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# Single units and conscious vision

## Nikos K. Logothetis

*Max Planck Institute for Biological Cybernetics, Spemannstrasse 38, 72076 Tübingen, Germany (nikos.logothetis@tuebingen.mpg.de)*

Figures that can be seen in more than one way are invaluable tools for the study of the neural basis of visual awareness, because such stimuli permit the dissociation of the neural responses that underlie what we perceive at any given time from those forming the sensory representation of a visual pattern. To study the former type of responses, monkeys were subjected to binocular rivalry, and the response of neurons in a number of different visual areas was studied while the animals reported their alternating percepts by pulling levers. Perception-related modulations of neural activity were found to occur to different extents in different cortical visual areas. The cells that were affected by suppression were almost exclusively binocular, and their proportion was found to increase in the higher processing stages of the visual system. The strongest correlations between neural activity and perception were observed in the visual areas of the temporal lobe. A strikingly large number of neurons in the early visual areas remained active during the perceptual suppression of the stimulus, a finding suggesting that conscious visual perception might be mediated by only a subset of the cells exhibiting stimulus selective responses. These physiological findings, together with a number of recent psychophysical studies, offer a new explanation of the phenomenon of binocular rivalry. Indeed, rivalry has long been considered to be closely linked with binocular fusion and stereopsis, and the sequences of dominance and suppression have been viewed as the result of competition between the two monocular channels. The physiological data presented here are incompatible with this interpretation. Rather than reflecting interocular competition, the rivalry is most probably between the two different central neural representations generated by the dichoptically presented stimuli. The mechanisms of rivalry are probably the same as, or very similar to, those underlying multistable perception in general, and further physiological studies might reveal much about the neural mechanisms of our perceptual organization.

**Keywords:** visual perception; visual awareness; binocular rivalry; multistable perception; monkey psychophysics; monkey physiology

## 1. INTRODUCTION

The primate visual system is thought of as a hierarchical series of processing stages, each consisting of different areas or modules that work—to some extent—parallel to each other, analysing different visual attributes (Hubel 1988; Zeki 1993). Information enters the visual system through the retina of the eye. The retinal image of each eye is channelled through about one million nerve fibres to a thalamic structure in the brain known as the lateral geniculate nucleus (LGN), from whence it is projected to the striate or primary visual cortex, also called area V1. Cells in the retina and LGN are activated by one eye or the other and respond to any spatial change in luminance or colour within their receptive field. Striate neurons, however, can usually be activated by either eye and often respond only to contours or edges with a specific orientation, that is, they show orientational selectivity. Moreover, many show selectivity for certain colours or directions of motion, or for a certain position in the depth of field. Cells sharing similar stimulus preferences tend to be grouped together in columns spanning the entire thickness of the cortex.

One can imagine the striate cortex as a two-dimensional array of functional units, each of which has a sufficient number of columns to examine contours in all orientations with both eyes (Hubel 1988). Roughly speaking, then, a simple geometrical pattern in the visual field (e.g. a hexagon) will generate an isomorphic pattern of excited cortical units, each having a number of active orientation columns. But is the concurrent activation of such columns what our perception of the hexagon is all about? Neuroscientific data say not.

For one thing, visual processing does not end in V1. Information is transmitted to more than two dozen other extrastriate cortical areas (Felleman & Van Essen 1991; Zeki 1978) that also contain maps of the visual field (Cowey 1979; Kaas 1978; Van Essen 1979, 1985) and are organized in two relatively segregated cortical streams of visual processing: a dorsal stream stretching towards the parietal lobe and a ventral one towards the temporal lobe (Merigan & Maunsell 1993). Selective damage to different areas shows that the dorsal stream processes information about the location and motion of objects, whereas the temporal stream processes information related to object recognition (Mishkin *et al.* 1983; Ungerleider & Mishkin 1982).

Individual extrastriate areas show various degrees of functional specialization that is evident in the stimulus selectivity of their neurons (Zeki 1978). Cells in the dorsal area MT (or V5), for example, show a pronounced directional selectivity, whereas neurons in the temporal
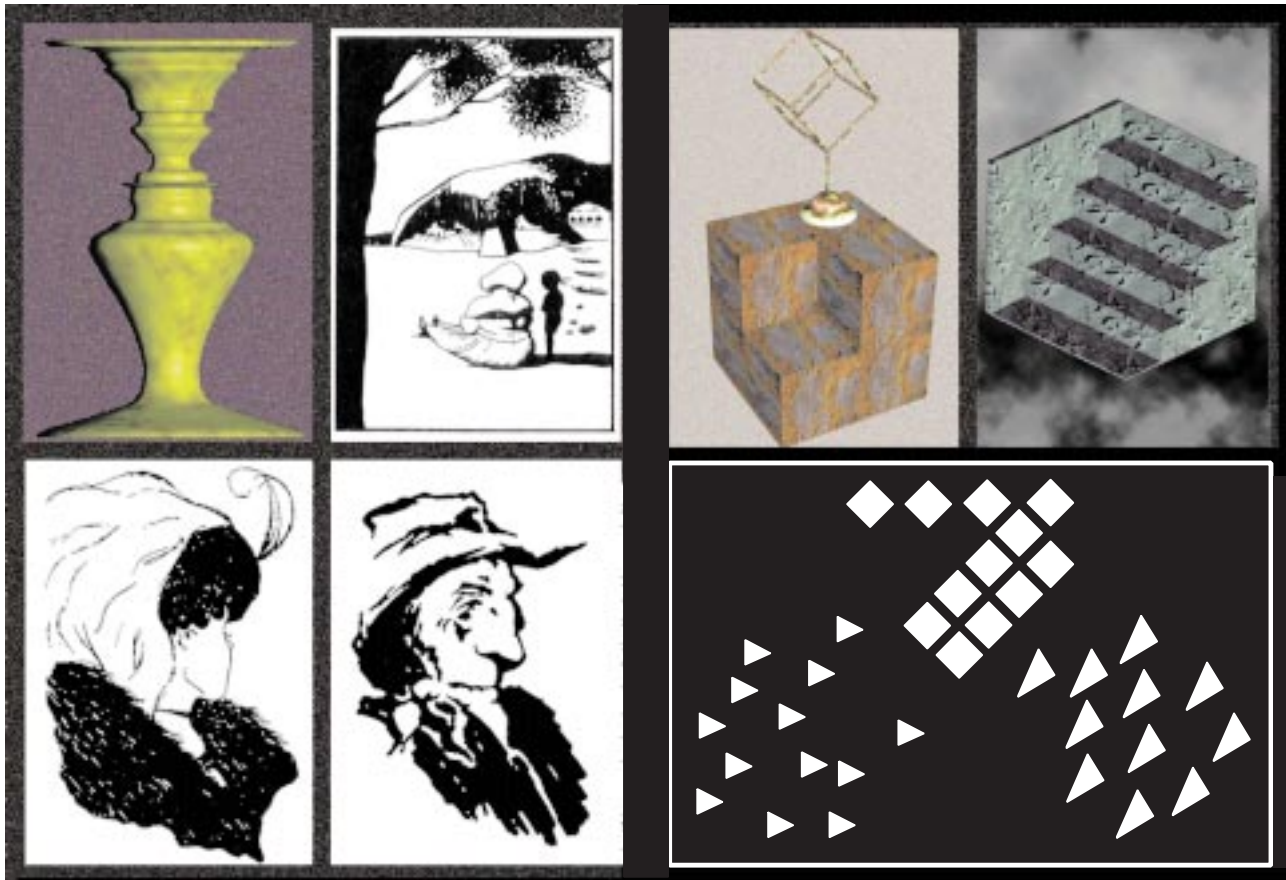
Figure 1. Ambiguous figures such as figure–ground, depth, or object reversals can tell us much about the nature of the perceptual system, because changes in perception while viewing such figures are endogenous rather than a result of changes in the stimulus itself. The figure shows different types of ambiguous picture, such as figure–ground reversals (top left pair), perspective reversals (top right pair), ambiguous objects (bottom left pair), and reversals of axis of symmetry (bottom right). Ambiguous figure–ground relations: the goblet-and-faces illusion was introduced by Edgar Rubin (1915). In it we see either two faces or a vase, with perception alternating between the two interpretations. On its right is a reversible figure–ground pattern drawn by Salvador Dali ('The three ages'). Ambiguous perspectives: the Necker cube and the Schroeder staircase. Another example of reversibility is the 'missing cube', which can be seen as a block with a cube missing from the corner nearest to the viewer, or as a cube in the upper corner of a room! Ambiguous objects: the 'young girl–old woman' figure was brought to the attention of psychologists by Edwin Boring in the 1930s. It was published in *Puck* in 1915 by the cartoonist W. E. Hill with the title 'My wife and my mother-in-law'. A few years later Jack Botwinick produced 'My husband and my father-in-law'. Ambiguous orientations: a multistable stimulus reported by Fred Attneave (Attneave 1971). The triangles (or the diamonds) change orientation, sometimes pointing one way, sometimes another, and sometimes a third way. The ambiguity here is probably due to the existence of more than one axis of symmetry. For example, an equilateral triangle has three axes. A scalene, in contrast, has none, but it can be perceived as an isosceles triangle seen at an angle, thus yielding both symmetry and depth reversals.

areas V2, V3 and V4 respond selectively to visual form (orientation, colour or depth cues) and those of the inferior temporal cortex—the highest end of the temporal processing stream—to views of entire objects, including human and monkey faces (Van Essen 1979, 1985).

Second, the activity of cells in the extrastriate areas is often not determined solely by local image properties, as it usually is in the striate cortex. For instance, the neurons in area V2 already show the same orientational specificity towards illusory contours, such as those of the Kanisza triangle, as they do towards real contours that are specified by local intensity changes (von der Heydt *et al.* 1984). Similarly, the response of many MT cells to a moving pattern can be influenced by the motion of other moving objects far outside the classical receptive field of the cells (Allman *et al.* 1985).

Finally, many areas of cortex change their activation level depending on whether or not the monkey is paying attention to or is required to remember a particular stimulus (Colby 1991; Desimone & Duncan 1995; Maunsell 1995), a finding suggesting that these areas might be involved in the perceptual organization of the visual input by combining the activity elicited by the sensory data with endogenous activity that reflects past experience and anticipation of the future.

