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Binocular Rivalry and the Cerebral Hemispheres

With a Note on the Correlates and Constitution of Visual Consciousness

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Abstract. In addressing the scientific study of consciousness, Crick and Koch state, "It is probable that at any moment some active neuronal processes in your head correlate with consciousness, while others do not: *what is the difference between them?*" (1998, p. 97). Evidence from electrophysiological and brain-imaging studies of binocular rivalry supports the premise of this statement and answers to some extent, the question posed. I discuss these recent developments and outline the rationale and experimental evidence for the interhemispheric switch hypothesis of perceptual rivalry. According to this model, the perceptual alternations of rivalry reflect hemispheric alternations, suggesting that visual consciousness of rivalling stimuli may be unihemispheric at any one time (Miller *et al.*, 2000). However, in this paper, I suggest that interhemispheric switching could involve *alternating unihemispheric attentional selection* of neuronal processes for access to visual consciousness. On this view, visual consciousness during rivalry could be *bi*hemispheric because the processes constitutive of attentional selection may be distinct from those constitutive of visual consciousness. This is a special case of the important distinction between the neuronal *correlates* and *constitution* of visual consciousness.

Key words: attentional selection, bipolar disorder, binocular rivalry, caloric vestibular stimulation, coherence rivalry, consciousness, interhemispheric switching, neural correlates, transcranial magnetic stimulation

1. Neural Correlates of Visual Consciousness During Binocular Rivalry

Binocular rivalry has intrigued investigators for centuries (Wade, 1998). The presentation of two dissimilar images, one to each eye (in the same retinal location), results in alternating perception and suppression of each image, for as long as the subject views the conflicting stimuli (Figure 1a, b). Despite the accumulation of a considerable amount of experimental evidence on the psychophysics and neurophysiology of binocular rivalry (Blake, 1989; Fox, 1991; Howard and Rogers, 1997; Logothetis, 1998a), there has been no consensus on the neural mechanism(s) underlying the phenomenon.

While binocular rivalry has traditionally been of interest to visual scientists, it has recently gained wider prominence as a tool for studying visual consciousness. Indeed, the scientific study of consciousness has emerged as a legitimate interdisciplinary pursuit.[1] Crick and Koch (1998) suggest that understanding the mechanisms of visual consciousness may provide a framework for understanding mechanisms of consciousness in general. They summarize the core issue: "It is probable that at any moment some active neuronal processes in your head correlate with consciousness, while others do not; *what is the difference between them?*" (p. 97, original italics).

The correlational approach is indeed a powerful scientific method and Crick and Koch's premise is certainly consistent with general principles of organizational and functional modularity in the brain. Such principles were established by clinical neurologists in the nineteenth century and became fundamental to twentieth century neuroscience (Albright *et al.*, 2000; Gazzaniga, 2000; Kandel *et al.*, 2000). It is not surprising therefore, that as we enter the twenty-first century, there is widespread interest in identifying the 'neural correlates of consciousness' (Atkinson *et al.*, 2000; Block, 1996; Chalmers, 1996; Cleeremens and Haynes, 1999; Crick and Koch, 1998; Frith *et al.*, 1999; Heeger, 1999; Metzinger, 2000).

Binocular rivalry is a useful tool in the search for neural correlates of consciousness for several reasons. It consists in abruptly alternating perceptual states, isolated both in time and character. This enables the precise mapping of an individual's visual consciousness trajectory (Cleeremans and Haynes, 1999). Moreover, single-unit and regional correlation studies can be based on the stimulus-specificity of individual neurones (Engel *et al.*, 1999; Logothetis, 1998a) and particular brain regions (Tong *et al.*, 1998), respectively. Most importantly however, the phenomenon enables the comparison of neural activity that depends on the (constant) presentation of stimuli and neural activity that depends on the (changing) *perception* of stimuli (Crick and Koch, 1998; Engel *et al.*, 1999; Flanagan, 1995; Logothetis, 1998a; Logothetis and Schall, 1989). This distinction has justifiably attracted wide interest because the latter, but not the former, can be considered a neural correlate of visual consciousness (at least during rivalry).

Logothetis and Schall (1989), Leopold and Logothetis (1996) and Sheinberg and Logothetis (1997) recorded the activity of neurons through various stages of the visual pathway while alert, trained monkeys reported their perceptual alternations during binocular rivalry (see also Myerson *et al.*, 1981). The model of rivalry proposed by Blake (1989; see also Lehky, 1988; Tong, this issue), based on reciprocal inhibition between monocular neurons (neurons that respond preferentially to one eye), predicts perception-dependent neuronal activity prior to the site of binocular convergence in the primary visual cortex (V1). However, Leopold and Logothetis (1996) demonstrated that the firing of monocular neurons was not correlated with the monkeys' perceptual reports. Although the activity of around 20% of V1 neurons was perception-dependent, all but one of these

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[1] See *Cognition* (2001, vol. 79, issues 1–2); *Consciousness and Cognition* (1999, vol. 8, issue 2; 1995, vol. 4, issue 2); *Nature Neuroscience* editorial (2000, vol. 3, issue 8); *Neuropsychologia* (1995, vol. 33, issue 9); *Philosophical Transactions of the Royal Society B Biological Sciences* (1998, vol. 353, issue 1377).

were *binocular* (responsive to either eye). Moreover, increasing percentages of neurons demonstrating perception-dependent activity were found as the investigators progressed through V4 ($\sim$40%) and the middle temporal area (MT; $\sim$40%),[2] finally reaching around 90% in the inferotemporal (IT) cortex and the superior temporal sulcus (STS) at the highest level of visual processing (Leopold and Logothetis, 1996; Logothetis and Schall, 1989; Sheinberg and Logothetis, 1997; reviewed in Logothetis, 1998a). Thus, perception-dependent single-unit activity during rivalry occurs increasingly through higher levels of visual processing, but not at all at the monocular level.

These electrophysiological results can be compared with the results of several recent functional magnetic resonance imaging (fMRI) experiments in humans undergoing rivalry. Polonsky *et al.* (2000) demonstrated perception-dependent neural activity in V1 (*striate* cortex) but could not determine whether monocular or binocular neurons were responsible for such activity. Tong and Engel (see Tong, this issue) found purely *monocular* perception-dependent fMRI activity during rivalry, by assessing the V1 blind-spot representation in humans. However, perception-dependent blind-spot monocular neuron activity does not necessarily imply perception-dependent activity amongst the rest of V1 monocular neurons, and cannot therefore be considered conclusive evidence that binocular rivalry is the result of interocular competition (c.f. Tong, this issue). Indeed, the single-unit data of Leopold and Logothetis (1996) suggest that blind-spot monocular perception-dependency does not extend to V1 monocular neurons outside this unique cortical representation (Concurrent measurements of blind-spot fMRI and non-blind-spot single-unit activity in monkeys could assess such issues directly).

