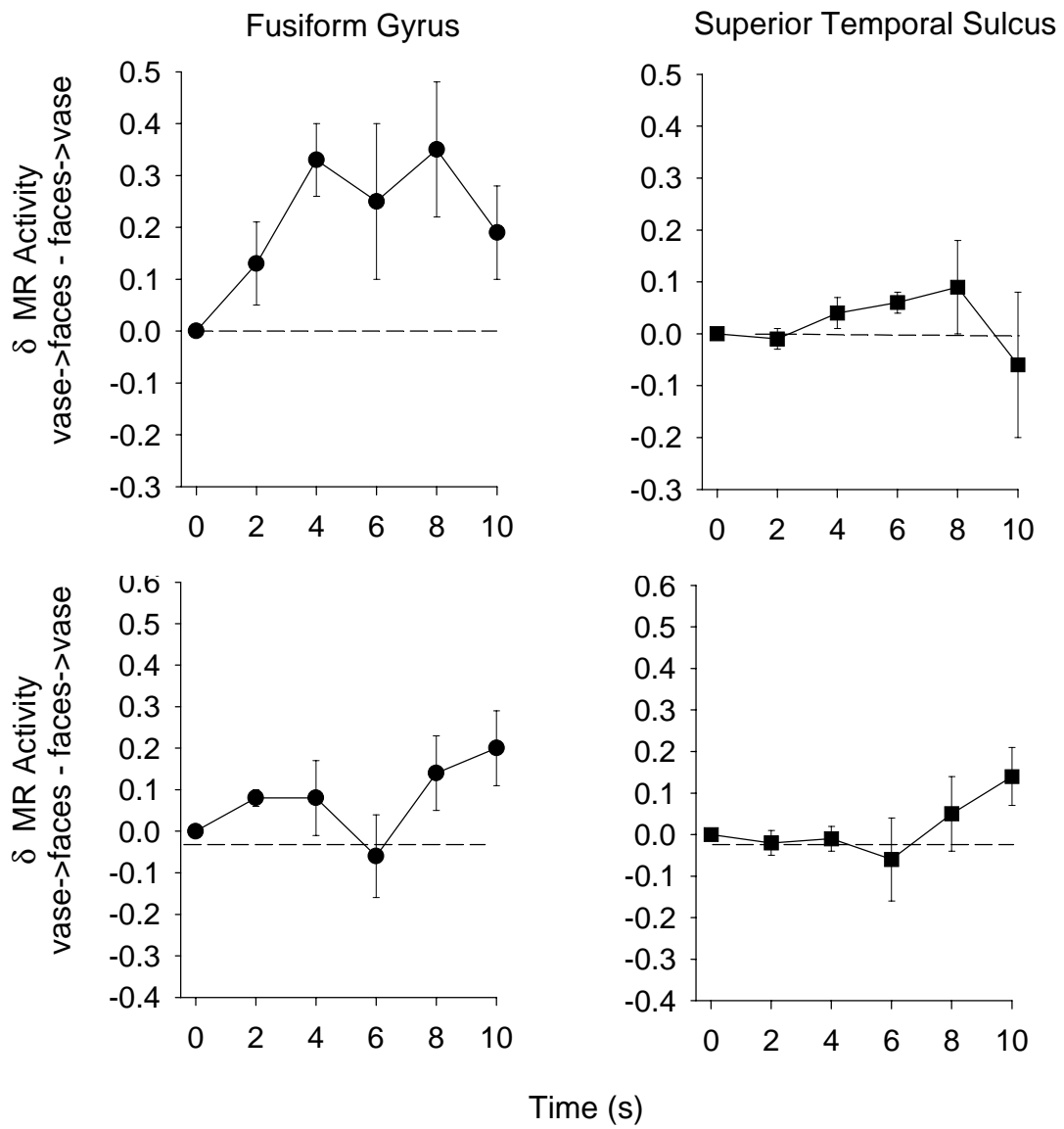
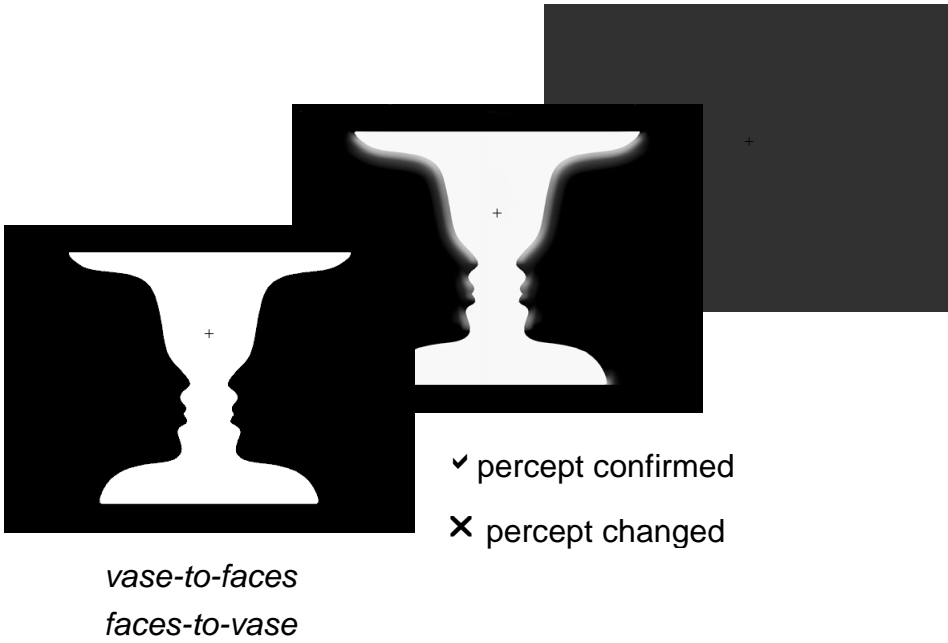
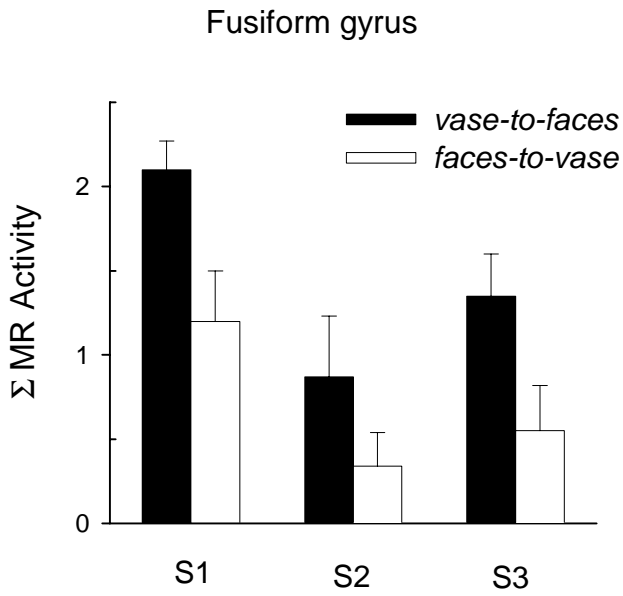