It seems, then, that the visual cortex as a whole has all the machinery requisite for analysing an image, but how is this machinery used by the brain to make us aware of the visual environment? Why is it, for example, that many cells in both the striate and the extrastriate cortex are known to respond to their 'preferred' stimulus even when an animal is
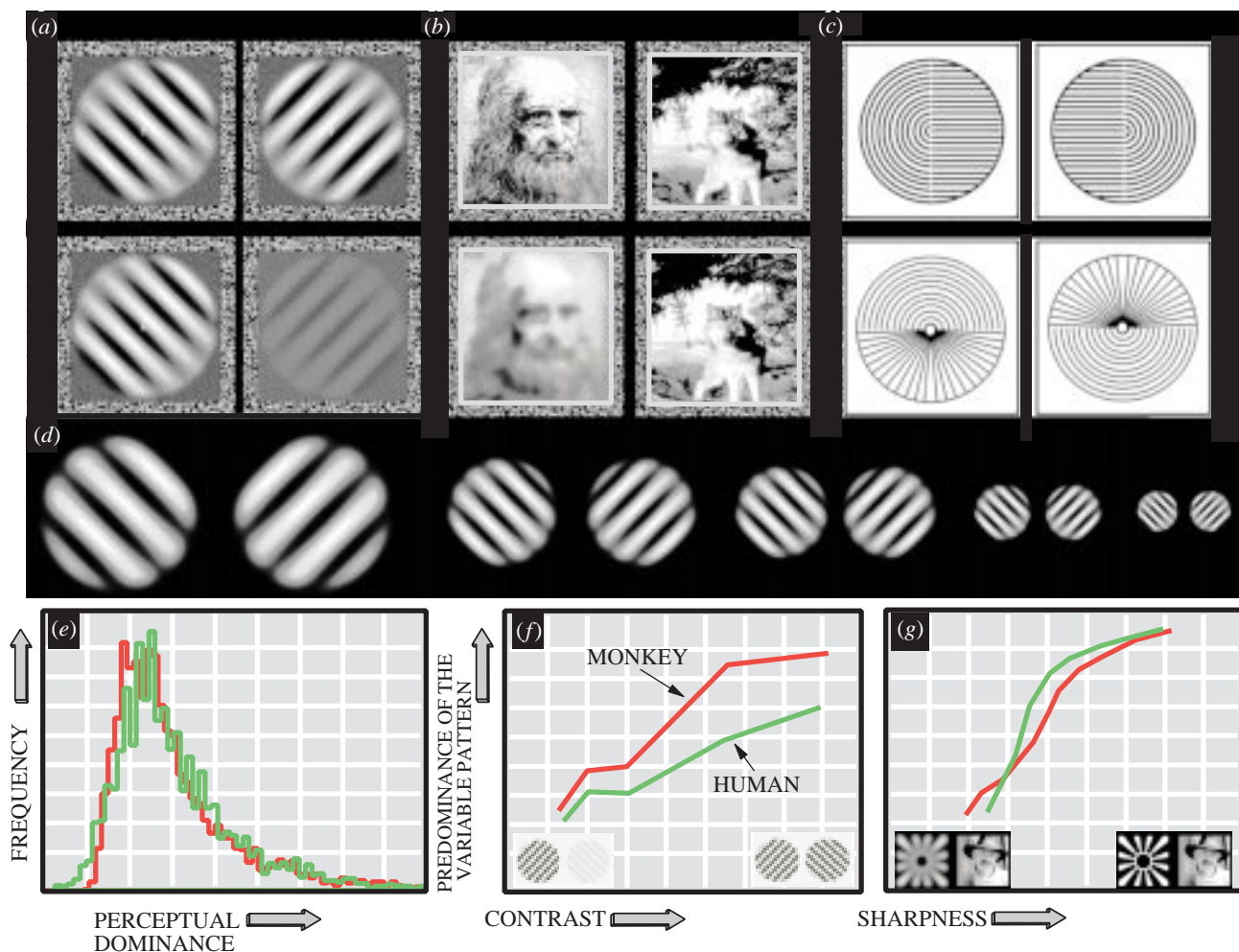
Figure 2. (*a*) Grating patterns of orthogonal orientations that are usually employed in the study of binocular rivalry. The patterns are also suitable for the study of the physiological mechanisms of rivalry, as they differentially activate orientation-selective neurons in a number of visual areas. Varying the strength of the patterns (e.g. contrast) changes the predominance of each stimulus. Strong stimuli remain suppressed for shorter periods. (*b*) Rivalling complex patterns like those used to study the role of the inferior temporal cortex in the awareness of a stimulus. The strength of such stimuli is determined by the pattern's spatial frequency range (Fahle 1982). Limiting the range (here by just blurring the image) decreases the predominance of the stimulus. (*c*) Patterns demonstrating that rivalry does not occur just between the two eyes or the two cerebral hemispheres (Diaz-Caneja 1928). When the Caneja patterns are presented dichoptically, rivalry occurs between the circles and the horizontal (or radial) lines. What compete against each other are thus the two most coherent percepts that can be derived by combining the two halves of the patterns interocularly and inter-hemispherically. (*d*) Exclusive dominance of pattern during rivalry depends on both the size and the spatial frequency of the stimulus (O'Shea *et al*. 1997). Stimuli of low spatial frequency (left) that are much larger than patterns of higher spatial frequency can still yield frequent phases of exclusive dominance. (*e*) Distribution of alternation phases for human and monkey subjects. (*f, g*) Both humans and monkeys show the same predominance–strength functions for two different stimulus types.

anaesthetized and thus unaware of the stimulus? What is it that determines what we see? Are there populations of neurons that are only activated when a stimulus is perceived?

## 2. MULTISTABLE PERCEPTION

### (*a*) *Ambiguous figures*

Such questions can be addressed in combined psychological and electrophysiological experiments in which the response of neurons to ambiguous stimuli is studied. These are stimuli that on continuous inspection spontaneously change appearance with no concomitant

changes in the retinal stimulus. Classic examples are the well-known perspective reversals such as the Necker cube or Schroeder's staircase, various ambiguous objects like the much celebrated 'young girl–old woman' illusion, and a large number of images with labile figure–ground organizations such as the vase-and-faces by Edgar Rubin and many of the famous drawings by M. Escher (figure 1). Ambiguous figures have long been used by psychologists to study the principles of perceptual organization (Attneave 1971) and could, in principle, also be used in experiments with behaving animals to investigate the neural mechanisms underlying the visual awareness of a pattern.

Let us assume that a neuron responds selectively to the unambiguous version of a stimulus, say to the lateral view of a face, as many neurons do in the inferior temporal cortex of the monkey. Would the same cell fire when presented with the faces–goblet pattern? And if so, would it do so only when the faces are perceived? If neurons indeed exist whose responses are contingent upon the perception of a stimulus, are such neurons located in specific areas or are they distributed throughout all levels of the visual processing hierarchy?

In an attempt to answer these questions, D. Leopold, D. Sheinberg and I conducted a number of experiments in monkeys trained to report the perceptual changes experienced during dichoptic stimulation, i.e. when the two eyes receive dissimilar images that cannot be fused into a single percept. Under these conditions both human and monkey observers experience fluctuating perceptual dominance and suppression of each monocular stimulus, a condition known as 'binocular rivalry' or simply 'rivalry'. Dichoptic stimulation offers an exquisite experimental paradigm for the study of visual awareness. First, any patterns presented dichoptically will compete for awareness (figure 2). To elicit rivalry, the experimenter needs only to determine which stimuli excite the neuron under study and which do not. A rivalling pair could be a simple orientated grating pattern, which typically excites many neurons in the early visual cortex, presented to one eye, and a grating of a different orientation (a difference of more than 20–30° is sufficient to induce rivalry) presented to the other. Alternatively, one stimulus could be a complex visual object, such as the view of the face or the body of an animal, which often elicits selective responses in the visual areas of the temporal lobe, and the other a geometrical pattern that fails to elicit neural responses. Second, each of the rivalling patterns can be readily presented as an unambiguous stimulus to which a monkey can be trained to respond in the desired way. Finally, recent psychophysical and electrophysiological studies suggest that the neural processes underlying the perceptual dominance of a pattern during rivalry might be closely related to those underlying the selection of a percept when viewing ambiguous figures. The study of rivalry can therefore provide us with direct evidence pertaining to the neural mechanisms of perceptual organization in general.

### (b) *Binocular rivalry*

Pattern rivalry was first reported by the inventor of the stereoscope, Wheatstone (1838), who noticed that two letters presented dichoptically do not fuse but instead compete for visual awareness. Typically one letter alone is seen for a while, after which it breaks into fragments that mingle with patches of the other, to be immediately replaced entirely by the other letter. Similar perceptual changes had been already reported for conditions under which the two eyes were presented with two different colours (DuTour 1760). Sometimes one colour dominated perception for a while, during which time the other one was phenomenally suppressed, and at other times bits and pieces of both colours could be perceived simultaneously.

The first comprehensive account of rivalry was given by Breese (1899, 1909) around the turn of the century. Since then, a large number of studies have extended Breese's initial findings by detailing the dichoptic conditions that trigger perceptual oscillations (Blake 1989; O'Shea 1983). Further research has elucidated the nature of phenomenal suppression of a rivalling pattern and promoted different theories that attempt to explain the mechanisms and site of stimulus selection (Blake 1989; O'Shea 1983; Walker 1978).

A characteristic property of rivalry is that the successive periods of visibility and invisibility of a pattern—which are usually referred to as the pattern's (or the eye's) 'dominance' and 'suppression' phases—are truly stochastic (Blake *et al*. 1971; Fox & Herrmann 1967; Levelt 1965, 1967; Walker 1975); in other words, the seemingly random alternations of rivalry are not due to the chaotic behaviour of a dynamic neural system (Lehky 1995). The average dominance and suppression periods vary both with subject and with stimulus type. Yet when individual phase-durations are normalized, e.g. expressed as fractions of their mean, their distribution can be very closely approximated by gamma functions, the parameters of which show considerable inter-subject similarity between humans and monkeys (Leopold & Logothetis 1995; Levelt 1965; Myerson *et al*. 1981; Sheinberg & Logothetis 1997). Interestingly, the same distribution of phase-durations has been reported for other multistable phenomena, such as the perspective reversals (Borsellino *et al*. 1972).