In earlier experiments, Tong *et al.* (1998; see Tong, this issue) used fMRI to measure brain activation during the two perceptual states of binocular rivalry. They used face and house images to elicit rivalry, thus taking advantage of the regional specificity associated with the processing of such stimuli. Face perception is known to be associated with activation in a specific region of the right hemisphere, the fusiform face area (Kanwisher *et al.*, 1997), while perception of houses and places, but not faces, is associated with activation bilaterally in the parahippocampal place area (Epstein and Kanwisher, 1998). Tong *et al.* (1998) demonstrated that the alternating perception of face and house images during rivalry is indeed correlated with alternating increases and decreases in brain activation in these respective *extrastriate* processing regions.

Lumer *et al.* (1998), also using fMRI, concentrated their investigation on perceptual transitions during binocular rivalry, comparing brain activation associated with rivalrous perceptual alternations and brain activation associated with non-rivalrous physical stimulus alternations. They reasoned that the former, but

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[2] About a third of neurons in V4 and MT, though perception-dependent, increased their firing rate when their *non*-preferred stimulus was perceived. This suggests that such neurons may be "part of an inhibitory mechanism that that is separate from, and to some extent independent of, the mechanisms of perception" (Logothetis, 1998a, p. 1808).

not the latter, could be implicated in the mechanism of perceptual transitions during rivalry. Finding transition-dependent activation in a right-lateralized fronto-parietal region, the authors argued (given this region's role in processes of selective attention) that during rivalry, it is this network that is responsible for the selection of neuronal processes for access to visual consciousness.

2. Eye, Stimulus and Coherence Rivalry

The topical issue of 'eye' versus 'stimulus' rivalry is discussed in detail by Blake (this issue) and Tong (this issue). According to Blake (1989, p. 146, original italics), "During a suppression phase of binocular rivalry, neural activity is inhibited within *all* monocular neurones innervated by the eye viewing the currently suppressed stimulus, not just those neurones selective for the features specifying that stimulus. In other words, it is a region of an eye that is suppressed during rivalry, not information about a particular set of stimulus features". This line of reasoning is supported by the fact that the detection thresholds of test probes (with stimulus features different to those of an initially suppressed stimulus) are elevated 0.3–0.5 log units when presentation of the probes occurs during perceptual suppression, compared with during perceptual dominance (Fox and Check, 1966; Fox and Check, 1968; Wales and Fox, 1970; see also Blake, 1989, and this issue).

Non-selective suppression suggests rivalry between corresponding regions of each eye, thus supporting monocular neurone models. However, other psychophysical observations challenge this notion of eye rivalry. For example, rapidly exchanging each eye's presented image (every 333 milliseconds) does not interfere with the smooth and slow perceptual alternations of normal rivalry, demonstrating that rivalry can occur between stimulus representations at a high level of the visual pathway (Logothetis *et al.*, 1996; see also Wei and Sun, 1998). On the other hand, Lee and Blake (1999; see Blake, this issue) found that the existence of stimulus rivalry during stimulus-exchange experiments is limited to specific conditions such as low-contrast, rapidly flickering stimuli that are exchanged abruptly between the eyes.

Using a different approach, Diaz-Caneja (1928), and more recently Kovács *et al.* (1996; see also Papathomas *et al.*, 1999) and Ngo *et al.* (2000), demonstrated the brain's capacity for rivalry between stimulus representations.[3] Diaz-Caneja (1928; see also Logothetis, 1998a and Alais *et al.*, 2000) reported that dichoptic (separate-eye) presentation of half-field stimuli such as those shown in Figure 1c, does not induce rivalry between two half-field percepts (Figure 1d), but rather, between coherent images of concentric circles and horizontal lines (Figure 1e). This finding was recently replicated (with some methodological differences) and quantified (Ngo *et al.*, 2000) and 'coherence rivalry' was found to occupy roughly half of an individual subject's total viewing time (n = 16 subjects, stimulus size = $2.8° \times 2.1°$, see Figure 1e). As Diaz-Caneja first reported in 1928, rivalry with half-

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[3] See also Kulikowski (1992); Treisman (1962); Whittle *et al.* (1968); and Blake (this issue).

field stimuli occurs (for at least half the viewing time) between coherent stimulus representations.[4]

Alais and Blake (1999; see also Breese, 1899; Blake, this issue) note that large standard rivalry stimuli induce piecemeal rivalry (mosaicism, see Figure 1b) in which stimulus features from each eye are perceptually mixed. This suggests that perceptual dominance during rivalry is established within local 'zones' throughout the visual field (see Sengpiel, this issue). They further suggest that the interaction between local zones is responsible for perceptual grouping during rivalry. However, there is a clear difference in the type of interaction occurring between zones of suppression in conventional rivalry and in coherence rivalry (see Figure 1)[5] and the difference exists only by virtue of 'information about a particular set of stimulus features'. This information determines *which* regions of an eye are suppressed at which time. The physiological mechanism(s) by which this occurs remains unclear. Plausible candidates include bottom-up processes (Alais and Blake, 1999; Blake, 1989), top-down (though *involuntary*) selection of coherent stimulus features (Leopold and Logothetis, 1999; Ooi and He, 1999; Papathomas *et al.*, 1999) or some interaction of these mechanisms (Logothetis, 1998a; Ooi and He, 1999; Papathomas *et al.*, 1999; Polonsky *et al.*, 2000; see also Reynolds and Desimone, 1999; Strüber and Stadler, 1999).

It is also unclear to what extent coherence and conventional rivalry are similar processes. Indeed, the stimulus characteristics determining the relative proportions of each during a given viewing period are only beginning to be studied (Blake, this issue; Kovács *et al.*, 1996; Ngo *et al.*, 2000; Papathomas *et al.*, 1999) and a variety of experimental and theoretical issues await investigation. For example, would the suppression in both eyes during coherence rivalry be non-selective? If not, a significant physiological difference exists between coherence and conventional rivalry. On the other hand, if test probes presented to suppressed regions of both eyes during coherence rivalry *are* associated with elevated detection thresholds, then it can be surmised that regional suppression (on the basis of particular stimulus features) temporally precedes non-selective suppression within those regions. Both contingencies suggest a role for high-level (though not necessarily cognitive/semantic) processing during coherence rivalry. As Blake (this issue, pp. 5–38) suggests, "perhaps attention is providing part of the neural glue".