Figure 5 Activity in face- and object-selective areas when viewing the vase-face stimulus. A) An event-related paradigm was employed in which the sudden onset of perception of either the faces or the vase was prolonged by adding subtle local contrast gradients (embossing) to one edge or other of the figure-ground boundary. Thus, following a vase-to-faces transition, the standard image was replaced by an embossed-face version of the same stimulus (top), whereas subsequent to a *face-to-vase* change, an embossed-vase version (bottom) replaced the standard. B) Face-selective voxels in the fusiform gyrus, but not the superior temporal sulcus, reflected the perceptual interpretation of a face in the Rubin figure, when prolonged by the embossing technique. Object-selective voxels in the parahippocampal gyrus or lateral occipital complex did not show selectivity for the perceptual interpretation of the vase. Each curve represents a mean time course from 3 subjects. Error bars show 1 SEM.

A



B



C

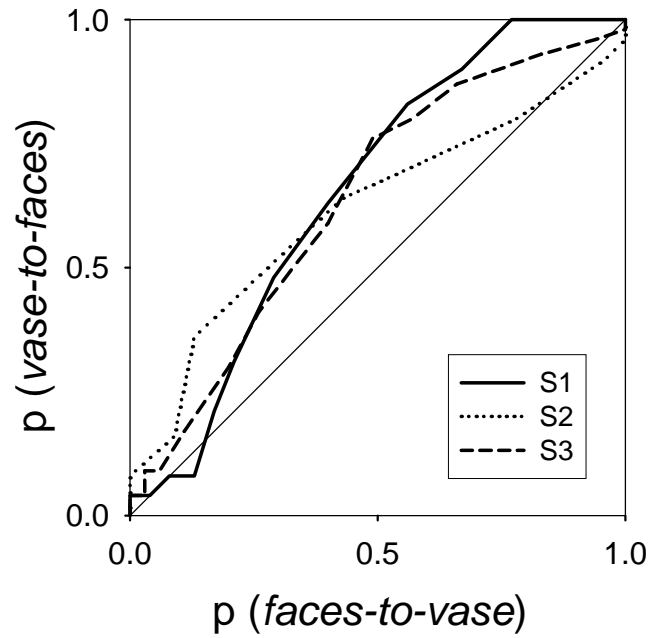


Figure 6 Activity in the fusiform gyrus predicted conscious perception of the vase-face stimulus (modified from Andrews et al., 2002). A) Responses were selected for all sequences in which a change of perception for the standard Rubin's stimulus, signalled by a button press, was followed by embossing of the *face* contours, thus biasing subsequent perception toward the faces percept. B) Each bar represents the integrated MR response for 6 sec after the spontaneous shift of perception. The sequence of physical images was identical in both conditions, yet more activity occurred if the perception of faces in the ambiguous figure was confirmed by the embossing than if it was changed. C) To assess whether the activity of the fusiform gyrus could predict perception when viewing the ambiguous stimulus on a trial-by-trial basis, we calculated the proportion of trials in which the MR activity correctly (hits) and incorrectly (false alarms) predicted the direction of perceptual change. Analysis of the data showed significant choice probabilities were apparent in the fusiform gyrus for each subject.