The temporal dynamics of rivalry depend strongly on the stimulus strength, a term specifying the combined effect of such stimulus parameters as luminance, contrast, spatio-temporal frequency, and amount of contour per stimulus area (Levelt 1965, 1966). The stimulus strength influences the overall visibility of a monocular pattern (also called its predominance) in a complex way. An increase in the stimulus strength in one eye increases the predominance of this stimulus only by decreasing the contralateral eye's mean dominance (Fahle 1982; Fox & Rasche 1969; Leopold & Logothetis 1995; Levelt 1965; Sheinberg & Logothetis 1997). The mean dominance of the eye receiving the stronger stimulus is hardly affected. One possible explanation of this finding is that the neural populations that underlie the visibility of a stimulus are different from those involved in the inhibition of the contralateral pattern.

## 3. RIVALRY HAS A CENTRAL ORIGIN

Early research showed that the perceptual changes during rivalry have a central origin, reflecting a selection process that takes effect subsequent to the analysis of the two monocular stimuli, rather than fortuitous changes in the patterns of retinal stimulation. For example, rivalry was demonstrated to occur between afterimages (Breese 1899) or optically stabilized images (Ditchburn & Pritchard 1960), as well as when the intrinsic ocular muscles were paralysed or artificial pupils were adopted (Lack 1971). Thus, factors such as eye movements, local adaptation, and shifts in accommodation, although they were found to influence the rate of rivalry to a limited degree (Lowe & Ogle 1966; Richards 1966), could safely be eliminated as causes in the generation of the perceptual alternations (Walker 1978).

Although rivalry has a central origin, it can only be controlled voluntarily to a limited degree and is only

partly related to visual attention. Initially, Breese and Helmholtz (Breese 1899; Helmholtz 1909) argued that although bright and distinct stimuli generally prevail over weaker contralateral stimuli, this trend could be reversed by directing attention toward the latter. Helmholtz (1909) further reported that it was possible to control rivalry at will by making one stimulus 'interesting', say, by counting its various contours, or by making voluntary eye movements perpendicular to the contours of a pattern. Later experiments, however, could not replicate these results. Whereas naive subjects can learn to control the rate of binocular rivalry (Meredith & Meredith 1962) and their ability to do so improves with practice (Lack 1970), the systematic, voluntary selection of one eye's stimulus, and the maintenance of a given perceptual state for an arbitrarily long time, are impossible tasks. This suggests that cognitive capacities such as attention are not the cause of rivalry, but rather that they have a modulatory influence on the spontaneously triggered perceptual alternations (Lack 1978).

To some extent, the predominance of a stimulus during rivalry also seems to be influenced by familiarity. For example, when two portraits, one of which is inverted, are presented dichoptically for one minute, subjects report seeing the upright face more completely than the inverted face (Engel 1956). Similar results were obtained in experiments with dichoptically presented words, in which the more frequent of the two words was reported most often (Davis 1959). Finally, the induction of content was shown to be a powerful determinant of which of the two stimuli is perceived. The presentation of dichoptic stimuli immediately after another 'inducing' word that provides a contrasting or contingency context showed that induction was critical in choosing one of the rivalling words (Rommetveit *et al.* 1968).

The effects of cognitive processes on rivalry not only implicate central processes in the phenomenon but also, as Helmholtz was the first to notice, offer proof that the two monocular fields remain independent and that the information within each field is fully analysed regardless of the state of dominance, because it is only then that the system can 'select' between two alternatives.

## 4. THE NEURAL SITE OF SUPPRESSION

### (a) *Psychophysical evidence*

Extensive psychophysical research has showed that the perceptual disappearance of a pattern during dichoptic stimulation ought to be due to a disruption of the normal flow of visual processing within or beyond the primary visual cortex. This conclusion was drawn after carefully studying the magnitude of the visual after-effects of stimuli engaged in binocular rivalry.

After-effects are measurable distortions in the perception of a pattern caused by the prolonged inspection of other patterns. For example, after tilted or curved lines have been gazed at for a certain length of time, physically vertical lines appear off-vertical in the direction opposite to that of the initial inspection (Gibson & Radner 1937). Similarly, observation of high-contrast gratings interferes the detection of gratings with the same spatial frequency (Blakemore & Campbell 1969), prolonged inspection of gratings of one spatial frequency

influences the perceived spatial frequency of other gratings (Blakemore & Sutton 1969), and prolonged observation of a field of steadily moving contours makes a stationary test field seem to move in the opposite direction (Wohlgemuth 1911). The magnitude or strength of such after-effects is estimated by their persistence after the adapting stimulus has been terminated, and it is found to increase—up to a certain limit—with the length of exposure to the adapting stimulus.

In a series of such studies, Robert Fox, Randy Blake and their collaborators asked the following simple and clever question: does a steadily present stimulus cause the same after-effects whether it is perceived continuously or intermittently? In other words, is an invisible stimulus still analysed by the visual system and how far does such an analysis go? It was shown that rivalry exerts no influence on the growth of contrast-threshold elevation and spatial frequency shift after-effects (Blake & Fox 1974a), of the linear motion after-effect (Lehmkuhle & Fox 1975) or of the tilt after-effect (Wade & Wenderoth 1978), as the recovery time from all of these after-effects was found to be proportional to the physical and not to the perceived stimulus presentation (figure 3). Taking into account the orientation selectivity of these after-effects (Blakemore & Campbell 1969; Blakemore & Nachmias 1971; Blakemore *et al.* 1970) and the fact that visual attributes such as orientation and direction are first processed in the striate cortex of the primate, these findings suggest that the processing of information pertaining to the suppressed stimulus is unaffected at least up to the level of the striate cortex.

The same conclusion was derived from experiments demonstrating the interocular transfer of various after-effects (Blake & Overton 1979; Blake *et al.* 1981; O'Shea & Crassini 1981; Wade & Wenderoth 1978). All simple after-effects produced by adapting one eye during rivalry were also experienced with the unadapted eye on monocular inspection, showing that at least some binocular neurons—which also do not appear until V1—remain unaffected during the perceptual suppression of the stimulus. Disruption of information before it reaches the binocular neurons in V1 would most probably severely reduce any interocular transfer, as it does in humans lacking stereopsis (Movshon *et al.* 1972).

The processing of some complex stimulus attributes, on the other hand, was found to be disrupted during binocular suppression. For instance, after-effects produced by continuous inspection of spiral motion (Wiesenfelder & Blake 1990) or subjective contours (Van der Zwan & Wenderoth 1994) were reduced when adaptation occurred under rivalry conditions. Neural-response selectivity for such stimuli does not appear until the visual areas MST (Graziano *et al.* 1994; Tanaka & Saito 1989) and V2 (von der Heydt *et al.* 1984), respectively.

In terms of neural mechanisms the results of these psychoanatomical experiments can be interpreted in three possible ways, the last two interpretations not necessarily being mutually exclusive:

1. Information about the stimulus is blocked after the input layers of V1, and thus is not available to the other extrastriate areas such as V2 or MT. Because neurons in the striate sublayers 4Ca and 4B are orientation-selective and direction-selective and because more than
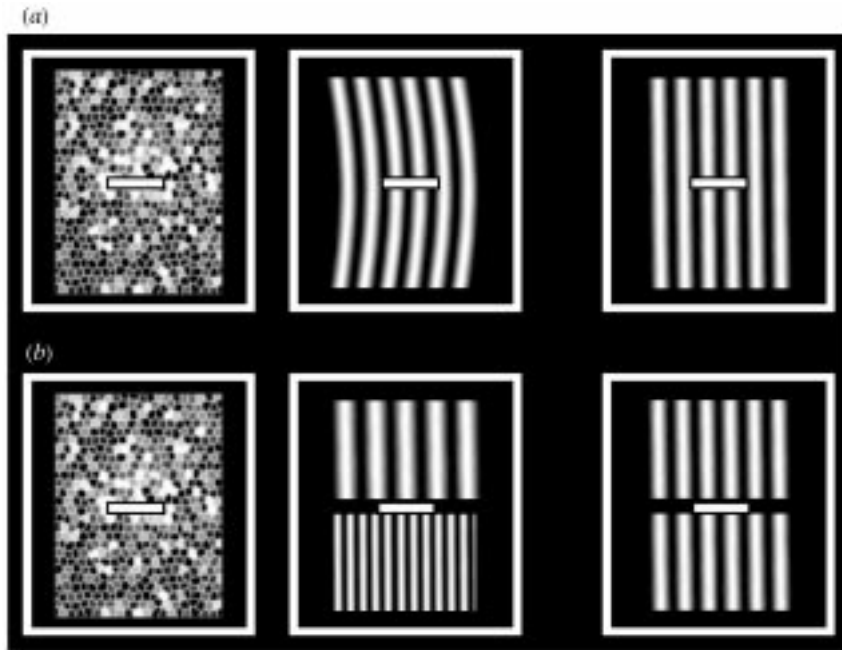
Figure 3. The tilt after-effect (*a*), and the spatial frequency shift after-effect (*b*), during binocular rivalry. Adapt for about 60 s by scanning back and forth along the fixation bar in the middle of the pattern, then quickly shift your gaze to the fixation bar of the vertical grating on the right (or to the fixation bar between the two equal-frequency gratings in the lower row). The upper grating should now appear to curve away from the adapting grating, whereas the two lower gratings should clearly appear to have different spatial frequencies. Repeat the procedure by fixing your gaze on the leftmost pattern with the adapting stimulus, and compare the endurance of the after-effect in the two conditions (see the text for references).

half of the cells in layers 4B and 4A are binocular, undiminished activity in layer 4 should be sufficient for generating the orientation and direction adaptation after-effects, as well as their interocular transfer.

2. The disruption in the flow of visual information is unrelated to anatomical or functional borders. Instead it reflects changes in the firing rate of certain types of neurons that might be distributed across different areas. Such neurons might be evenly distributed across the different cortical layers or clustered in one or more layers (see Crick (1996) for discussion).

3. The perceptual dominance or suppression of a stimulus is associated with changes in the degree of correlation between the firing of cells, rather than with the mean firing rate of single neurons. In this case, adaptation after-effects can be thought of as the result of undiminished activity of individual neurons, whereas dominance and suppression of the visual stimulus might be due to changes in coherence in the activity of the neural population.

In what follows we review recent neurophysiological evidence showing that the first interpretation is unlikely to be correct in the monkey visual system. Moreover, even though perception-related coherence changes cannot be excluded during rivalry, the existence of a large number of cells that strongly increase their firing rate during the dominance of the stimulus and decrease it during suppression indicates that response synchronization—if it occurs—cannot be, by itself, the 'neural correlate' of perceptual organization.