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[4] Ngo *et al.* (2000) dubbed the phenomenon first demonstrated by Diaz-Caneja 'coherence rivalry' to refer to the perceptual re-organization of each eye's presented stimuli into rivalling coherent images. Although coherence rivalry is consistent with the notion of stimulus representation rivalry, the latter does not necessarily imply such re-organization.

[5] With the small stimuli we used in our coherence rivalry experiments, piecemeal rivalry was minimized and excluded (Ngo *et al.*, 2000).

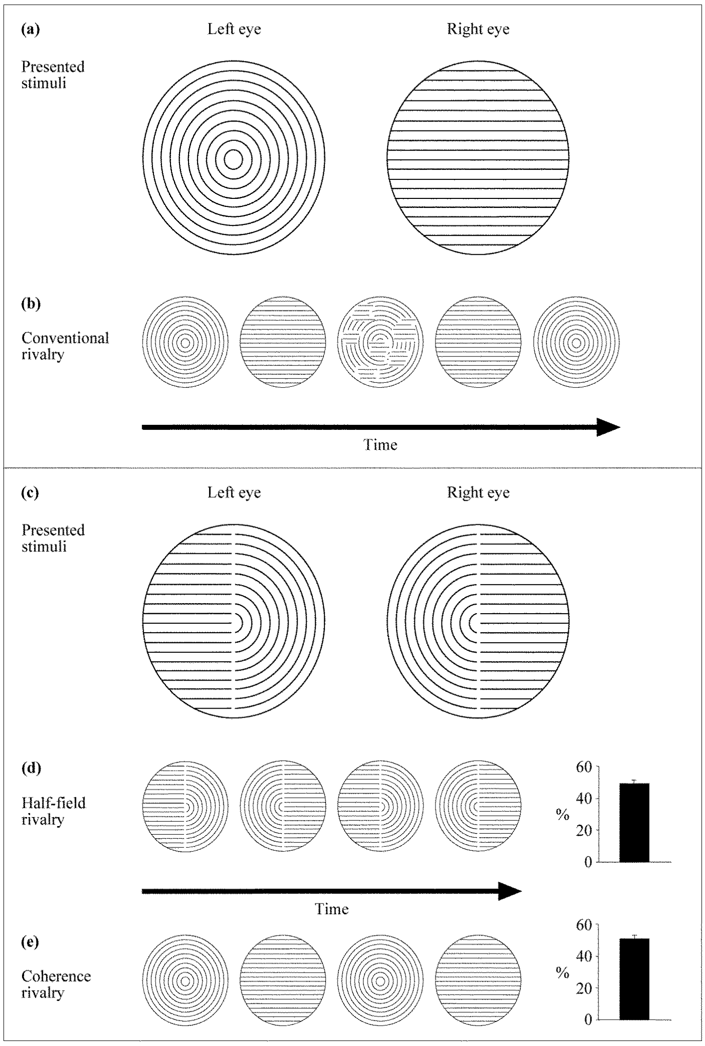

Figure 1. Stimuli and perceptions during conventional rivalry (a, b) and coherence rivalry (c, d, e). The constant presentation of concentric circles to the left eye and horizontal lines to the right eye (a) induces perceptual alternations between the two stimuli, every few seconds (b). Also shown in (b) (middle circle) are the occasional mosaic perceptions in which aspects of each eye's image are perceived. The time spent perceiving mosaic periods is relatively insignificant when small stimuli are used (as in Ngo *et al.*, 2000). In contrast to conventional rivalry, the constant presentation of complementary half-field stimuli (c) induces half-field rivalry for half the viewing time (d), and coherent perceptions of concentric circles and horizontal lines for the other half (e). The latter periods demonstrate the brain's capacity to organize aspects of each eye's presented stimuli into rivalling coherent percepts (coherence rivalry). The suppressed regions of an eye in standard rivalry displays and in half-field displays of the same size differ by virtue of particular stimulus features that determine *which* regions of an eye are suppressed at which time. This re-organization process suggests the involvement of high-level, though not necessarily cognitive/semantic, processing (see text). (Reprinted in part, from *Current Biology* 10, Ngo *et al.*, Binocular rivalry and perceptual coherence, R134–R136, Copyright (2000), with permission from Elsevier Science.)

3. Two Hemispheres, Two Percepts – the Interhemispheric Switch Hypothesis

A novel hypothesis for the neural mechanism of binocular rivalry, consistent with the existence of high-level stimulus rivalry and a role for attentional factors, was recently proposed by Miller, Liu, Ngo, Hooper, Riek, Carson and Pettigrew (2000). The fact that there are two perceptual states during rivalry and two cerebral hemispheres in our brains suggests that each hemisphere might select one, but not the other percept, and the perceptual alternations might therefore be mediated by hemispheric alternations or, as we have called it, *interhemispheric switching*. On this view, visual consciousness of rivalling stimuli may be unihemispheric at any one time (Miller *et al.*, 2000). This notion is consistent with the fact that a single cerebral hemisphere can sustain a coherent visual percept (as evidenced by residual visual function following surgical excision of an entire hemisphere (Bogen *et al.*, 1998; Engel, 1993)). As Bogen *et al.* (1998, p. 73) state, "one hemisphere suffices for fully human consciousness and the mechanisms for awareness are double."

Furthermore, independent hemispheric attentional processing has been demonstrated in both split-brain and normal subjects (Luck *et al.*, 1989; Zaidel *et al.*, 1990). For example, a split-brain subject in a task requiring visual search for particular stimulus features can employ each hemisphere's attentional resources independently (Luck *et al.*, 1989). The hemispheres search their respective hemifields in *parallel*, and the task is completed earlier than in normal subjects who are forced to search each hemifield *serially*. This advantage only exists when target arrays are presented in both hemifields, and disappears when the same number of targets is presented to a single hemifield (Luck *et al.*, 1989).[6] (The role of attentional factors in binocular rivalry is discussed in section 7.)

