1. INTRODUCTION

Binocular rivalry is experienced when the left and right eyes are viewing incompatible images: one eye's image is seen while the other is suppressed. This phenomenon was first noticed in the sixteenth century and was carefully investigated after the invention of mirror stereoscope in the nineteenth century (Wade, 2004). There has been a renewal of interest in the topic in the last few years (Blake & Logothetis, 2002).

Two features make binocular rivalry an attractive tool for exploring visual awareness. Firstly, it consists of perceptual fluctuations in the presence of constant visual stimulation. Any place in the brain where neural activity varies in synchrony with the rivalry must be instrumental in perception. Secondly, a number of recent studies have contributed to identifying the neural modulation in binocular rivalry. Studying binocular rivalry has therefore helped to unfold the underlying neural mechanisms in sensation, and provided an invaluable contribution in understanding the transformation from retinal image to perception.

Three methods have been used to study binocular rivalry. Psychophysical studies have described the perceptual fluctuations and the loss of visual awareness in binocular rivalry suppression. Physiological studies have recorded the firing of the visual cells and their correlation with the perceptual alternations. Recently, these alternations have been monitored by using functional magnetic resonance imaging. These three types of experiments will now be described in turn.

Psychophysics of binocular rivalry

Conditions for binocular rivalry

The brain normally combines the information from the two eyes to form a single percept that betrays no trace of its monocular origins. The two monocular images may not always fall on exactly corresponding areas of the retina, but the images can still be seen as one. Why are we aware of only a single object even though the two retinal images are not identical? There are two possible solutions, fusion and suppression. When the two retinal images differ little, they are fused. The small discrepancy is tolerated and contributes to depth perception.

When the two images are incompatible, fusion is disrupted. For instance, when vertical contours are presented to one eye and horizontal ones to the fellow eye, they are not combined. In order to solve the conflict between the images, binocular cooperation gives way to rivalry resulting in one eye's image being seen while the other is perceptually suppressed. This situation periodically reverses, with the suppressed image becoming visible and the previously dominant image suppressed, as long as the incompatible stimuli are present.

Brief presentation of incompatible images, however, yields fusion rather than rivalry. For instance, when a pair of orthogonal gratings is presented to the two eyes for less than 150 milliseconds, a subject perceives a grid, a mixture of the two gratings (Wolfe, 1983; Wolfe, 1986). Rivalry becomes more probable as the viewing time is prolonged. When stimuli cover a large area of the visual field, rivalry is patchy: some patches are dominated by the right eye and others by the left eye (Blake, O'Shea & Mueller, 1992). In such case, various segments of the stimuli are in relatively independent states of dominance and suppression at a particular time. Furthermore, the spatial extent of the rivalrous regions can dynamically change as the percept alternates (Hochberg, 1964). The neural mechanism of this piecemeal suppression has not yet been well established but some cooperation or interaction between neighbouring cortical areas may be involved (Kovács, Papathomas, Yang & Fehér, 1996).

Temporal properties

Spontaneous perceptual alternation is a distinguishing feature of binocular rivalry; alternation is maintained as long as the dichoptic stimuli are presented. The duration of a dominance interval has a mean of approximately 2 seconds (Fox & Herrmann, 1967; Levelt, 1965), and it will reduce after prolonged exposure to the stimuli, due possibly to fatigue and/or adaptation (Hudenell & Hollins, 1979).

Is the sequence of perceptual alternation regular or irregular? To address this question, Levelt (1965) measured a sample of dominance durations. He found a unimodal distribution of durations with a mode less than its mean, and a long tail of large durations; the sample was well-fitted with a gamma distribution. Levelt (1965) therefore proposed the hypothesis that a dominance interval contains a fixed number of independent neural events. Fox and Herrmann (1967) also recorded dominance durations during rivalry. They analysed the dependence of each interval on its neighbouring intervals. The results showed that durations were independent of each other. Rivalry induced with kinetic stimuli has the same temporal statistics (Norman, Norman & Bilotta, 2000).

The above studies and others (Fox & Check, 1972; Lack, 1973), suggested that binocular rivalry alternation is a local phenomenon which is not governed by a central time-keeper. What mechanism triggers the alternation? Eye movement, blinking and accommodation have been found to have little effect on the time course (Lack, 1974). Visual adaptation had also been suggested as an explanation for the alternation process. It was hypothesised (Fox & Check, 1972) that while the dominant eye is adapting to the visible stimulus, the suppressed eye is not. Thus, the non-adapted suppressed eye should improve in relative sensitivity as the suppression progresses until it takes over dominance. If that were true, the magnitude of suppression should decline during a suppression period. Fox and Check (1972) measured the detection threshold at different times during suppression. A test flash was introduced to one eye after the subject signalled the onset of suppression in that eye's stimulus. Detectability was measured as the probability of correct responses, and the probability was found to be unaffected by the timing of the test stimulus. It was therefore concluded that the magnitude of suppression is independent of the duration of suppression, throwing the adaptation theory into doubt.

This conclusion was based on static rivalry-inducing stimuli. Is there any difference if the inducing stimuli are dynamic? Norman, Norman and Bilotta (2000) used two types of rivalry-inducing stimuli, namely stationary and drifting sinusoidal gratings, to measure the suppression magnitude at different times. A small test stimulus of variable luminance was presented in one of four locations. The luminance detection thresholds were measured as the luminance producing 75 to 80% correct responses. The results confirmed the findings of Fox and Check (1972) in that the magnitude of suppression is constant throughout a suppression interval.