### (b) *Physiological evidence*

Much electrophysiological research has been conducted on the neural mechanisms of binocular vision. However, only a few of these studies are directly pertinent to binocular rivalry. Most experiments on binocular interactions were actually done with non-specific stimuli that do not induce binocular rivalry in humans. Recordings were

performed in cats and monkeys in both the LGN and the visual cortex.

#### (i)  *Lateral geniculate nucleus*

The LGN has often been considered to be the site of suppression, mainly because of its anatomy and the organization of its retinal and cortical inputs (Singer 1970). In cats and monkeys, as well as in many other species with well-developed binocular vision, the retinal terminals reaching the LGN remain segregated by projecting to different layers that are separated by the koniocellular zones, which contain numerous tiny neurons whose function is still unclear. Each layer receives excitatory input from one eye and contains a detailed retinotopic map of the contralateral visual field. Moreover, the maps of different layers are in perfect register, providing an ideal substrate for local or global inhibitory interactions between the two eyes. Finally, the LGN receives substantial feedback from the striate cortex (Gilbert & Kelly 1975; Lin & Kaas 1977; Robson 1983), which can provide a control signal indicating the detection of rivalry.

However, physiological experiments have found no evidence for a neural correlate of binocular rivalry in the LGN of cats and monkeys. Early studies of interocular interactions in the LGN typically involved stimulation of the dominant eye with one stimulus and intermittent presentation of a second stimulus to the non-dominant eye. For any given layer the dominant eye is the eye providing the excitatory drive; the other is non-dominant. Early experiments reported some inhibitory interocular interactions in the LGN of cats (Pape & Eysel 1986; Rodieck & Dreher 1979; Sanderson *et al.* 1969; Singer 1970) and monkeys (Marrocco & McClurkin 1979; Rodieck & Dreher 1979; Schroeder *et al.* 1990). However, almost all of these effects were not stimulus-specific and thus not directly correlated with those stimulation conditions that elicit binocular rivalry in human experiments. Furthermore, experiments in alert monkeys
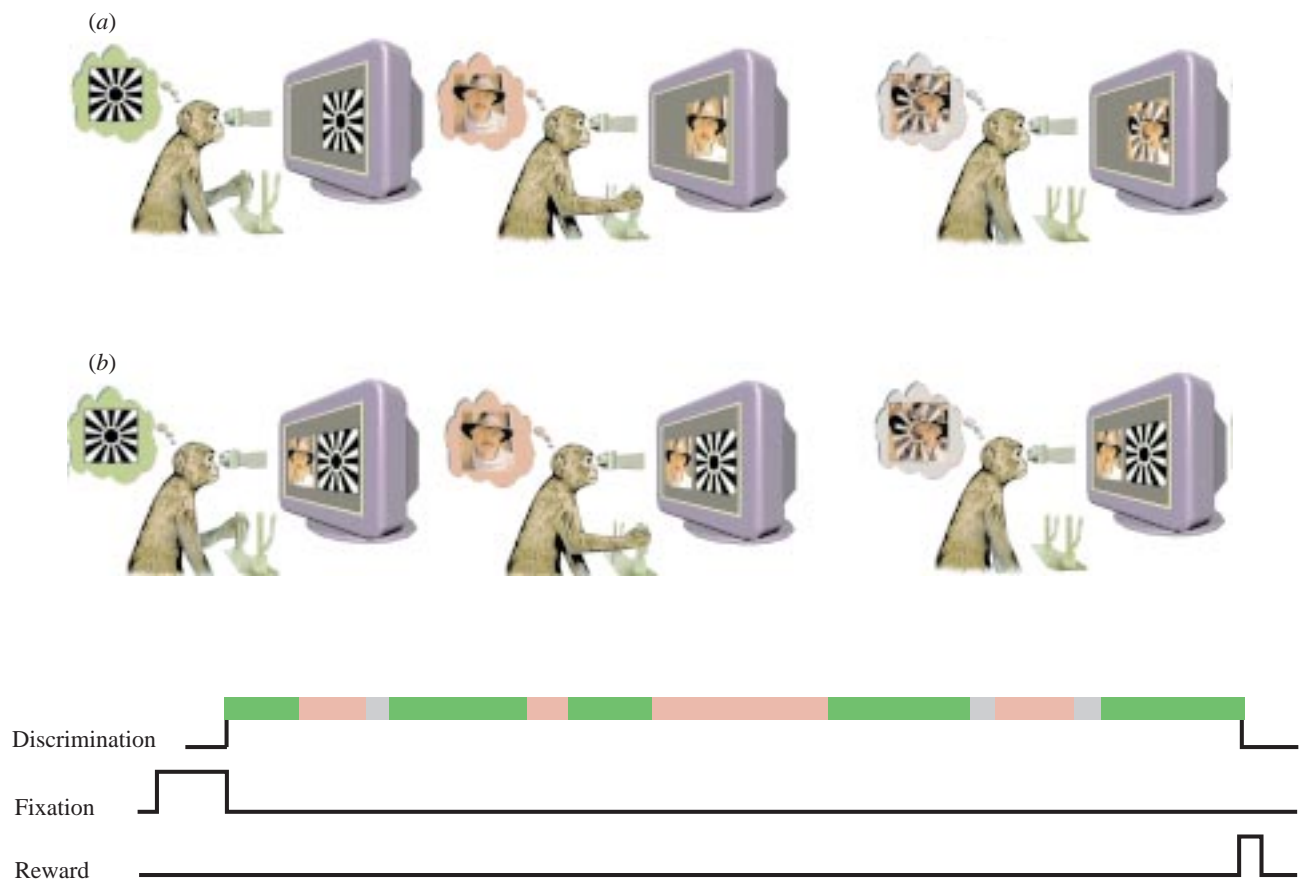
Figure 4. (*a*) Non-rivalry; (*b*) rivalry. The monkeys were taught to pull and hold the left lever whenever a sunburst-like pattern (left-object) was displayed, and to pull and hold the right lever upon presentation of other figures (right-objects), including images of animate objects. In addition, they were trained not to respond or to release an already pulled lever on presentation of a physical blend of different stimuli (mixed objects). During the behavioural task, individual observation periods consisted of random transitions between presentations of left-objects, right-objects and mixed objects. A juice reward was delivered only after the successful completion of an entire observation period. During rivalry periods, the monkeys indicated alternating perception of the left-objects and right-objects.

did not reveal any measurable non-specific inhibitory interactions (Lehky & Maunsell 1996) such as those reported with anaesthetized cats and monkeys (Marrocco & McClurkin 1979; Rodieck & Dreher 1979; Sanderson *et al.* 1969; Schroeder *et al.* 1990).

An experiment using rivalling stimuli was conducted by Varela & Singer (1987), who recorded from the lateral geniculate body of anaesthetized cats and found that the cell response to a drifting grating presented to the dominant eye was inhibited by stimulation with an orthogonal grating through the non-dominant eye. Ablation of the visual cortex abolished these feature-dependent inhibitory interactions. However, later studies in two different laboratories failed to confirm these findings (Moore *et al.* 1992; Sengpiel *et al.* 1992, 1995). In fact, in their study, Sengpiel *et al.* (1995) could not find a single case of orientation-selective suppression during dichoptic stimulation in the cat LGN. About 40% of the neurons showed inhibitory interactions that were not orientation-specific, which means that inhibition was as strong when the two gratings were of the same orientation as when they were orthogonal. Inhibition did not vary in strength with the relative interocular spatial phase for any combination of orientations (Sengpiel *et al.* 1995).

Further conclusive evidence of the absence of any inhibition at the subcortical level in the geniculostriate system came from the recent electrophysiological finding that neurons in the LGN of the alert monkey do not exhibit any temporal modulation of their activity when an animal is presented with moving rivalrous gratings during a fixation task (Lehky & Maunsell 1996).

(ii) *Visual cortex*

The behaviour of monocular neurons in the primary visual cortex of the cat was found to be strikingly similar to that of the LGN neurons. Their response was independent of interocular differences in orientation or spatial phase (Sengpiel *et al.* 1995). In contrast, roughly half of the binocular neurons in the primary visual cortex of cats showed a significant depression of their response to their preferred stimulus when a rivalling stimulus was presented to the other eye (Sengpiel & Blakemore 1994; Sengpiel *et al.* 1995). However, this orientation suppression was contingent upon the neuron's having been previously adapted to its preferred orientation. Simultaneous rivalrous presentation after several seconds of a blank screen did not result in suppression of the response. In their experiments, Sengpiel and colleagues mostly used

short (5 s) presentations of the rivalling stimuli, during which fluctuations resembling 'perception during rivalry' would not be easily discernible, yet even in those few experiments in which the activity of the neurons was examined during prolonged (30 s) exposure to orthogonal gratings, only one unit showed the kind of unstable behaviour that might be expected to occur during dichoptic stimulation.

Entirely different neural behaviours, however, were observed in experiments with behaving monkeys trained to report rivalry (Leopold & Logothetis 1996; Logothetis & Leopold 1995; Logothetis & Schall 1989*a,b*, 1990; Sheinberg & Logothetis 1997). Initial experiments in the middle temporal area (MT or V5) revealed different cell populations whose activity was, to a greater or smaller extent, modulated in a complex way during binocular motion rivalry (Logothetis & Schall 1989*a,b*). A number of cells seemed to fire only when the neuron's preferred direction was perceived, but because MT neurons receive direct input from both layers 4B and 6 of the striate cortex, it was not clear whether perception-related response modulation in MT was a property of this area or whether it reflected activity changes occurring in the striate cortex. In an attempt to improve our understanding of the physiology of rivalry, David Leopold and I studied the responses of neurons in the different early visual cortices of trained, behaving monkeys starting with the primary visual cortex (Leopold & Logothetis 1996). The animals were first taught to fixate a central spot of light and to report the perceived orientation of dioptically (both eyes presented with the same stimulus) presented gratings by pulling levers. The duration of single observation periods was gradually increased until the animals learned to fixate and report continuous perceptual changes for periods of up to 25 s. Once proficient with the task, the monkeys were gradually exposed to increasing periods of dichoptic stimulation, during which they indicated alternating perception of the two gratings. The psychophysical data collected with the trained monkeys were remarkably similar to those obtained with human subjects in our laboratory and others (figure 2*e–g*). This suggests first that the mechanisms of this phenomenon are likely to be the same in humans and monkeys, and second that the monkeys did indeed perceive the usual alternations experienced by humans and reported them with high reliability.