Evidence for interhemispheric switch mechanisms in non-human organisms includes the phenomenon of alternating unihemispheric slow-wave sleep (USWS) which has been observed in birds (Rattenborg *et al.*, 1999) and aquatic mammals (Mukhametov *et al.*, 1977; Mukhametov *et al.*, 1985; reviewed in Rattenborg *et al.*, 2000). During USWS, one eye is closed with its contralateral hemisphere in slow-wave sleep, while the other eye is open with its contralateral hemisphere awake. Moreover, birds can control which eye is kept open according to the direction from which a predator is likely to approach (Rattenborg *et al.*, 1999).[7]

Other comparative evidence for an interhemispheric switch mechanism includes the finding by Jack Pettigrew, Josh Wallman and Kerstin Fritsches, of independent alternating patterns of eye-movements in the sandlance, a small teleost lacking callosal connections between the hemispheres (Pettigrew *et al.*, 1999; Wallman

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[6] Chelazzi *et al.* (1993) demonstrate that neurons in monkey inferotemporal cortex (the same region in which single-unit activity is highly correlated with perception during binocular rivalry), are involved in visual search.

[7] Hemispheric asynchrony in slow-wave activity also occurs in cats, but only following sagittal transection of the lower brainstem (Michel, 1972).

et al., 1995).[8] In humans, chronobiologists have documented ultradian rhythms of alternating cerebral activation (Shannahoff-Khalsa, 1993; Werntz *et al.*, 1983) and at least two other side-to-side alternations are known to exist. The nasal cycle (Shannahoff-Khalsa, 1991), recently demonstrated with fMRI (Sobel *et al.*, 1999), reflects alternating autonomic tone in the vasculature of the right and left nasal turbinates, resulting in alternating relative patency of each nostril, with a cycle in the minutes–hours range. In one study of humans, the nasal cycle was shown to alternate in phase with cerebral activation patterns measured by electroencephalography (EEG; Werntz *et al.*, 1983), and in cats the nasal cycle can be manipulated by stimulation of the brainstem reticular formation (Bamford and Eccles, 1982). Another side-to-side rhythm known to exist in humans is the pathological condition of periodic alternating nystagmus. Lesions of the cerebellum and brainstem can cause nystagmic eye movements that alternate in direction every few minutes (Baloh, 1976; Waespe *et al.*, 1985).

4. Caloric Vestibular Stimulation During Rivalry

The interhemispheric switch hypothesis suggests a testable prediction. Activation of a single hemisphere should increase the time spent perceiving the activated hemisphere's image. The time spent perceiving one image relative to the other during rivalry is referred to as *predominance*. Specifically then, activation of a single hemisphere should alter the predominance of rivalling stimuli if rivalry is indeed mediated by a process of interhemispheric switching.

We first tested my prediction using the unilateral hemisphere activation technique of caloric vestibular stimulation (Miller *et al.*, 2000). The procedure involves instilling iced water into the external auditory canal to induce stimulation of the vestibular system. With the subject's head oriented at 30 degrees from the horizontal plane, the iced water induces a signal from the vestibular apparatus, through brainstem nuclei, resulting in activation of contralateral cortical regions (Figure 2). The subject experiences vertigo and exhibits horizontal nystagmus with the brisk phase in the direction opposite to the stimulated ear.

Brain-imaging studies of human subjects following caloric stimulation demonstrate cortical activation in contralateral temporo-parietal, anterior cingulate and insular cortex, and the putamen in the basal ganglia (Bottini *et al.*, 1994; Vitte *et al.*, 1996; the latter study also found ipsilateral hippocampal activation). These structures have been implicated in attentional processing (including visual search and conflict resolution) (Posner, 1994; Posner and DiGirolamo, 2000; Posner and Petersen, 1990; Nobre *et al.*, 1997), and caloric stimulation has a dramatic effect on attention in cases of unilateral neglect. Right-sided brain lesions (affecting

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[8] Around the same time, Ramachandran (1994) proposed that the two cerebral hemispheres in humans exhibit antithetical cognitive styles and Pettigrew reasoned that such antithetical styles would not be employed concurrently but rather, in alternation, thus suggesting the existence of an interhemispheric switch mechanism in humans.

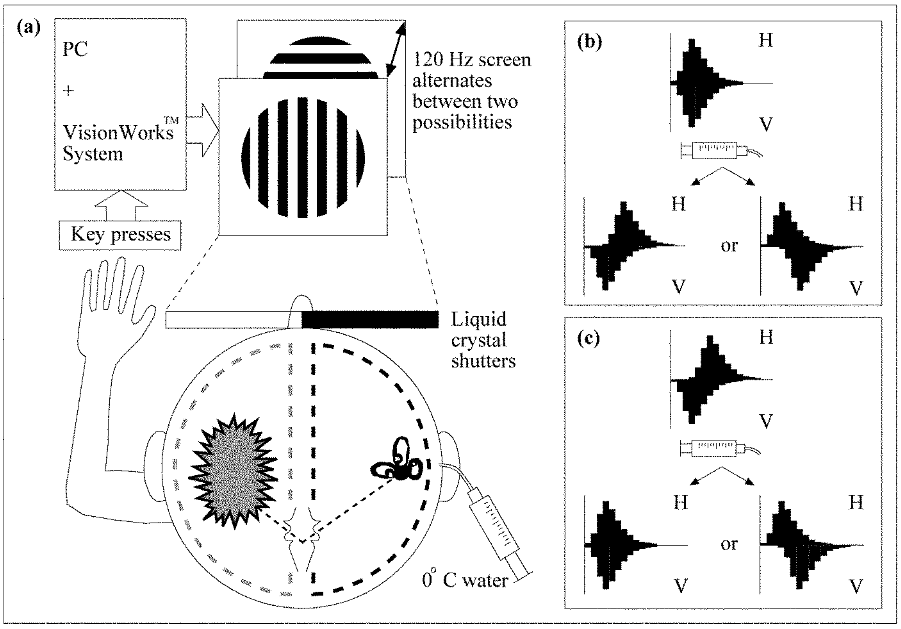

Figure 2. Set-up for caloric stimulation and binocular rivalry experiments and the effects on perceptual predominance predicted by the interhemispheric switch hypothesis. The rivalry set-up (a) shows a right-drifting vertical grating being presented to the left eye and an upward-drifting horizontal grating being presented to the right eye using liquid crystal shutters to restrict the presentation of each image to its intended eye. The orthogonal gratings induce binocular rivalry and subjects report their perceptual alternations using response keys on a keyboard. The caloric stimulation procedure involves irrigating the external ear canal with iced water and acts via the semicircular canals and brainstem to produce activation of contralateral structures involved in attentional processing. The expected effects on rivalry alternations from unilateral hemisphere activation (according to the interhemispheric switch hypothesis) are depicted by frequency histograms (b, c). These represent the frequency (y-axis) of horizontal and vertical perceptual intervals in seconds (x-axis) during the rivalry-viewing period. In (b), there is no baseline predominance of either horizontal or vertical percepts so unilateral hemisphere activation is expected to induce either a horizontal (bottom left) or vertical (bottom right) predominance. In (c), there is a baseline predominance of the horizontal percept that is expected to disappear (bottom left), or even reverse to a vertical predominance (bottom right) following unilateral hemisphere activation by caloric stimulation. (Reprinted from *Current Biology* 10, Miller *et al.*, Interhemispheric switching mediates perceptual rivalry, pp. 383–392, Copyright (2000) with permission from Elsevier Science.)