In general, then, perception randomly alternates approximately every two seconds during binocular rivalry, and the depth of suppression is independent of time during suppression.

Effects of stimulus strength

Several studies have shown that the capacity of a stimulus to induce binocular rivalry depends on its characteristics such as contrast, texture, and motion. This 'strength' can be considered as the stimulus energy required to induce neural responses. Stimulus strength has been measured through the predominance of a stimulus, which is commonly defined as the duration for which a stimulus is dominant, divided by the total viewing time. Equal stimulus strength in each eye results in equal predominance of the two monocular stimuli. An increase in stimulus strength to one eye results in an increase in the predominance of that stimulus, and also in the rate of alternation, by reducing the time for which it is suppressed (Levelt, 1965). However, a system for rating stimulus strength has not been well established (Blake & Logothetis, 2002). Eye dominance or preference, which is usually defined by standard sighting tests, has less influence on predominance (Coren & Kaplan, 1973).

In general, a high-contrast stimulus predominates over a lower one; a stimulus with sharp edges predominates over a blurred one; a moving stimulus predominates over a static one (Levelt, 1965). Spatial frequency and orientation also influence the predominance: a stimulus with lower spatial frequencies tends to predominate over one with higher frequencies and a figure with vertical contours predominates over a horizontal one (Fahle, 1982; Wade, 1974). Moving stimuli produce stronger rivalry than static ones (Springbett, 1961) and parametric investigations of motion rivalry have been performed (Wade, de Weert & Swanston, 1984).

Psychoanatomy

A number of psychophysical studies have attempted to localise the cortical site(s) at which binocular rivalry is initiated. These studies tested the effect of rivalry on visual properties such as adaptation and after-effects in an approach called psychoanatomy. Depending on the property chosen, psychoanatomy yields different results.

The first set of studies examined the after-effects of viewing gratings for extended periods of time. Blake and Fox (1974a) assessed the effect of binocular rivalry suppression on the production of adaptation after-effects to contrast and spatial frequency. The subject viewed a grating of 3 or 6 cycles per visual degree to build up adaptation. The contrast and spatial frequency after-effect was measured by comparing the appearance of the adapted grating to an adjacent reference visual stimulus. Elevation in contrast threshold and a frequency shift were determined for monocular stimulation. During suppression, although the adapting stimulus was present continuously, it was visible only half of the time. Interestingly, the contrast and spatial frequency after-effects were unperturbed. It is thought that grating adaptation occurs in the primary visual cortex (Blakemore & Nachmias, 1971). Since binocular rivalry does not interrupt this adaptation, Blake and Fox came to the conclusion that binocular rivalry suppression takes place at a site higher than the primary visual cortex.

In a similar context, Wade and Wenderoth (1978) showed that binocular rivalry suppression does not interrupt the build-up of the tilt after-effect, which is probably a property of the orientation-selective cortical neurons in the primary visual cortex (Carpenter & Blakemore, 1973). The same is true for the linear motion after-effect (Blake, 1995; Lehmkuhle & Fox, 1975; O'Shea & Crassini, 1981). These observations also suggested that binocular rivalry occurs beyond the primary visual cortex.

On the other hand, the involvement of the primary visual cortex cannot be completely excluded. Lehky & Blake (1991) found that the contrast after-effect, which is specific to primary visual cortex (Blakemore & Campbell, 1969), was affected by binocular rivalry. Rivalry was induced by two orthogonal gratings, one with a fixed luminance contrast and the other with a variable contrast. The visibility of the fixed-contrast grating varied with the contrast of the other grating. Detection sensitivity was tested in the eye that viewed the fixed-contrast grating immediately after building up adaptation. The detection sensitivity was slightly reduced as the visibility of the fixed contrast grating increased, indicating that adaptation has a slight effect on binocular rivalry. It therefore suggested that some component of binocular rivalry depended on the primary visual cortex.

The relationship between binocular rivalry and the filling-in effect has also been studied. In normal viewing, humans are not consciously aware of the physiological blind spot in the visual field, because the filling-in mechanism compensates for the absence of retinal projection. The filling-in mechanism is thought to depend on neural activity in the primary visual cortex (Komatsu, Kinoshita & Murakami, 2000). Recently, He and Davis (2001) questioned whether the filling-in information could compete with retinal projection to form binocular rivalry. A stimulus with a radial pattern, a star burst, was centred on the blind spot of the left eye. A dichoptically-paired stimulus, consisting of three concentric rings, was placed on the corresponding location for the right eye. The subject was required to signal when seeing the right-eye stimulus. The visibility of the non-blind-spot (right-eye) stimulus was found to be similar to that in binocular rivalry. The filled-in information from the left eye's blind spot interfered with the visibility of the right eye stimulus to yield binocular rivalry. This experiment provided further evidence that binocular rivalry has a component in the primary visual cortex.

Does binocular rivalry exert an influence on visual cortex higher than the primary area? Subjective contours evoke activity mainly in V2 but little in the primary visual cortex (Shipp & Zeki, 1985; Zeki, 1975). Van der Zwan and Wenderoth (1994) assessed the involvement of rivalry in the cortical area V2, which is adjacent to the primary visual cortex. Rivalry was induced by a purely subjective contour with a single orientation formed by multiple concentric rings bisected through the centres. The two bisected images were shifted with respect to each other and were basically orthogonal in orientation. After building up adaptation, the stimuli were replaced by a test, which was binocularly presented. The perceived orientation of the test, rotated away from or towards the adapting stimulus, reflected the magnitude of adaptation to the rivalry-inducing stimuli. There was a substantial reduction in adaptation during suppression, leading to the conclusion that binocular rivalry exerts some effect on V2 because of its disruption to the subjective contour after-effect. This conclusion led to the idea that binocular rivalry influences neural activity in V2.