In our V1/V2 recordings we found a small percentage of neurons whose response was contingent upon the visibility of the stimulus. All except one of these neurons were binocular. In area V4, by contrast, 38% of the recorded neurons modulated their activity with the monkey's report. Curiously, about one-third of the response-modulating cells fired more strongly when their non-preferred orientation was perceived; only two-thirds of the neurons were excited when the stimulus was visible. Almost the same classes of neurons were found in the area MT (or V5) of the monkeys reporting binocular motion rivalry (Logothetis & Schall 1989*b*). The neurons whose activity seems to be in anti-correlation with the animals' perception of the driving stimulus might be part of an inhibitory mechanism that is separate from, and to some extent independent of, the mechanisms of perception. Such an independent mechanism was predicted by

psychophysical experiments on the effects of the strength of a stimulus on its predominance (Fahle 1982; Fox & Rasche 1969; Levelt 1965).

Taken together, the physiological results of recording in early visual cortices suggest that the response of a large number of cells (about 80% in V1/V2 and 60% V4/MT) in the visual cortex is independent of the perceptual dominance of the stimulus. The notion that the striate cortex, or indeed any one visual area, is the 'site' of suppression is therefore incorrect. The proposition that rivalry depends on inhibitory interactions between monocular channels before or at the site of binocular convergence (Blake 1989; Lehky & Blake 1989, 1991) is also incorrect. In both cats (Sengpiel *et al.* 1995) and monkeys (Leopold & Logothetis 1996), monocular neurons showed no activity changes that could provide the physiological substrate of rivalry. The physiological data, however, are consistent with the psychophysical observations on adaptation after-effects, although not necessarily with the traditional interpretation of these observations. Our results indicate that after-effects remain undiminished during rivalry because the most cells in the striate or extrastriate cortices are unaffected by suppression. In other words, perceptual adaptation and suppression are not mediated by mechanisms that have a serial, hierarchical relationship to each other, but rather involve different populations of cells at any given processing stage.

Whereas the cells that were unaffected by suppression can be seen as the neural correlate of our residual capacity to process different attributes of an invisible pattern, the role of the neurons whose activity depended on perceiving the stimulus remains elusive. At present it is not clear whether the responses of these units mediate the perception of the stimulus or simply reflect the stimulus selection that might occur in higher visual centres. To evaluate the possibility that perception-related neural changes in the early visual cortices are induced by feedback from higher visual areas, David Sheinberg and I decided to examine first the responses of neurons in the inferior temporal cortex during rivalry.

The inferotemporal cortex (IT) is a large cortical area extending approximately from just anterior to the inferior occipital sulcus to a couple of millimetres posterior to the temporal pole, and from the fundus of the superior temporal sulcus (STS) to the fundus of the occipitotemporal sulcus (Logothetis & Sheinberg 1996). Cytoarchitectonically this cortical region is subdivided into the areas TE anteriorly and TEO posteriorly (Von Bonin & Bailey 1947). Area TEO forms a band extending from the lip of the STS to a few millimetres medial to the occipitotemporal sulcus. Its posterior border is close to the lip of the ascending portion of the inferior occipital sulcus, and its posterior–anterior extent is 10–15 mm (Boussaoud *et al.* 1991). Area TE extends further anteriorly to about the sphenoid. On the basis of topography and the laminar organization of projections, the IT can also be subdivided into a posterior (PIT), a central (CIT) and an anterior (AIT) region, each with a ventral and a dorsal portion (Felleman & Van Essen 1991). On the basis of cytoarchitectonic and myeloarchitectonic criteria, as well as the pattern of afferent cortical connections, the temporal cortex has been further subdivided into a large
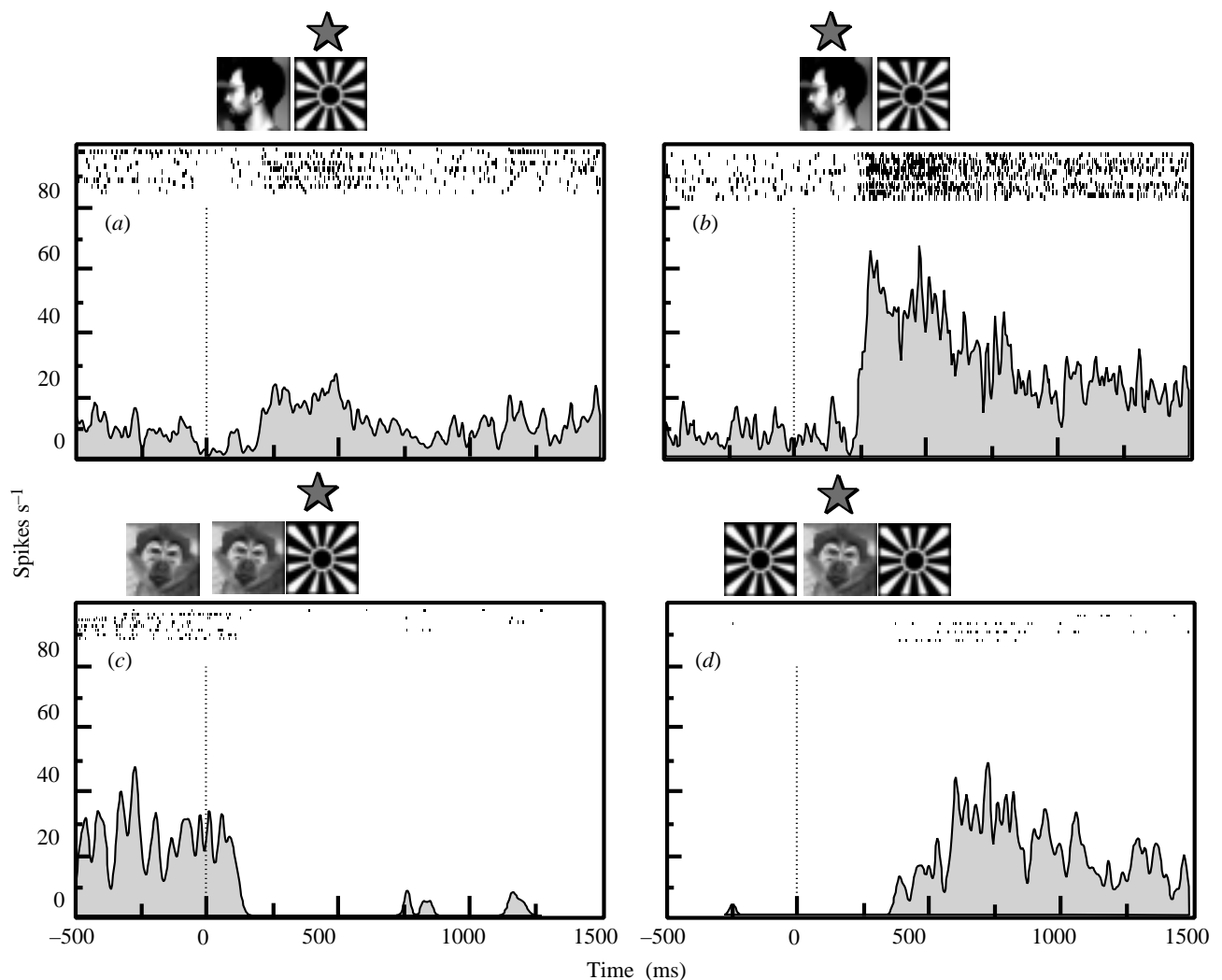
Figure 5. Neural responses during rivalry. (*a*, *b*) The response of an STS neuron during the dominance and suppression of its preferred pattern, here the profile of a face. The two stimuli are presented simultaneously (rivalry condition). (*c*, *d*) The responses of another cell during the dominance and suppression of a stimulus in the flash-suppression condition. In this condition, one of the two stimuli used to instigate rivalry is first viewed monocularly for 1–2 s. After the monocular preview, rivalry is induced by presenting the second image to the contralateral eye. For a couple of seconds human subjects and monkeys invariably perceive only the newly presented image, whereas the previewed stimulus is rendered invisible. Here, too, the neuron fires exclusively when its driving stimulus is perceived. Note that the rivalling stimuli (in (*c*) and (*d*)) which follow the short monocular presentation of one stimulus are usually the same; only the animal's report is different as is the response of the IT neuron. The small star indicates the monkey's report.

number of separate visual areas (Seltzer & Pandya 1978, 1994), several of which have distinct physiological characteristics (Baylis *et al*. 1987).

The inferotemporal cortex has long been known to have an essential role in visual object recognition. Damage to the IT produces severe deficits in perceptual learning and object recognition even in the absence of any significant changes in basic visual capacities (Gross 1972, 1994; Logothetis & Sheinberg 1996). The findings of ablation studies are consistent with the discovery of IT neurons that respond to complex two-dimensional visual patterns or even entire views of objects (Logothetis & Sheinberg 1996; Perrett *et al*. 1989; Perrett & Oram 1993; Rolls 1994; Tanaka 1996). Particularly prominent is the class of neurons responding to animate objects, including faces, bodies or body parts (Wachsmuth *et al*. 1994). Face-selective neurons responsive to the identity of faces are found in the inferior temporal cortex, whereas cells that

respond to facial expressions, gaze direction and vantage point have been reported in the STS (Hasselmo *et al*. 1989; Perrett & Oram 1993). Configurational selectivity, such as that demonstrated for face objects, can also be induced by experience as a result of extensive training in subordinate level recognition (Logothetis & Pauls 1994; Logothetis *et al*. 1995).