structures such as those above) can cause a lack of attention to the left side of space, which is temporarily ameliorated by left ear (right hemisphere) cold caloric stimulation (Vallar *et al.*, 1993).[9]

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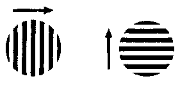
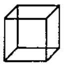
[9] Denial of disease (anosognosia) is also temporarily ameliorated by caloric stimulation (Cappa *et al.*, 1987; Ramachandran, 1994). See Kinsbourne (1977) for a different notion of hemisphere rivalry in the context of unilateral neglect.

Table I. Summary of the effects of unilateral caloric stimulation during two types of conventional rivalry (Miller *et al.*, 2000), viewing of the Necker cube (Miller *et al.*, 2000), and coherence rivalry (Ngo *et al.*, in preparation).

Stimuli	Left Hemisphere Activation	Directional Bias of Left Hemisphere Activation Effects	Right Hemisphere Activation	Control
	✓ (n=20)	✓ (n=20)	✗ (n=14)	✗ (n=12)
	✓ (n=20)	✓ (n=20)	✗ (n=20)	✗ (n=20)
	✓ (n=26)	✗ (n=26)	✗ (n=16)	✗ (n=26)
	✓ (n=16)	✗ (n=16)	✗ (n=16)	✗ (n=16)

✓ = significant change in image predominance
✗ = no significant change in image predominance
n = total number of subjects for each condition

We therefore assessed whether unilateral activation of attentional structures (by caloric stimulation) would alter perceptual predominance during rivalry, beginning our investigations with drifting, horizontal and vertical gratings.[10] Activation of the left hemisphere was found to induce a significant change in predominance during rivalry, and most often caused an increase in the time spent perceiving the horizontally oriented grating (always presented to the right eye) (Table I). Some subjects however, demonstrated increased perception of the vertical grating following stimulation, and other subjects showed no effect at all. Interestingly, right hemisphere activation did not change predominance.

The fact that left hemisphere activation tended to increase perception of the horizontal rather than the vertical grating (i.e., demonstrated a directional bias) raised the possibility that the observed effect was due to undetected nystagmic eye movements from the caloric stimulation.[11] Such horizontal eye movements could alter image predominance by reducing the spatial frequency and contrast of the vertical, but not the horizontal, grating (Fahle, 1982). This interpretation was excluded by repeating the experiment with orthogonal, obliquely oriented

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[10] For detailed description of methods and analysis procedures, see Miller *et al.* (2000).

[11] Post-stimulation rivalry testing only began after the visible signs of nystagmus had ceased, but eye movements undetectable to the naked eye may have persisted.

stimuli. In these experiments, the oblique gratings were also stationary to ensure that drifting gratings were not required for the effect to be observed. The same pattern of predominance changes due to caloric stimulation was demonstrated, including a directional bias favouring again, the stimulus presented to the right eye (Table I).

Trung Ngo then demonstrated that left hemisphere activation by caloric stimulation also significantly altered perceptual predominance during viewing of the Necker cube (Miller *et al.*, 2000). Necker cube rivalry has temporal properties in common with binocular rivalry, suggesting the two phenomena may be mediated by similar neural mechanisms (Borsellino *et al.*, 1972; Leopold and Logothetis, 1999; Logothetis, 1998a; Logothetis *et al.*, 1996; Walker, 1975). The finding of a similar effect of left hemisphere activation on both types of perceptual rivalry further supports this suggestion.[12] The Necker cube experiments, like the binocular rivalry experiments, failed to demonstrate a significant effect on predominance following right hemisphere activation. However, unlike the binocular rivalry experiments, the significant left hemisphere activation effects with the Necker cube were not associated with a directional bias (Table I).

Finally, we assessed the effect of caloric stimulation during coherence rivalry (Ngo *et al.*, in preparation). In the context of coherence rivalry, the interhemispheric switch model predicts an effect of caloric stimulation on the predominance of rivalling coherent images (Miller *et al.*, 2000). Not surprisingly, we found that left hemisphere activation significantly altered the predominance of rivalling coherent images while right hemisphere activation did not. In these experiments, like the Necker cube experiments, no directional bias was observed (Table I).[13]

5. Transcranial Magnetic Stimulation During Rivalry

Caloric stimulation's effects are long lasting (around 10 minutes in most subjects) and result in unilateral hemisphere activation. Jack Pettigrew suggested that single-pulse transcranial magnetic stimulation (TMS), with its high temporal resolution, could be used to further test the interhemispheric switch hypothesis. We therefore used this technique to disrupt a single hemisphere at one or the other phase of the perceptual alternations during binocular rivalry (Miller *et al.*, 2000). According to the interhemispheric switch hypothesis, unilateral hemisphere disruption should cause perceptual disruption when delivered at one phase of the perceptual switch, but not the other (Figure 3). We concentrated our investigation on the left hemisphere's temporo-parietal regions based on the previous caloric stimulation experiments.

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[12] Two subjects who experienced normal baseline Necker cube rivalry exhibited such a strong effect that they effectively failed to perceive one of the two depth perspectives following stimulation.

[13] We are currently assessing the effect of caloric stimulation on half-field perceptual periods (Ngo *et al.*, in preparation).