The middle temporal cortex (MT), a high-level cortical area, is more sensitive to rotating images than are lower cortical areas (Graziano, Andersen & Snowden, 1994). Rotating images therefore provide a sensitive tool for finding the site of binocular rivalry suppression. Wiesenfelder and Blake (1990) used rotating spirals to induce adaptation. After adaptation to a contracting rotating spiral, the subject perceived expansion when viewing a static stimulus. The strength of the after-effect was measured by measuring its duration. In the monocular condition, the duration lengthened as the adapting period extended. During binocular rivalry, this duration was also lengthened but relative to the cumulative visible time, not the total time, of the rotating spiral. This result indicated that binocular rivalry suppression restricted the adapting effect of rotation to the time for which it was visible. The authors therefore concluded that binocular rivalry is exerted before MT.

Other high-level visual tasks show similar effects during binocular rivalry. Semantic processing, for example, has been found to be interrupted by binocular rivalry (Zimba & Blake, 1983). In this experiment, a priming word was presented during the dominance and suppression phases of binocular rivalry and was followed by a test word. The reaction time for detecting the test word was measured. The reaction time was longer when the prime appeared during suppression than when it appeared during dominance. This result showed that suppression slows down the recognition of the word. Semantic processing presumably occurs in high-level cortex (Buchel, Price & Friston, 1998; Malach, Reppas, Benson, Kwong, Jiang, Kennedy, Ledden, Brady, Rosen & Tootell, 1995). Binocular rivalry is therefore presumed to occur before the high-level site at which semantic processing takes place.

In general, binocular rivalry exerts influence to not only the high-level visual cortex (Wiesenfelder & Blake, 1990; Zimba & Blake, 1983), but also to low-level cortex (van der Zwan & Wenderoth, 1994) and the primary visual cortex (Lehky & Blake, 1991). This reflects the idea that binocular rivalry suppression occurs at a variety of sites along the visual processing pathway (Blake & Logothetis, 2002).

Physiology of binocular rivalry

There are indicators of binocular rivalry that do not rely on subjects reporting their perceptions. These are optokinetic nystagmus, visual evoked potentials (VEP), single-neuron recordings, and magnetic resonance imaging. They will be discussed in turn.

Ocular motor indicators

Two ocular motor indicators, optokinetic nystagmus and pupil reactivity, have been claimed to objectively reflect perceptual fluctuations in binocular rivalry. The relationship between pupil reactivity and binocular rivalry is equivocal (Regan, 1991a) and is therefore excluded from this review.

Optokinetic nystagmus, the reflex eye movements induced by a steadily moving stimulus, correlates well with the perceptual alternation in binocular rivalry. Fox, Todd & Bettinger (1975) induced binocular rivalry with vertical contours moving leftward in front of one eye, and rightward in front of the other eye. The subject was asked to nominate the direction of movement of the dominant stimulus, and the subject's nystagmus, including the fast and slow component eye movements, was recorded. The direction of the slow eye movement correlated with that of the dominant stimulus. In addition, the intervals of the slow components with the same direction were examined by a stochastic analysis. These intervals were found to be independent of each other, and had a gamma distribution, revealing characteristics similar to those in binocular rivalry (Fox & Herrmann, 1967; Levelt, 1965). Optokinetic nystagmus was therefore proven to be a reliable indicator of binocular rivalry perception.

Visual evoked potentials

Several studies have used scalp electrodes placed over the occipital lobes to record visual evoked potentials (VEP) while subjects experienced binocular rivalry. Early experiments used time-averaged recordings pooled over the left and right eyes, without perceptual reports (Lansing, 1964; MacKay, 1968). Binocular rivalry resulted in a reduction in the amplitude of VEP signals. Brown & Norcia (1997) linked electrical signals with perception by separately tagging the left- and right-eye components of the VEP. When the left- and right-eye stimuli drifted at 5.5 Hz and 6.6 Hz respectively, Fourier components corresponding to these two stimuli appeared. The authors successfully demonstrated that the frequency-tagged VEP signals mirrored the stimuli that subjects reported to be dominant during binocular rivalry, in that when the amplitude of one rivalry-inducing stimulus was large, that of the other stimulus was invariably small. Moreover, these modulations were tightly phase-locked to the perceptual reports of the rivalry status: the presence of one eye's stimulus frequency in the electrical record corresponded with the perception of that eye's stimulus. The results suggested that binocular rivalry could be studied in non-verbal human or animal subjects using this technique.

Single-neuron recordings

Although both optokinetic nystagmus and VEP establish a firm coupling between physiological signals and perceptual fluctuations in binocular rivalry, they do not tell us where in the visual system the rivalrous percepts are arising. Single-neuron recordings in the lateral geniculate nuclei (LGN), primary visual cortex and higher cortical areas have helped to establish the visual areas involved in binocular rivalry. Early recordings used anaesthetised animals, making it difficult to relate neural activity to concurrent perceptual experience. More recently, however, several experiments have recorded action potentials from neurons in awake monkeys trained to report rivalry perception.