Of particular interest for our discussion is the connectivity of this cortical region. The area TEO, which is adjacent to V4, receives feedforward, topographically organized cortical inputs from areas V2, V3 and V4 and sparser inputs from areas V3A, V4t and MT. Fibres from TEO project feedforwardly to the areas TEm, TEa and IPa (Distler *et al*. 1993). The area TE, in contrast, sends feedback projections to TEO, which in turn projects back to the areas V2, V3, V3A, V4, V4t and MT (Distler *et al*. 1993; Rockland *et al*. 1994; Saleem & Tanaka 1996). Both TE and the STS also send direct feedback projections to
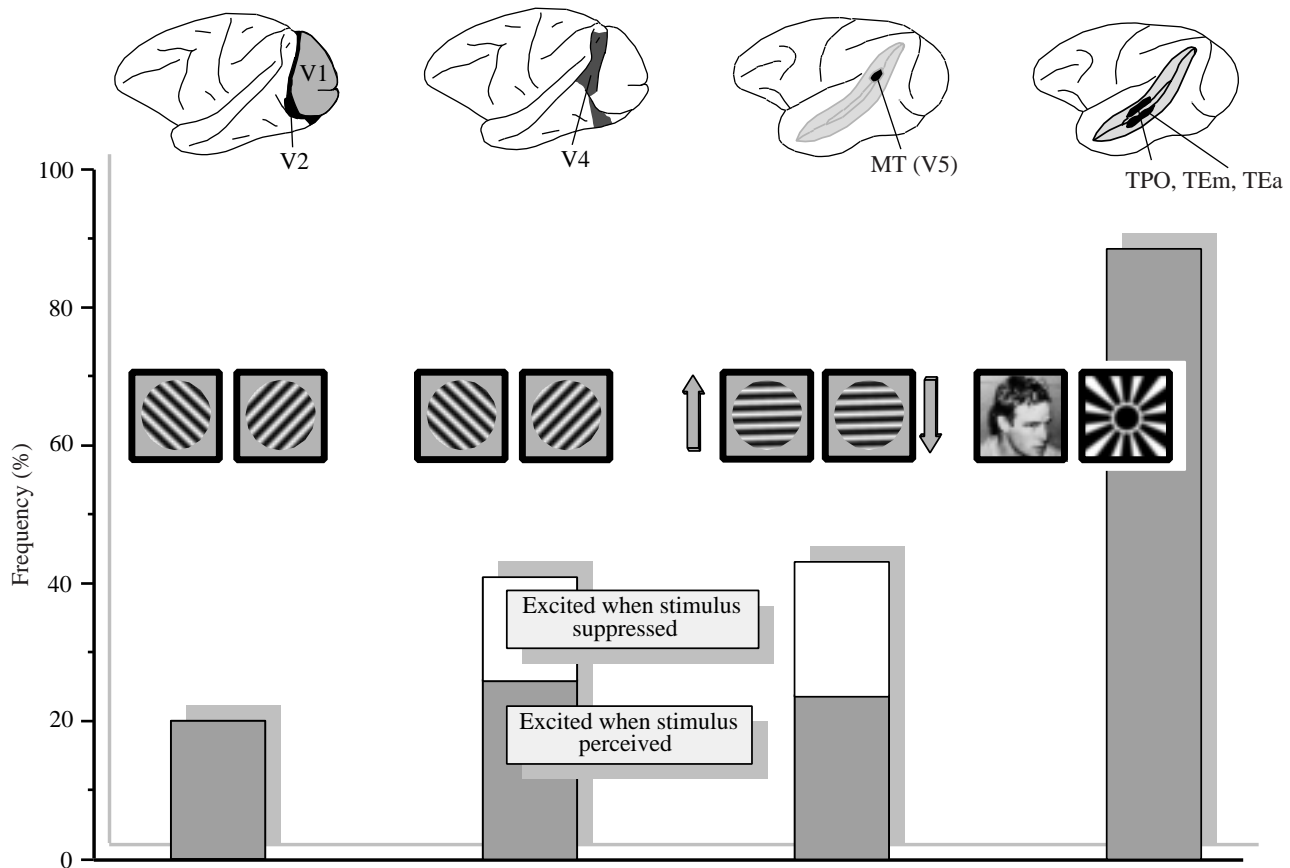
Figure 6. Distribution of perception-related activity in visual cortex.

the striate cortex, projections that originate only from layer 6 (Rockland & Van Hoesen 1994). Finally, and not surprisingly, TE is also connected with different prefrontal areas, specifically with the areas 8 and 45 in the inferior limb of the anterior bank of the arcuate sulcus, with area 12 on the inferior prefrontal convexity, and with areas 11 and 13 on the orbital surface. In contrast, the connections of area TEO are limited to areas 8, 45 and 12 (Webster *et al.* 1994). Neurons in the visual areas of the temporal lobe might therefore be in a position to influence the activity of cells in the early extrastriate or striate cortex in the process of forming unified percepts. If so, one might expect that the periods of excitation and inhibition of the neurons in the temporal lobe closely reflect the phases of perceptual dominance and suppression of their preferred pattern. Recordings in these areas showed that this is indeed so for the STS and TE areas in the monkey (Sheinberg & Logothetis 1997).

The monkeys participating in the IT experiments were trained to fixate a light spot and to perform a categorization task by pulling one of two levers attached to the front of their primate chair (figure 4). They were taught to pull and hold the left lever whenever a sunburst-like pattern was displayed, and to pull and hold the right lever on presentation of other figures, including images of humans, monkeys, apes, wild animals, butterflies, reptiles and various man-made objects. In addition, they were trained not to respond or to release an already pulled lever on presentation of a physical blend of different stimuli.

To ensure that the monkeys reliably reported what they perceived we followed the same training procedure that was used successfully in the experiments described above (Leopold & Logothetis 1996). Each observation period typically consisted of randomly intermixed periods of rivalrous and non-rivalrous stimulation, during which left-objects and right-objects were displayed monocularly to permit control of the animal's behaviour. To train the monkey to report only exclusive visibility of a figure, mixed objects mimicking piecemeal rivalry were randomly intermixed within each observation period. The monkeys reliably withheld response during these mixed periods, even when such periods constituted an entire observation period. At the end of the training period the psychophysical performance of the monkeys was remarkably similar to that of human subjects (Sheinberg & Logothetis 1997).

Figure 5 shows typical responses of two different STS neurons under two different stimulation conditions. The top plots show a face-selective neuron that fired more when the profile of a face was dioptically displayed. Presenting the sunburst pattern elevated only slightly the baseline activity of the neuron. During dichoptic viewing the neuron was excited only when the monkey reported seeing the face object. The response of another face-selective cell is shown in the bottom plot (see figure 5 for a description of the stimulus). Once again, perceptual suppression was strongly correlated with the neuron's response-inhibition.

The main result of these experiments is that the activity of the vast majority of the inferotemporal or STS
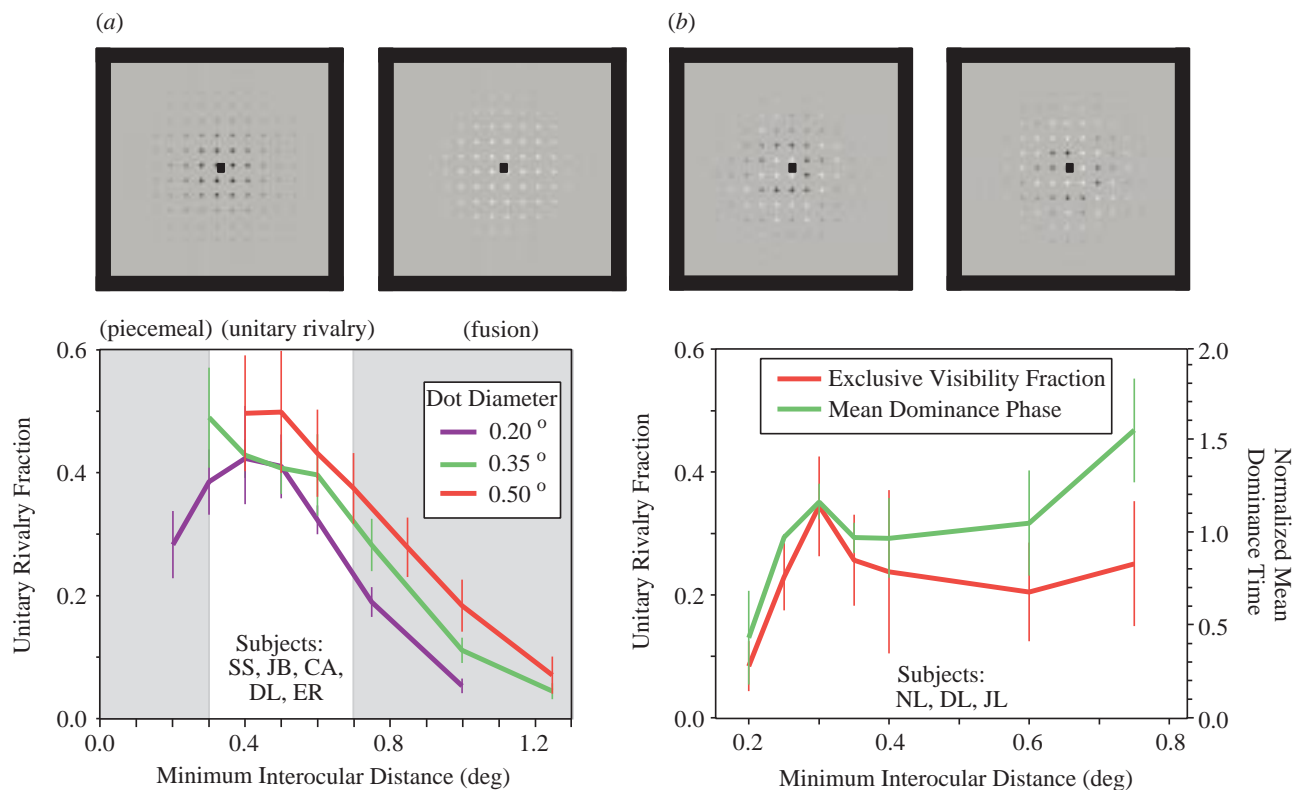
(*a*)   (*b*)



Figure 7. (*a*) Each curve represents the unitary rivalry fraction as a function of the minimum interocular distance for a given dot diameter. Average unitary fractions are shown for five subjects, with the bars signifying the standard error. (*b*) Data from three subjects in the mixed dot experiment. The insets show the stimuli used in the types of experiment.

neurons (*ca.* 90% of the recorded cells) is contingent upon the perceptual dominance of an effective visual stimulus. It was also striking that there were no cells that were active exclusively during the phenomenal suppression of the stimulus, a finding suggesting that the studied areas represent a stage of processing beyond the resolution of ambiguities, where neural activity might indeed be the physiological correlate of conscious perception. Excitation associated with the suppression of the stimulus was also absent from the striate cortex. It is tempting to speculate that the latter type of activity—so far described only in areas V4 and MT—might be present only in those areas that are most likely to be involved in perceptual organization. In such visual areas pattern coherence might be the result of strong inhibitory and facilitatory interactions between neurons coding for simple visual attributes.