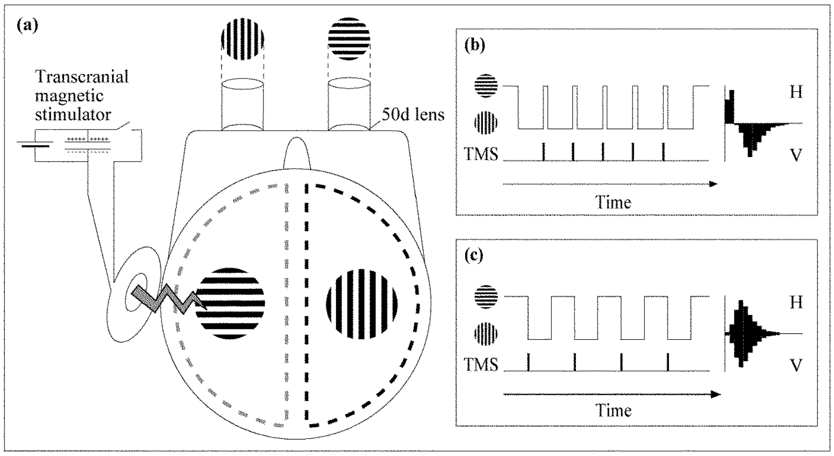

Figure 3. Set-up for transcranial magnetic stimulation (TMS) and binocular rivalry experiments and the perceptual interference effects predicted by the interhemispheric switch hypothesis. The circular coil delivers a single pulse to the temporo-parietal region of the left hemisphere. The subject views orthogonal stationary gratings and reports their perceptual alternations using two response keys, one of which triggers the magnetic stimulation (a). The time course of perceptual alternations shows the predicted disruptive effects of TMS triggered by a switch to the horizontal percept (b). If the left hemisphere selects the horizontal percept, TMS applied to this hemisphere when horizontal is perceptually dominant will disrupt this percept and allow the vertical percept to assume dominance. The frequency histogram (right) therefore depicts very short horizontal interval durations. When the stimulation is delivered under identical conditions, but at the opposite phase of the perceptual switch (i.e. triggered when the subject reports a switch to vertical), disruption of the left hemisphere has little effect because it is the right hemisphere that has selected the vertical percept (c). Thus the frequency histogram (right) for this contingency shows normal interval durations. Although not shown by frequency histograms, it follows that if another subject shows shortened vertical interval durations following left hemisphere TMS in one contingency, and no effect in the other, this would indicate that the left hemisphere has selected the vertical rather than the horizontal percept. (Reprinted from *Current Biology* 10, Miller *et al.*, Interhemispheric switching mediates perceptual rivalry, pp. 383–392, Copyright (2000) with permission from Elsevier Science.)

Phase-specific effects of left hemisphere TMS were demonstrated in five of seven subjects tested. In some subjects, TMS delivered when the subject signalled a switch to the horizontal percept caused an immediate return to the vertical percept. However, in the same subjects, no effect was observed when TMS was delivered *in the same location* but on a switch to the vertical percept. This phase-specific pattern was present but reversed in other subjects, suggesting again that not all subjects represent the horizontal stimulus in the left hemisphere. Irrespective of the direction of TMS-effects, phase-specific perceptual disruption strongly suggests between-hemisphere rivalry.[14]

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[14] An interpretation based on TMS-induced activation rather than disruption offers the same support for the interhemispheric switch hypothesis. To count as evidence against the interhemispheric

6. Interpreting the Results

The effect of caloric stimulation and transcranial magnetic stimulation on image predominance during binocular rivalry, and of caloric stimulation on perspective/image predominance during Necker cube and coherence rivalry, supports the notion that interhemispheric switching mediates perceptual rivalry. All of these effects are difficult to explain using current models of rivalry, but are predicted by the interhemispheric switch model.

The fact that there was no effect of right hemisphere activation on image/perspective predominance in all four perceptual rivalry experiments requires explanation. The right fronto-parietal cortex activation asymmetry associated with perceptual transitions during rivalry (Lumer *et al.*, 1998) suggests that right hemisphere activation by caloric stimulation could affect that hemisphere's image *and* this transition-related network. This dual activation could mitigate the expected effects on predominance.

An alternative explanation for the lack of right hemisphere activation effects on predominance may lie with the known hemispheric asymmetry of spatial representation. The right hemisphere represents both sides of space, whereas the left hemisphere represents only the right side of space (Heilman and van Abell, 1980; Nobre *et al.*, 1997; for a more detailed discussion see Roberston and Marshall, 1993). Indeed this is why it is usually right-sided rather than left-sided lesions that cause unilateral neglect; the intact right hemisphere in the latter case can still represent all of space. Thus, if the right hemisphere selects *both* percepts during rivalry (retaining all information as it does for spatial representation), activation of this hemisphere by caloric stimulation would not be expected to induce a change in image predominance.[15]

The directions of predominance changes observed in the four caloric stimulation experiments raise the issue of hemisphere-designation (Table I). Which image/perspective is represented in which hemisphere, and why? In the vertical/horizontal and oblique rivalry experiments, the majority of subjects spent more time perceiving the image presented to the right eye following left hemisphere activation. There was no such directional bias observed in the Necker cube and coherence rivalry experiments. Note however, there is no eye-of-origin in the

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switch hypothesis, it would need to be shown that TMS-induced perceptual disruption (or activation) occurs at *both* or *neither* phase of the perceptual switch. TMS could also be used to investigate perceptual grouping during coherence rivalry. Moreover, right hemisphere TMS, particularly with respect to the right fronto-parietal network implicated in perceptual transitions during rivalry (Lumer *et al.*, 1998), may shed light on the hemispheric asymmetries observed in the caloric stimulation experiments.

[15] The data of Tong et al. (1998; see Tong, this issue) fit this interpretation, but this is most likely due to their use of one right-lateralized stimulus (face) and one non-lateralized stimulus (house). According to this alternative explanation for the lack of right hemisphere activation effects, the expected fMRI findings when rivalry involves stimuli that activate homologous brain regions (see note 24) would be right hemisphere activation during one perceptual state (transition-related activity aside) and bilateral activation during the rival perceptual state.

Necker cube experiments (it is not viewed dichoptically), and in coherence rivalry, eye-of-origin is shared. Taken together, the predominance changes are suggestive of the following interpretation. The stimulus presented to an eye in conventional dichoptic situations is usually selected by the contralateral hemisphere and when rivalry does not involve dichoptic presentation (as in Necker cube rivalry), or when dichoptic presentation mixes image components between the eyes (as in coherence rivalry), hemisphere-designation is arbitrary.