In species with well-developed binocular vision, the retinal projections from each eye terminate in different laminae of LGN, so that they remain segregated. Single-unit recordings show that interocular suppression occurs, as a reduction of firing rate in an individual neuron, as early as in LGN and the primary visual cortex (V1). Sengpiel, Blakemore and Harrad (1995) found neurons whose activity was reduced by interocular mismatches in the LGN or in layer 4 of V1 in anaesthetised cats with normal binocular vision. The optimal monocular grating was selected for each cell by finding the stimulus with a spatial frequency and orientation that produced the maximal response. Gratings of various orientations were then presented to the fellow eye. The authors found that introduction of an incompatible stimulus reduced the responses of a neuron in laminae A and A1 in the LGN to about 40% of that during monocular viewing. A reduction of response, measured as about 35%, was also found in the neurons in V1. Although these LGN neurons exhibit inhibitory interaction, the inhibition was independent on the interocular difference of the grating orientation. For the majority of the binocular cortical cells, the response to a grating of optimal orientation in one eye was suppressed by a grating of very different orientation shown to the other eye. Sengpiel et al. (1995) proposed that the perceptual switches during binocular rivalry depend on the interaction at the level of binocular neurons of the primary visual cortex.

While LGN cells are liable to inhibitory interocular interaction in the cat, similar modulation has not been found in the monkeys. Lehky & Maunsell (1996) studied neural correlates of binocular rivalry in LGN by using alert macaque monkeys. Orthogonal drifting gratings were presented binocularly to the monkeys and the gratings were centred over receptive fields to induce interocular suppression. The only task of the monkey was to fixate the stimulus. The results showed that there was no difference between the responses of LGN neurons under rivalrous and non-rivalrous conditions, as determined by the ratios of their respective power spectra. They claimed that there was no evidence for interocular suppression at the subcortical level. The authors, however, found that there was a curious "temporal afterimage" effect in which LGN cells continued to be modulated at the drift frequency of the grating for several seconds after the visual stimulus disappeared. In another study (Varela & Singer, 1987), ablation of visual cortex abolished these LGN activity and feature-dependent interferences. This activity might have been due to feedback responses from the primary visual cortex (McClurkin, Optican & Richmond, 1994). The power spectrum is the Fourier transform of the temporal autocorrelation function and as such conveys no information about the phase or delay of signals. In addition, the responses can have the same second-order autocorrelation function and radically different third- or higher-order correlation. The lack of responses from the power spectrum therefore does not rule out the involvement of the LGN in binocular rivalry suppression. LGN activity has been shown in functional imaging studies (Haynes, Deichmann & Rees, 2005; Wunderlich, Schneider & Kastner, 2005), which will be discussed later in this chapter. The first expression of binocular rivalry could therefore be in the LGN.

A series of papers assessing the neural activity during binocular rivalry have been published by Nikos Logothetis and his colleagues. Their work arose from the correlation of psychophysical and single-unit data in awake monkeys. Monkeys were trained to report their perception during rivalry by pulling levers to signal which stimulus was seen, and cortical neural activity was recorded at the same time. During non-rivalry viewing, presentation of an optimal stimulus caused a significant increase in firing rate, which correlated well with the monkey's viewing report. In binocular rivalry, cells fired strongly when their optimal stimulus was perceptually dominant, and markedly reduced their response when the non-optimal stimulus was dominant. The cells that were affected by suppression were almost exclusively binocular, and their proportion was found to increase in the higher processing stages along the visual cortical pathways.

Along the dorsal visual pathway, Logothetis and Schall (1989) examined the middle temporal cortex (MT) and found that the firing activity of 42% of the recorded neurons correlated with the perceptual alternation during binocular rivalry. For the ventral pathway, Leopold and Logothetis (1996) examined visual areas V1, V2 and V4. They found that 18% of their recorded neurons in V1 and V2 fired in a way that matched the perceptual fluctuation in rivalry. This proportion increased two-fold in V4, where the responses of 38% of the recorded cells correlated with perceptual alternation during binocular rivalry. Further along the ventral pathway, Sheinberg and Logothetis (1997) showed that up to 90% of the neurons recorded in the superior temporal sulcus and inferior temporal cortex had neural activity correlated with perceptual rivalry. They suggested that binocular competition had reached perceptual awareness at this level of cortex. In general, therefore, there was weak binocular rivalry in the primary visual cortex, and the proportion of cells that correlate with the percept increase along the visual cortical pathways.

These results, however, must be treated with a little caution. Perceptually, binocular rivalry is a high-level cognitive activity, in which there is intriguing complexity and diversity of neural activity involving competition between conflicting visual stimulation. How does the study of single units reflect this complex cognition? The answer to this question is far from simple. For example, the perceptually significant activity occurs not at the single-neuron level but in groups of neurons (Churchland & Sejnowski, 1992; Douglas & Martin, 1991). In addition, the absence of firing rate changes in any cortical areas should not be interpreted as an absence of perceptual activity, as populations of neurons can increase and decrease the coherence of their firing as a function of time. Such increases in coherence have significant effects on the other stages of processing, as synchronised inputs produce stronger depolarisations for equal numbers of spikes (Blake & Logothetis, 2002).

Functional magnetic resonance imaging

Functional magnetic resonance imaging (fMRI) refers to a technique that non-invasively measures neuronal activity by determining regional changes of blood perfusion and metabolism (Orrison, Lewine, Sanders & Hartshorne, 1995). The relationship between neural activity and blood flow may be explained by metabolic processes, in that the generation of synaptic and action potentials results in metabolic deficits and consequent increases of regional cerebral blood flow. This relationship has been observed for over 100 years. For instance, William James observed regional brain pulsation and Paul Broca measured regional brain temperature changes when subjects performed mental tasks (Berns, 1999).