Areas V4 and MT are certainly excellent candidates for neural sites of image segmentation and grouping. Neurons in both areas have moderately complex receptive fields (Gallant *et al.* 1993; Tanaka *et al.* 1991), receive inputs from both the lower cortical areas and the areas of the temporal lobe (Felleman & Van Essen 1991), and are known to reflect strongly the attentional requirements associated with various tasks (Luck *et al.* 1997; Moran & Desimone 1985; Treue & Maunsell 1996). Although attention has been convincingly shown not to be the cause of the perceptual fluctuations experienced during rivalry, the neural principles of stimulus selection that takes place when attending to a visual pattern might have a great deal in common with those principles underlying perceptual dominance during rivalry.

The results of a recent adaptation study performed under dioptic viewing conditions (He *et al.* 1996) support this notion. He *et al.* presented subjects with gratings of high spatial frequency displayed in the periphery of the visual field. When the gratings were presented alone, the subjects were aware of their orientations. When, however, they were flanked by other similar gratings (a condition known as 'crowding'), orientation became impossible to discern. The orientation-specific adaptation, however, was not affected by the 'perception-suppressing' crowding. In that the resolution of the grating patterns under these conditions is most probably limited by an attentional filter acting beyond the primary visual cortex, the results of He *et al.* indicate—just as in binocular rivalry—that the attentional selection of a stimulus and the encoding of its primary visual attributes might occur in different processing stages, with the earlier stages (presumably V1) making no direct contribution to the awareness of a stimulus (Crick & Koch 1995).

In contrast, an experiment in which the effects of attention on the tilt after-effect were studied (Spivey-Knowlton & deSa 1994) hints at differences between the mechanisms of rivalry and attention. Specifically, subjects were adapted to two equidistant gratings tilted 15° from the vertical. During adaptation the subjects were instructed to attend to either the left or the right grating. After adaptation, the subjects adjusted a grating to the apparent vertical in either the attended or the unattended region. The magnitude of the direct tilt after-effect in the attended regions was found to be significantly greater than that for the unattended region, suggesting that

attentive processing of one stimulus might inhibit the subconscious processing of the other.

Similarities between attention and rivalry can also be seen in physiological experiments. Indeed, the response of neurons in V4 and MT might be considerably enhanced or inhibited when the monkey attends to the cell's preferred or non-preferred stimulus, even when there is no concomitant change in the stimulus itself and the mechanisms underlying such changes are also considered to be of competitive nature (Desimone & Duncan 1995). Obviously, it would be interesting to find out in concurrent multiple-electrode recordings how the responses of neurons in the early extrastriate cortex correlate with those of the neurons in the areas of temporal lobe, and whether or not the 'inter-area' neural interactions when stimulus selection is under voluntary control (e.g. selective attention) are similar to those when it is determined by processes of self-organization (e.g. perceptual multistability).

In summary, the neurophysiological experiments on binocular rivalry showed that perception-related modulations of neural activity occur to different extents in different visual areas (figure 6). The cells that are affected by suppression are almost exclusively binocular, and their proportion increases as one moves to higher processing stages of the visual system. The strongest activity inhibition is observed in the firing patterns of cells in the IT and STS rather than in those of the striate neurons. At present it is not clear whether the activation of even those neurons that most closely follow the percept of stimulus forms the 'sufficient and necessary condition' for the awareness of that stimulus. Future studies, in which the effects of activation (for an elegant series of relevant stimulation studies see Celebrini & Newsome (1995), Groh *et al.* (1997) and Salzman *et al.* (1990)) or inactivation of these neurons on the perceptual report of the monkey is examined, might provide better insights into the mechanisms of perceptual organization and stimulus awareness.

The findings discussed above also raised the following questions, among others: given that no evidence was found to favour interocular competition and eye suppression, what is actually rivalling during binocular rivalry? Which aspects of rivalry have their origin in the workings of the binocular visual system, such as those of fusion and stereoscopic depth perception, and which are directly related to the processes of perceptual organization? Is the mechanism that triggers rivalry the same as that yielding the intermittent but unified perception of each pattern?

## 5. THE MECHANISMS OF BINOCULAR RIVALRY

### (a) *Triggering competition*

The effectiveness of the phenomenal suppression of an otherwise salient monocular stimulus is undoubtedly one of the most striking things about binocular rivalry. Indeed, when a stimulus is suppressed during rivalry it becomes invisible, just as though it were switched off! Even more striking is the fact that the visual pattern that is blocked from awareness for several seconds might be orders of magnitude stronger than the pattern that dominates perception. In fact, as soon as one of the competing stimuli reaches its threshold visibility, it will compete for

perceptual dominance regardless of how strong the contralateral stimulus is (Blake 1977).

However, fluctuations between the exclusive dominance and the profound suppression of a pattern, commonly called 'unitary rivalry', are not the only perceptual outcome of dichoptic stimulation. Viewing large dissimilar patterns results in alternating periods of exclusive visibility of one or the other eye's view, interspersed by a mosaic-like collage ('piecemeal rivalry') consisting of different portions of each eye's stimulus-pattern (Breese 1899, 1909; Levelt 1965). Moreover, distinct perceptual states can be experienced when the stimuli are viewed at very low contrast or when their spatial frequencies differ greatly, with the former condition yielding a stable summation between the two images, resulting in the perception of a plaid (Liu *et al.* 1992), and the latter favouring the perception of transparency, wherein a 'surface' of higher spatial frequency is experienced in front of a lower spatial-frequency 'surface' (Yang *et al.* 1992).

There exist certain conditions, then, under which the visual system can create two different intact representations of two dissimilar overlapping patterns, despite the fact that such conditions violate the fundamental principle that two different objects cannot be in the same place at the same time. The fact that such conditions exist suggests that rivalry is triggered at a processing level that is different from, and probably earlier than, the level of central representation of each pattern. This (early) mechanism might be related to fusion or stereopsis, but it could also be related to the processes underlying the formation of higher geometrical representations such as curves, surfaces and other object primitives by means of simple, local attributes such as orientated line segments, angles, small velocity fields, or colour patches. Local image processing is inherently ambiguous. A number of different strategies, including feedforward, lateral and feedback cortical interactions, are probably used by the visual system to impose constraints and disambiguate information during the process of figure–ground segregation, an assumption that finds ample support in physiological experiments studying the effects of context on single unit activity (Allman *et al.* 1985; Gilbert *et al.* 1990; Gilbert & Wiesel 1990; Knierim & Van Essen 1992; Lamme 1995; Levitt & Lund 1997; Li & Li 1994; Olavarria *et al.* 1992; Schmidt *et al.* 1997; Sillito *et al.* 1995; Sillito & Jones 1996; Zipser *et al.* 1996). Superposition of two different stimuli might strongly interfere with this disambiguation procedure. Evidence for the latter comes from the observation that dichoptic viewing is not a necessary condition for the development of the competitive interactions leading to instability and perceptual fluctuations.

Rivalry can occur even under monocular viewing conditions (a phenomenon often called non-dichoptic or perceptual rivalry) when both stimuli are presented to the same eye (Atkinson *et al.* 1973; Breese 1899; Campbell *et al.* 1973; Campbell & Howell 1972). For instance, two orthogonal sinusoidal gratings projected on a white screen will continuously change in appearance (Campbell & Howell 1972). The effect is even more marked when the gratings have different colours (which probably increases the pattern's coherence). Orthogonal red and green gratings of

matched intensities rival, so that sometimes the red grating is seen on its own and at other times only the green grating is perceived. Just as with binocular rivalry, periods of mixed perception are intermingled with periods of exclusive visibility of one or the other pattern.

Monocular and binocular rivalry have many common characteristics (Sindermann & Luddeke 1972; Walker 1976). The threshold conditions instigating either type of rivalry are very similar. For instance, the orientation disparity eliciting monocular rivalry is 15–20° and the difference in spatial frequency is about one octave (Campbell *et al.* 1973; Campbell & Howell 1972). About the same thresholds are known to instigate binocular rivalry (Blake 1989). The two phenomena differ somewhat in appearance; monocular rivalry manifests itself more frequently in the attenuation of one or other of the gratings rather than in its complete disappearance (Wade 1975). It is not unreasonable to assume that attention, monocular rivalry and binocular rivalry are manifestations of competitive interactions differing in the strength of inhibition, with attention resulting in the weakest and binocular rivalry in the strongest suppression of the non-dominant pattern.

## (b) *Selecting a representation*

Once instigated, rivalry most probably involves two separate and perhaps antagonistic processes: (*a*) the ongoing local inhibitory interactions (the same interactions that trigger the phenomenon), which might be the cause of the fragmentary appearance of larger (more than 1°) stimuli (piecemeal rivalry), and (*b*) those interactions that underlie the stimulus selection. Our proposition of a second mechanism operating independently of the local cross-inhibitory events is motivated both by the physiological data described above and by the accumulating evidence against the eye-suppression theories.

Traditionally, rivalry has been studied in a manner that does not clearly differentiate between eye and stimulus competition. When a stimulus is seen, it could in principle be the monocular channel receiving this stimulus that dominates, or alternatively the neural representation of the stimulus, regardless of which eye the representation comes from.

An observation favouring the eye-suppression hypothesis is that immediately after a subject reports the exclusive suppression of one eye's stimulus, this stimulus instantly becomes visible when it is rerouted into the eye that is dominating at that instant (Blake *et al.* 1980). The eye-suppression hypothesis is also supported by studies that demonstrate that the suppressed eye suffers a general reduction in sensitivity. In other words, test probes bearing no resemblance to the suppressed stimulus itself are more difficult to detect during suppression than during dominance (Blake & Camisa 1979; Blake & Fox 1974*b*; Fox & Check 1972; Wales & Fox 1970). For example, increases of approximately 0.5 log units were reported in detection thresholds (Blake & Camisa 1978; Makous & Sanders 1978; Wales & Fox 1970) and incremental detection thresholds (Wales & Fox 1970). It is therefore assumed that suppression is not selective for the rivalry-inducing stimulus, but instead completely blocks the processing of the information coming through the suppressed eye (Blake *et al.* 1980). An exception is the

processing of colour information, as suppression seems to affect the colour-opponent and the achromatic mechanisms differentially (Smith *et al.* 1982).