The contralateral eye-hemisphere observation is supported by physiological evidence demonstrating a higher proportion of binocular neurones with a dominant input from the contralateral eye in macaque monkeys (LeVay *et al.*, 1985). While this designation principle appears to fit the data, higher-order influences of hemispheric specialization may also have an effect on which image is selected by which hemisphere. The left hemisphere might select horizontal lines, for example, given the left-lateralization for (horizontal) sentence reading (Bavelier *et al.*, 1997). We are currently assessing such issues by repeating the caloric experiments with reversed eye-of-presentation.[16] If the majority of subjects show an increase in vertical grating perception following left hemisphere activation when the vertical grating is presented to the right eye, this will confirm the eye-of-origin principle. Increased horizontal predominance following left hemisphere activation when the horizontal grating is presented to *either* eye would argue for a higher-order effect. The eye-of-origin principle could also be assessed using caloric stimulation during monocular rivalry (Andrews and Purves, 1997; Atkinson *et al.*, 1973; Breese, 1899; Campbell *et al.*, 1973),[17] expecting no directional bias of predominance changes (because eye-of-origin is the same for both percepts).

7. Mechanisms of Interhemispheric Switching

Helmholtz (1910/1962) and James (1890) considered rivalry to be a paradigm case of *involuntary* attention, upon which voluntary attention could exert some effect (Fox, 1991; see also Blake, this issue, pp. 5–38, inset on Sherrington). Indeed, it was the conjunction of such attentional interpretations of rivalry with the evidence for independent hemispheric attentional processing in split-brain subjects (section 3), that lead me to propose that binocular rivalry might employ the sort of interhemispheric switch mechanism that Jack Pettigrew was confident would exist in humans (see note 8). The effect of caloric stimulation on attentional processing in cases of unilateral neglect further suggested that the technique could be used to test the interhemispheric switch hypothesis (section 4). Our demonstration that (left hemisphere) caloric stimulation can alter perceptual predominance during

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[16] We are also currently assessing the stability of hemisphere-designation by re-testing subjects on different occasions.

[17] When two differently coloured orthogonal gratings are superimposed in the same eye, perceptual rivalry between each grating occurs (similar to binocular rivalry).

rivalry bolsters the (involuntary) attentional interpretations of Helmholtz, James and Sherrington.

The notion of attentional processing has also been useful to other investigators of the rivalry phenomenon. Logothetis (1998a) and Leopold and Logothetis (1999) discuss the similarities and differences between perceptual multistability and processes of selective attention, noting that modulation due to rivalry and attention occurs in similar cortical regions (see also Ooi and He, 1999; Sheinberg and Logothetis, 1997; see below). Similarly, Lumer *et al.* (1998) interpreted their fMRI findings during rivalry in the context of selective attention. Ooi and He (1999; see also Blake, this issue; Breese, 1899; Fox, 1991; Hunt and Guilford, 1933; Lack, 1978; Logothetis, 1998a; Strüber and Stadler, 1999; Walker, 1978) recently demonstrated that a variety of voluntary and involuntary attentional factors (including the Cheshire cat and pop-out effects, and attention cueing) play a role in determining predominance during rivalry.

Given these and other findings (see below), I suggest that interhemispheric switching during perceptual rivalry involves *alternating unihemispheric attentional selection* of neuronal processes for access to visual consciousness.[18] Independent attentional mechanisms in each hemisphere may be alternately *involuntarily* directed (top-down) to (bottom-up) signals concerning stimulus characteristics such as those that determine stimulus strength (Levelt, 1965; see also Blake, this issue; Logothetis, 1998a; Ooi and He, 1999). On this view, the perceptual alternations of conventional rivalry can be seen as involuntary directions of (unihemispheric) attention, upon which, to some extent, voluntary attention may act.[19] Similarly, the involuntary perceptual grouping seen in coherence rivalry may involve the selection of coherent stimulus features of one global percept by attentional mechanisms in one hemisphere, with coherent features of the rival percept selected by attentional mechanisms in the other hemisphere (Miller *et al.*, 2000). The selection process in each hemisphere (for both conventional and coherence rivalry) could conceivably occur through the biasing of competition between populations of neurones (Desimone and Duncan, 1995; Kastner *et al.*, 1999; Reynolds and Desimone, 1999; Schwartz *et al.*, 2000).

On the basis of comparative and neuropsychological evidence (see note 8), Jack Pettigrew suggested that interhemispheric switching may be driven by brainstem or other subcortical oscillators (Pettigrew and Miller, 1998).[20] Such regions have

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[18] 'Unihemispheric' should not be confused with the one-sided fronto-parietal network implicated in perceptual transitions. Rather, in this context, it means each hemisphere in alternation.

[19] Alternating unihemispheric (involuntary) attentional selection during rivalry could facilitate voluntary attention directed towards the perceived stimulus (cf. Ooi and He, 1999), though voluntary attention itself may be constantly bilateral, alternating between hemispheres, or constantly lateralized (perhaps to the right – sustained attention appears to be lateralized to this side (Pardo *et al.*, 1991)). Experiments with fMRI could assess this directly.

[20] Thus suggesting that the corpus callosum is not the 'site' of the switch itself. However, this structure is likely to play a role in transferring visual information from the single hemifield representation of one hemisphere's early processing regions to the opposite hemisphere's higher visual regions.

been implicated in attention and arousal (Aston-Jones *et al.*, 1999; Guillery *et al.*, 1998; Kandel *et al.*, 2000; Kinomura *et al.*, 1996; Newman and Baars, 1993; Parvizi and Damasio, 2001; Robbins, 1997; Sarter and Bruno, 2000; Sturm *et al.*, 1999; see also *Consciousness and Cognition*, 1995, vol. 4, issue 2). Bistable oscillators (Marder, 1998; Marder and Calabrese, 1996) may account for a variety of biological phenomena (section 3) and could mediate alternating unihemispheric attentional selection.

Furthermore, the right-sided fronto-parietal network implicated in the generation of perceptual transitions (Lumer *et al.*, 1998) may play a role in attention shifting/switching (Corbetta *et al.*, 1993; Nobre *et al.*, 1997) through efferent projections to a brainstem/subcortical oscillator (Mega and Cummings, 1997; Newman and Baars, 1993; Wyss and Sripanidkulchai, 1984; see also Sturm *et al.*, 1999). Such projections may act to switch an oscillator's output to the previously suppressed or dominant hemisphere (depending, respectively, on whether such output induces dominance or suppression of its target hemisphere).[21] This lateralized network may also play the 'comparator' role proposed by Fox (1991; see also Blake, this issue, pp. 5–38) to initiate and maintain rivalry under dichoptic conditions, and may therefore be distinguished from the independent attentional selection mechanisms in each hemisphere.