The fMRI technique is based on the blood-oxygen-level-dependent (BOLD) signals in activated brain areas (Bradley & Stark, 1999). However, because fMRI relies on significant changes of regional cerebral blood flow, it cannot necessarily distinguish excitatory and inhibitory activity. In addition, some activated areas may be invisible during binocular rivalry due to the summation of BOLD signals due to dominance and suppression. Careful experimental design is therefore required to demonstrate the activity of such areas during rivalry.

Tong, Nakayama, Vaughan & Kanwisher (1998) used fMRI to monitor stimulus-selective responses of the human fusiform face area (FFA) and parahippocampal place area (PPA) during binocular rivalry. A face stimulus was presented to one eye and a house stimulus to the other eye. Fluctuations of magnetic resonance signals in FFA and PPA correlated well with subjects' perceptual alternations: activation of FFA when the face was seen and activation of PPA when the house was seen. The magnitude of signals in the FFA and PPA during rivalry was equal to that evoked when the stimulus was physically alternated between face and house. This result indicated the activity in these high-level areas is as pronounced during rivalry as during normal viewing.

Lumer, Friston & Rees (1998) designed an experiment to study the neural activity associated with perceptual transition in binocular rivalry. The rivalry stimulus consisted of a drifting grating presented to one eye and a static face to the other. The non-rivalrous control was constructed by physically switching the stimulus between grating and face with the same timing as in rivalry. Cortical activity was scanned in the two conditions, dichoptic and non-rivalrous control. Comparison of the fMRI signals in the two conditions revealed a cortical activation site in the right frontoparietal region. This region has been implicated in spatial attention (Desimone & Duncan, 1995) and the authors speculated that both rivalry and attention share a similar mechanism in that they can block the awareness of a monocular stimulus or an unattended stimulus, respectively.

Both of the above-mentioned studies revealed cortical activation during binocular rivalry in high-level cortical areas rather than in the primary visual cortex. Is the primary visual cortex silent during binocular rivalry? Two studies show the opposite. Polonsky, Blake, Braun & Heeger (2000) used a low contrast grating presented to one eye and a higher-contrast orthogonal grating to the other eye. Magnetic resonance activity in the primary visual cortex increased while the higher contrast pattern was perceived and decreased when the lower contrast pattern was perceived. The fluctuation in V1 activity was about 55% as large as that evoked by physically alternating the two monocular stimuli. Other cortical areas, such as V2, V3, V3a and V4v also showed fluctuations of activity of a similar magnitude. This experiment clearly demonstrated the involvement of the primary visual cortex in binocular rivalry.

Tong and Engel (2001) examined the effect of binocular rivalry in the primary visual cortex by monitoring the activity in the cortical representation of one eye's blind spot; activity in this region is almost all driven by the ipsilateral eye with little or no input from the contralateral eye. The rivalry-inducing stimulus was a grating to one eye and an orthogonal grating to the blind spot and surrounding region of the other eye. The results showed that the activity in the blind-spot representation increased when the ipsilateral eye's stimulus became dominant, and diminished when the other grating became dominant. Further, the activation was similar in magnitude to that during physical alternation between these gratings. This finding provided evidence that there is interocular competition in the primary visual cortex that could mediate binocular rivalry. It also implies that V1 may be important in the selection and expression of conscious visual information.

Very recently, there have also been reports that rivalry modulates activity in the lateral geniculate nucleus (Haynes et al., 2005; Wunderlich et al., 2005). Wunderlich et al. (2005) used fMRI to measure neural activity in the human LGN while subjects viewed contrast-modulated gratings presented dichoptically. They found that the amplitude of fMRI signals both in LGN and V1 increased monotonically when subjects perceived a high-contrast grating and the amplitude decreased when the subjects perceived a low-contrast grating. The other fMRI study, conducted by Haynes et al. (2005), demonstrated that the regions of LGN that show strong eye preference also show modulated activity during binocular rivalry: a region increases its activity when its preferred eye is perceptually dominant. These two studies provided evidence that neural correlation of binocular rivalry can be found even earlier than V1, that is, in the LGN.

In general, fMRI has revealed activations in multiple visual cortical areas during binocular rivalry. In agreement with the psychophysics and neurophysiology, therefore, imaging studies show that binocular rivalry suppression occurs at a number of cortical sites, including the primary visual cortex.

Binocular rivalry suppression

Suppression depth

Many binocular rivalry studies measure dominance durations. This can lead to practical problems, such as a variable criterion for dominance. The variability can apply to the visual field location on which the subject is reporting, or to the timing of perceptual switches. A more objective approach measures suppression depth. By definition, binocular rivalry suppression depth is the visual sensitivity loss or threshold elevation during suppression when compared to the dominance viewing condition. Suppression depth has been measured is several ways, which will now be described.

Fox and Check (1966) examined thresholds for three viewing conditions: dominance, suppression, and monocular viewing. The rivalry-inducing stimulus was a red grating to one eye and an orthogonally-oriented green grating to the fellow eye. In monocular viewing, one eye viewed a stimulus while the fellow eye viewed a blank field. The detection threshold was assessed by delivering three alphabetic letters with equal probability. Letter luminance was adjusted to obtain

50 to 70% correct responses by using a two-alternative forced-choice method. The threshold measured in dominance was similar to that in monocular viewing, and both were substantially lower than that in suppression. The suppression depth was, however, not quantified in this experiment.