However, a general, non-selective reduction in sensitivity during the suppression of a stimulus is not exclusive to binocular rivalry, but can also occur when viewing (non-dichoptically) ambiguous figures. For example, contour discontinuity is harder to detect in an area perceived as background than in an area perceived as a figure (Weitzman 1963), retinal image displacement is less visible in the ground region than in the figural region of an Escher picture (Bridgeman 1981), and the orientation of tilted lines is discriminated less accurately when it is flashed in the ground rather than the figural region of Rubin's reversible goblet–faces picture (Wong & Weisstein 1982). Once again, the thresholds are elevated by about 0.5 log units (Wong & Weisstein 1982). Thus, there is a plethora of evidence showing that the performance of perceptual tasks is often facilitated by perceived 'figureness' or conversely inhibited by perceived 'non-figureness'.

In contrast, a number of experiments have provided strong evidence in favour of the stimulus-suppression hypothesis. Stimulus specificity was evident, for instance, in experiments showing that suppression is instantly terminated if some feature of a suppressed stimulus—contrast, for example—is abruptly changed (Walker & Powell 1979). Rivalrous stimuli differing both in colour and in form occasionally yield a percept composed of one eye's form grafted onto the other eye's colour (Breese 1909; Crain 1961; Treisman 1962), an observation constituting a paradox for the eye-suppression hypothesis in that it requires that both eyes be simultaneously dominant and suppressed. Coherence was also found to determine perception when simple colour patches are presented dichoptically. When dichoptically stimulated with isoluminant red–green and green–red patterns, subjects consistently reported perceiving either solid red or solid green (Kulikowski 1992). In a similar vein, when rivalrous stimuli are composed of multiple parts, then those parts that form a Gestalt figure are more likely to dominate together perceptually, even if presented to opposite eyes (Whittle *et al.* 1968). The effects of Gestalt on the predominance of a stimulus were demonstrated very convincingly by Diaz-Caneja (1928). His stimuli (see figure 2*c*) show beyond any reasonable doubt that 'neither a monocular image nor one related to a particular hemisphere determines what constitutes a percept, but rather the goodness of the composite figure'.

Stimulus-rivalry is further supported by experiments showing that basic capacities of the binocular system, such as binocular summation (Westendorf *et al.* 1982) and stereopsis (Julesz & Miller 1975; Kaufman 1974; Ogle & Wakefield 1967; Ramachandran & Siram 1972; Treisman 1962; Wolfe 1986), which depend on the information received simultaneously from both eyes, can often coexist with binocular rivalry, in the sense that information received through the suppressed stimulus field can be combined to improve the detection of a stimulus or to extract depth information. Similarly, rivalry has been shown to coexist with the perception of coherent motion. Counterphase modulation of a red–green and yellow–black grating each presented to one eye was found to be
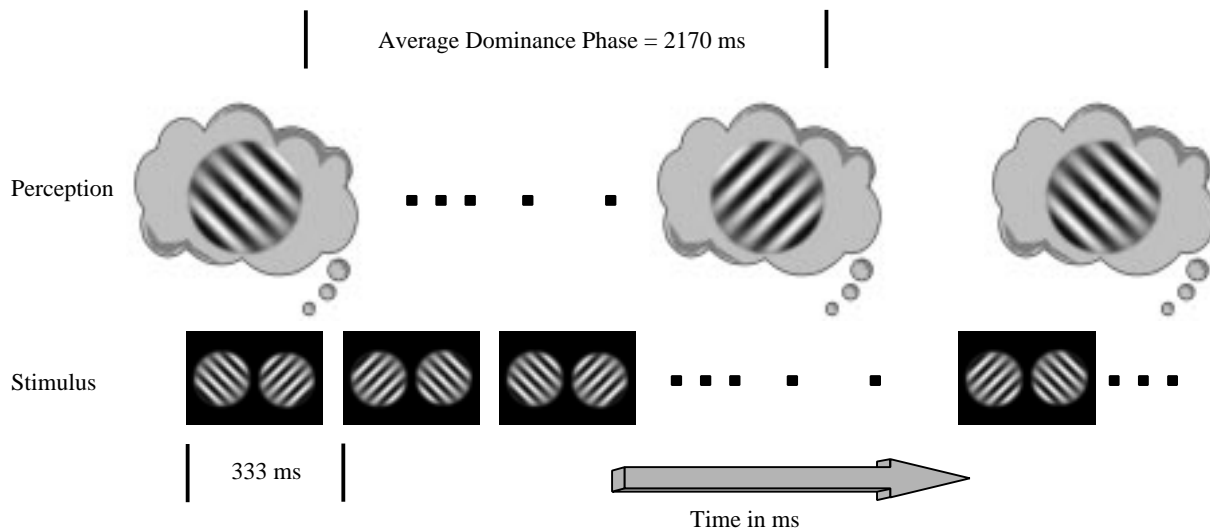
Figure 8. During an experimental session the observer viewed a pair of orthogonally oriented gratings tilted rightward to one eye and leftward to the other. The stimuli were turned on and off with a frequency of 18 Hz, and were exchanged between the eyes every 333 ms. The 18 Hz flicker was introduced to minimize the perception of the orientation swapping. In this condition each eye sees a grating that periodically switches between perpendicular orientations. In contrast, the subjects reported seeing slow alternations between the two orientations that were not correlated with the physical exchange of the stimulus configuration.

integrated into coherent motion, despite the fact that the colours engaged in perceptual rivalry (Carney *et al*. 1987).

If rivalry is between the two stimuli rather than between the eyes, one might expect an increase in the exclusive dominance of a pattern if the local inhibitory interactions are minimized. To examine this hypothesis David Leopold presented human subjects in our laboratory with sets of white and black dots, the latter shifted diagonally with respect to the former, to eliminate stereoscopic depth (Leopold 1997). The rationale behind these stimuli was the following: binocular suppression spreads beyond the actual point of dichoptic superposition (Blake *et al*. 1992; Kaufman 1963), usually to include regions of the 'background' surrounding the contour conflict. It is thus assumed that rivalry occurs between small, finite spatial zones, the size of which also determines the minimum size of a stimulus that can produce unitary rivalry. In the fovea this size is approximately $0.25°$. The dots were therefore shifted by about $0.2°$ and presented in different sizes and densities. Sizes ranged from $0.2°$ to $0.5°$ in diameter, and the minimum interocular distance varied from $0.2°$ to $1.25°$. The size of the entire stimulus was about $7°$.

Figure 7 shows the results of this experiment. Unitary perception was found to reach a maximum between $0.3°$ and $0.7°$ of inter-dot distance. At larger inter-dot distances there was a tendency for all the dots to be perceived at the same time, probably because the suppressive zones surrounding the dots in one eye no longer encroached on those from the dots in the other. For small distances, in contrast, the subjects reported piecemeal appearance. For the optimal distance, however, unitary rivalry occurred about 80% of the time in each observation period. Minimizing local interaction did in fact have a pronounced effect on the coherence of the rivalling percepts. We next tested whether there is interocular grouping in stimuli that consisted of mixed black and white groups. Figure 7*b* shows the stimuli used in this

experiment together with the performance of one subject. More than one-third of the time the subjects did indeed report rivalry between whole-white and whole-black dot sets, grouping different parts of each set together to form a coherent percept.

Similar experiments were conducted concurrently and independently by Kovacs *et al*. (1996), who generated complementary patchworks of intermingled rivalrous images and examined whether the visual system is able to unscramble the pieces of the patchwork arriving from different eyes to obtain coherent percepts. They, too, found that pattern coherency in itself can drive the perceptual alternations experienced during rivalry.

Finally, the hypothesis of stimulus rivalry was tested by using a new stimulus paradigm (figure 8) in which the rivalling patterns were periodically exchanged between the two eyes, thereby eliminating the possibility that perceptual alternations occur simply as a result of fatigue in one or the other monocular channel (Logothetis *et al*. 1996). In this paradigm, 'eye suppression' would lead to periods in which perception is dominated by a grating regularly switching orientation, the way it would appear if the subject were to close first one eye and then the other. In contrast, 'stimulus suppression', during which the central neural representation of a stimulus can be suppressed, would produce normal rivalry between the two continually exchanged patterns, because the conflicting central representations of these patterns remain the same regardless of which eye they are coming through.

The rivalry experienced when monocular stimuli are continually swapped between the eyes was found to be indistinguishable from conventional binocular rivalry, on the basis of the standard tests of the temporal dynamics of this phenomenon. The smooth, slow perceptual changes despite continuous alternation of the stimulus orientation in each eye rule out the possibility that rivalry is the result of a complete suppression of one monocular channel. Each monocular view in this paradigm is a

grating periodically changing orientation as though the stimulus were viewed first with one eye and then with the other. However, these physical changes of the monocular view are rarely visible, if ever, and perception is instead dominated for extended periods by one or the other orientation, with the left-tilted and right-tilted grating patterns alternating in conscious perception slowly and stochastically.

## 6. CONCLUSIONS

The experiments reviewed here shed new light on the phenomenon of binocular rivalry and visual perception in general. Rivalry has long been considered to be a phenomenon that is closely linked to fusion and stereopsis, demonstrating the existence of important underlying processes that operate constantly to establish unified vision (for a review see Blake (1989)). The sequences of dominance and suppression have been thought of as the result of competition between the two monocular channels at their early stage of convergence, namely the striate cortex. Both the psychophysical and the physiological evidence presented here are incompatible with this interpretation. Rivalry does not merely reflect interocular competition. It is true that neural inhibitory interactions most probably form the basis of the local perceptual conflicts that arise when two incompatible stimuli are superimposed; however, such conflicts can arise with or without dichoptic stimulation and are most probably the origin of the instability experienced during binocular, as well as monocular, rivalry. Although establishing the conditions for perceptual instability, these local conflicts are most unlikely to be the explanation of stimulus selection and percept generation. Rather than reflecting activation and inhibition of the right or left pool of monocular neurons, the dominance and suppression of a pattern during rivalry reflects the excitation and inhibition of cell populations in the higher visual areas, which are directly involved in the representation of visual patterns. Future experiments in which recordings are made in different areas concurrently might help us to understand better the role of neurons or neural assemblies at the different stages of visual processing in the generation of phenomenal suppression and the awareness of a stimulus.

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