The magnitude of threshold elevation was quantified in another experiment (Wales & Fox, 1970). Rivalry was induced by two circular disks with opposite contrast. A test stimulus was delivered to the left eye and the duration of its presentation was adjusted to obtain a detection threshold for correct identification. The threshold in suppression was three times higher than that in dominance. In term of sensitivity, which is calculated as the reciprocal of threshold, sensitivity in suppression was one third of that in dominance. This method was a relatively indirect way of measuring suppression depth. It was, however, the first quantification of suppression depth, and is commonly cited in the rivalry literature.

Direct measurements of contrast sensitivity in suppression can be found in other experiments, such as those of Makous and Saunders (1978) and Blake and Camisa (1979). The contrast sensitivity in suppression was estimated to fall to about 50% of that in dominance, regardless of the contrast levels of the orthogonal gratings.

Eye suppression

Early work in binocular rivalry suggested that suppression operates non-selectively over a broad range of stimulus types on the suppressed eye. The *eye suppression* hypothesis states that a suppressed eye is equally insensitive to any stimulus, regardless of its spatial, chromatic or dynamic properties (Blake, Westendorf & Overton, 1980). Coupled with this hypothesis is the idea that binocular rivalry is the result of reciprocal inhibition between left-eye and right-eye channels in the visual system. Eye suppression is therefore considered to be the result of competition between monocularly-driven cells.

Evidence for this hypothesis can be found in a number of psychophysical studies. In the study of Blake, Westendorf & Overton (1980), the monocular stimuli were alternated between eyes immediately after the subject reported suppression of one eye's image. The swapping of stimuli caused the percept to change from one monocular stimulus to the other, implying that dominance belonged to an eye, not a stimulus characteristic. Further the suppressed eye remained suppressed, despite the change in the stimulus presented to it. In another experiment (Nguyen, Freeman & Wenderoth, 2001), achromatic orthogonal gratings were used to induce binocular rivalry and a brief test stimulus was presented to one eye while its rivalry-inducing stimulus was dominant or suppressed. The test stimuli were varied widely across four stimulus domains: namely, the relative stimulation of medium- and long-wavelength-sensitive cones, duration, spatial frequency, and grating orientation. The result in each case was similar in that contrast sensitivity during suppression was around 65% of that during dominance. More importantly, suppression depth was found to be largely independent of the type of test stimulus.

Feature suppression

The *feature suppression* hypothesis, an alternative to the eye suppression hypothesis, states that binocular rivalry suppression is mediated by competition between neuronal populations tuned to differing stimulus features. These populations are assumed to be largely located in higher visual cortex and to respond to input from both eyes. This hypothesis challenges the eye suppression hypothesis on at least three lines of evidence.

There are two psychophysical studies supporting feature suppression. Logothetis, Leopold & Sheinberg (1996) were the first to make the distinction between eye and feature suppression (they called the latter stimulus suppression). In their experiment, the two rivalry-inducing stimuli were swapped between the two eyes three times per second. Perceptual alternations, however, were much slower, and were similar to the alternation in the absence of swapping. They concluded that neural representations of the two monocular stimuli compete for visual awareness independently of the eye through which the stimuli are presented.

Kovács et al. (1996) also provided evidence for feature suppression. They designed a patchwork rivalry paradigm in which one eye was presented with green patches interspersed with red patches, while the other eye was presented with the complementary pattern. Subjects, however, reported seeing an alternation between all-red and all-green patterns, and they did so more often than expected by chance. They also broke the coherency of conventional stimuli (a monkey face and a jungle face) and replaced them by complementary patchworks of the intermingled rivalrous images (each of them contained a mixture of pieces of a monkey and pieces of a jungle scene). The subjects again reported seeing the conventional images (either a monkey or a jungle scene). Kovács et al. concluded that there is interocular grouping of similar stimulus components, supporting the hypothesis of feature suppression.

Initiation of binocular rivalry

Eye suppression versus feature suppression

From the preceding discussion, it is clear that binocular rivalry exerts its effects at a number of sites along the visual pathway. It is not at all clear, however, where binocular rivalry is initiated. In the remainder of this chapter, four possibilities are considered: the primary visual cortex, high visual cortex, frontal lobe, and brainstem.

Eye suppression and feature suppression are the most commonly used hypotheses for the origin of binocular rivalry. There is evidence for and against each hypothesis. Nguyen et al. (2001) therefore developed a model that incorporates both forms of suppression. The model is shown in Figure 1.1. The main idea is that inhibition occurs between cell populations at a succession of stages in the visual pathway. In the primary visual cortex there is inhibition between left- and right-eye-driven cells, resulting in eye suppression. At higher cortical levels the inhibition is between binocular cells encoding opposing features such as horizontal and vertical orientation, producing feature suppression. At each stage, the dominant pathway inhibits the suppressed pathway, increasing the suppression of that pathway. Reciprocally, the suppressed pathway inhibits the dominant pathway less, increasing the dominance.

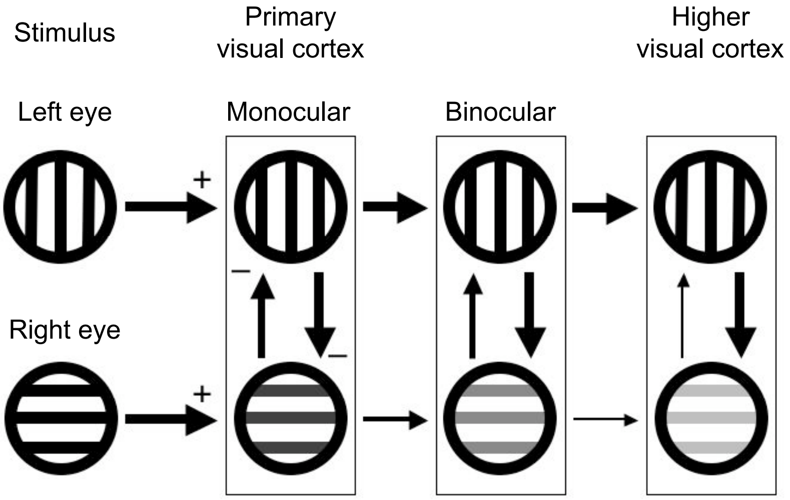

Figure 1.1. A model of binocular rivalry, from Nguyen et al (2001). This model assumes that binocular rivalry involves more than one neuronal population, and the visual pathways include monocular and binocular processing stages, and a feature-selective stage in higher cortex. A pathway leads from each eye, and there is mutual inhibition between these two pathways at each stage. The figure shows suppression in the right-eye pathway, depicted as a loss of contrast in the gratings representing the stages. Suppression deepens as the signal progresses to higher cortex. Sensitivity change is due to the suppression at the monocular stage, and perceptual loss is due to the suppressive effects at higher stages.

This model predicts that the depth of suppression increases as the visual signal progresses along its pathway. Nguyen, Freeman & Alais (2003) have provided experimental support for this prediction. In their experiments, visual stimuli were lobed circles of the form first described by Wilkinson, Wilson & Habak (1998). The test stimulus comprised two adjacent multi-lobed semicircles: one semicircle had two lobes while the second semicircle had fewer, such as 0, 0.5, 1 and 1.5 (examples as shown in Figure 3.2). This test stimulus was presented briefly to one eye during either its dominance or suppression phase. The subject was required to nominate which semicircle had more lobes, and lobe amplitude was adjusted to obtain 75% correct responses. The task became more difficult as the number of lobes in the second semicircle approached two. The results showed that suppression depth increased as the task became more difficult.

The increasing suppression depth was interpreted as follow. When the variable semicircle had zero lobes, the judgement consisted of deciding in which half of the tested eye's view there was a change. This was a judgement that presumably depended on the responses of cells in the primary visual cortex. The small suppression depth measured therefore reflected the relatively small effects of rivalry early in the cortical pathway. When the decision involved the discrimination of a 1.5-lobed semicircle from a 2-lobed one, higher centres were presumably required for the judgement; the deeper suppression in this case reflected the stronger effects of rivalry in these areas. The model shown in Figure 1.1 assumes that binocular rivalry is initiated in the primary visual cortex. The deepening suppression described by Nguyen et al. (2003) is consistent with this idea.

High-level cortical influence on binocular rivalry

The sequence of events leading to binocular rivalry begins with the visual stimulus, leading to activation of photoreceptors and other retinal cells, transmission through the thalamus, and activation of the visual cortex. This sequential flow is referred to as ‘bottom-up’. There are also high-level cortical influences affecting the perceptual process. In keeping with the terminology of 'bottom-up', this downward flow is called 'top-down'. If binocular rivalry originates in high-level cortex, top-down effects may heavily affect the perceptual decision-making. If the origin is in low-level cortex, the top-down selection will be less effective. How much top-down influence on binocular rivalry exists? To understand this question, voluntary control and attentive bias in binocular rivalry is here reviewed.

In binocular rivalry, fluctuations in dominance and suppression are irregular and unpredictable. Can these fluctuations be voluntarily controlled? This issue has been studied for more than 100 years. The result is that with prolonged practice, the dynamics of rivalry can be slightly affected by voluntary control. An early experiment (Breese, 1899) measured dominance durations under two conditions: 1. passive viewing of the stimulus; 2. with mental effort to keep one monocular stimulus visible in view. The result showed that mental exertion could measurably bias the duration of dominance. The bias was, however, not quantified. Lack (1969) recorded the dominance fluctuations in 32 subjects by asking them to report dominance. Subjects were instructed to decrease or increase the rate of alternation for a given test period. Over 10 days of practice, with approximately 50 minutes per day, the subjects were able to accelerate or decelerate the alternation rate.

However, these experiments also indicated that observers had difficulty maintaining dominance or suppression of one rivalrous stimulus to the exclusion of the other. In addition, these measurements relied on the subjective reports of perception: the reported changes in perception might reflect a change in a subject's criterion for signalling specific perceptual states. A more objective measurement of voluntary control over binocular competition is found in the work of Collyer and Bevan (1970). The test stimulus, an equilateral triangle, was presented at one of three orientations. The subject was required to identify the orientation of the triangle. Test luminance was set at a level producing 70% correct responses in the monocular viewing condition. Subjects then performed the same task during binocular rivalry with and without voluntary effort to bring a particular stimulus to view. The results showed that recognition was improved around 10 to 16% in the tasks when the subject was warned which eye was to be stimulated, and instructed to maintain the dominance of one eye's stimulus for a complete session. These results indicated that there is some degree of voluntary control over binocular rivalry.

Is the magnitude of interocular suppression altered by voluntary control? Lack (1973) examined this idea by measuring the discrimination threshold in suppression during passive and active viewing conditions. In passive viewing, subjects did not resist any perceptual changes, but in active viewing, tried to maintain dominance of a specific stimulus. The test stimuli were four English letters and when subjects triggered a test, one of these letters was presented after a 0.5 second delay. The test stimulus duration was set to obtain 60% correct responses in a normal viewing condition. The duration was substantially increased during suppression compared to that during dominance. The threshold elevation, however, was similar in the passive and active viewing conditions. Lack concluded that voluntary effort did not result in greater suppression depth.

Voluntary control over binocular rivalry has been compared with that in other forms of bistable perception. The Necker cube is a cube represented by its edges, not its faces, and can be perceived in two depth relationships. Meng & Tong (2004) compared voluntary control of dominance durations in binocular rivalry and Necker cube reversal. The results showed much weaker voluntary control over binocular rivalry than for Necker cube reversal, even for rivalry displays that maximised the opportunities for feature-, object, or space-based attentional selection. Other recent studies on voluntary control of perceptual bi-stability (van

Ee, 2005; van Ee, van Dam & Brouwer, 2005) also showed that voluntary control in binocular rivalry is very limited.

If binocular rivalry and Necker cube reversal were mediated by common mechanisms of stimulus-based competition, attentional selection should be equally effective in biasing these two forms of rivalry. The preceding results indicate this is not the case. Rather, binocular rivalry is strongly influenced by bottom-up factors such as stimulus contrast, contour and motion, while top-down attentional modulation is weak. These results favour the idea that binocular rivalry differs from bistable figure reversal and involves a more automatic form of visual competition. This reinforces the notion that binocular rivalry originates in low-level cortical areas.

Hemispheric switching theory in binocular competition

Subcortical regions, early visual cortex and high-level cortical areas have been suggested as neural sites for the initiation of binocular rivalry. Further, it has generally been assumed that rivalry operates through competition between neighbouring groups of cells. Pettigrew and his colleagues have made a very different suggestion, namely, that rivalry alternation results from switches in activation between the left and right hemispheres, triggered by a bistable oscillator located in a subcortical region such as the midbrain. This theory challenges the idea that binocular rivalry is cortically originated and deserves careful consideration.

The evidence for the hemispheric switching theory is as follows. First, the rate of binocular rivalry alternation is slow in euthymic subjects with bipolar disorder compared with normal controls (Pettigrew & Miller, 1998). Pettigrew & Miller proposed that bipolar disorder is the result of a genetic propensity for slow interhemispheric switching mechanisms and the patient becomes manic when the switching favours the left hemisphere, and depressed when the switch changes to the right hemisphere. Because of the slow interhemispheric switching their bipolar subjects had a slow perceptual alternation rate. Second, activation or disruption of a single hemisphere in human affects the perceptual alternations of binocular rivalry (Miller, Liu, Ngo, Hooper, Riek, Carson & Pettigrew, 2000). To demonstrate this effect, Miller et al. (2000) used caloric vestibular stimulation to stimulate a hemisphere, or single-pulse transcranial magnetic stimulation to disrupt a hemisphere. Both of these two methods caused striking changes in the pattern of binocular rivalry alternations, with complete reversals of pattern of predominance.

Pettigrew (2001) argued that the primary visual cortex was not a candidate for initiating binocular rivalry, on the following basis. The period of the binocular rivalry cycle is 2 to 3 seconds, which is too slow for a V1 process. The 'attentional spotlight' in V1 has been found to operate at 30 to 40 Hz measured in serial search tasks (such as in (Wolfe, Alvarez & Horowitz, 2000)). If alternation takes place in V1, the switch rate would be as fast as 30 Hz. However, binocular rivalry is much slower than this, around 0.5 Hz (Levelt, 1965). It must be originating in some other location that is nevertheless receiving input from V1 but is unable to follow V1's high-speed oscillation. In addition, the V1 neuronal activity is relatively consistent in firing rate, which cannot explain the fact that there is a large individual variation in rivalry rate.

To complete the hemispheric switching theory, Pettigrew (2001) proposed that the trigger for interhemispheric oscillation be located in the ventral tegmentum area: a number of paired midline structures in the neuraxis fitted his criteria. These structures included the hypothalamus, the midbrain tegmentum, the raphe system, the locus coeruleus and the medulla. Generally speaking, the selection was based on the anatomical location, timing of oscillation and functional imaging results.

The theory of hemispheric switching tries to place rivalry in the larger context of individual variations, circadian rhythms and some psychiatric conditions (such as mood disorder and schizophrenia). There are, however, a lot of questions unanswered about the theory; the following are some of the unsolved issues. First, the subcortical structure of the ventral tegmentum is only weakly linked to the visual pathway. How can the tegmentum identify the visual conflict between the two eyes? Second, although the tegmentum has a similar oscillation rate to binocular rivalry, there is so far little evidence that can link this oscillation with binocular rivalry. Third, if the hemispheric switching theory is true, then we can expect that the whole hemisphere will be simultaneously activated. However, the single-unit studies show that the cell populations correlated to perceptual alternations increase along the visual pathways (Logothetis, 1998). Fourth, if binocular rivalry is the result of hemispheric oscillation, the communication between hemispheres would be critical. There is, however, binocular rivalry in split-brain patients (O'Shea & Corballis, 2000). These conflicts throw doubt on the hemispheric switching idea.