Subcortically-driven alternate unihemispheric attentional selection could explain other empirical observations such as perception-dependent neuronal response synchronization in V1,[22] and perception-dependent fMRI activity in V1 (Polonsky *et al.*, 2000), during rivalry.[23] It could also account for the fact that the magnitude of single-unit responses in higher visual regions (Sheinberg and

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Monkey IT cortex neurons have large, bilateral receptive fields which lose input from the ipsilateral visual field when the corpus callosum and anterior commissures are sectioned (Gross *et al.*, 1993). Because the highest proportion of perception-dependent neuronal activity during rivalry has been found in IT and STS cortex, the interhemispheric switch hypothesis proposes rivalry between the hemispheres at high levels, not between V1 visual hemifield representations. It should also be added that the corpus callosum could play a more fundamental role in mediating alternating unihemispheric attentional selection (Schwartz *et al.*, 2000; Zaidel *et al.*, 1990) whether or not the oscillator account is accurate.

[21] On this view, the right-sided network would have bilateral efferent projections (to both sides of a reciprocally-coupled oscillator). This should not however discount the possibility of projections from the left hemisphere to a subcortical or brainstem oscillator.

[22] Fries *et al.* (1997, p. 12699) report that in strabismic cats undergoing rivalry, "at early stages of visual processing the degree of synchronicity rather than the amplitude of responses determines which signals are perceived and control behavioural responses." A brainstem oscillator driving perceptual rivalry could help explain such temporal correlation (synchrony) of neuronal firing (Engel *et al.*, 1997). Stimulation of the mesencephalic reticular formation is known to synchronize neuronal firing at distant sites in cat extrastriate cortex (Munk *et al.*, 1996; Engel *et al.*, 1999). However, the role of neuronal response synchronization in perception remains unclear. Several authors have suggested that response synchrony at low levels may be the result of top-down attentional selection mechanisms (Engel *et al.*, 1999; Leopold and Logothetis, 1999; Polonsky *et al.*, 2000).

[23] It should be noted that each single hemisphere presumably selects neuronal processes for access to visual consciousness from *both* hemispheres (see note 20).

Logothetis, 1997) and of fMRI activation in lower visual regions (Polonsky *et al.*, 2000) during rivalrous visual stimulation, is *half* that during normal visual stimulation. Voluntary attention to stimuli is known to increase single-unit and regional (fMRI) responses even in the absence of visual stimulation (reviewed in Chelazzi and Corbetta, 2000; Desimone and Duncan, 1995; Kastner *et al.*, 1999; Mangun *et al.*, 2000; Reynolds and Desimone, 1998). Alternate unihemispheric (involuntary) attentional selection – compared with *bi*-hemispheric (involuntary) attention during physical stimulus alternation (normal vision) – might therefore be expected to produce the half response magnitude findings mentioned above.[24] It has indeed been shown that not only voluntary attention, but also involuntary ('reflexive') attention, can modulate visual processing (see Mangun *et al.*, 2000).

A further example of how the interhemispheric switch hypothesis provides a new framework within which to re-interpret existing empirical data stems from Sengpiel's (2000) comment that the contralateral eye-hemisphere designation tendency in our caloric stimulation data may help to explain some of the psychophysical data in support of eye rivalry (though not monocular channel rivalry).[25] As Blake (this issue, section 4) rightly notes, eye over stimulus rivalry is supported by the fact that swapping a newly dominant stimulus into the other eye causes a reversal of perceptual dominance; stimulus rivalry predicts no perceptual reversal under these conditions. However, stimulus rivalry does predict perceptual reversal under these conditions if, as the interhemispheric switch model suggests, the two rivalling stimuli are represented in opposite hemispheres.[26,27]

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[24] Tong *et al.* (1998; see Tong, this issue) did not find such reduced activation during rivalry, perhaps due to the fact that non-homologous brain regions were activated in their study. For an alternative explanation of the half response magnitude data, based on the fact that physical removal of a stimulus is not the same as phenomenal suppression, see Polonsky *et al.* (2000).

[25] According to the caloric stimulation data, eye-of-origin information, instead of being lost at binocular convergence, can be maintained in terms of hemisphere-designation.

[26,] It should be noted that the spatial separation of each stimulus representation is enough to predict perceptual reversal in the re-routing experiments, even in cases where the hemisphere-designation principle appears to be ipsilateral rather than contralateral. However, if higher-order effects cause horizontal stimuli to be represented most often in the left hemisphere *irrespective of eye-of-presentation* (see section 6), then perceptual reversal would not be predicted in re-routing experiments.

[27] It is also interesting to re-interpret Breese's (1899) experiments on unilateral muscle contraction during rivalry, in light of the hemispheric asymmetry in our caloric stimulation results. Breese had subjects (including himself) contract limb muscles on either side of the body (in separate sessions), during binocular rivalry with coloured gratings. Although his own data did not show an asymmetric pattern, it is clear from the overall data presented for six individuals (p. 31, Table IX), that right-sided muscle contractions (left hemisphere activation; Schiff *et al.*, 1998) had a greater effect on image predominance than left-sided muscle contractions (right hemisphere activation).

8. Further Testing the Interhemispheric Switch Hypothesis

Although we have provided data that supports the interhemispheric switch hypothesis, a convergence of evidence from a variety of approaches could settle the issue. Such approaches might include simultaneous bilateral electrophysiological recordings of single neurones, pairs of neurones, and populations of neurones in cortical and subcortical structures. If interhemispheric switching is occurring during rivalry, some indication of the process is likely to be detectable (see for example, Schwartz *et al.*, 2000). Brain-imaging studies, EEG and event-related potential studies, and magnetoencephalography studies (see, e.g., Srinivasan *et al.*, 1999; Tononi *et al.*, 1998) could also be performed but should employ non-lateralized stimuli and should analyse signals derived while one percept is dominant separately from those generated during its suppression. Results should also be assessed on an individual basis because hemisphere-designation is arbitrary for non-dichoptic stimuli such as the Necker cube, and is not always fixed even in conventional rivalry. Group analyses may therefore average out real hemispheric asymmetries. Such studies should also take account of the fact that the presence of bilaterally symmetrical neuronal activity in some regions/circuits does not imply the absence of bilaterally asymmetrical neuronal activity in other regions/circuits during rivalry (see note 23 and section 10). Spatial resolution is therefore an important methodological factor (with respect to regions at least).

Other than our own data presented above, the only other test to date of the interhemispheric switch hypothesis is interesting but inconclusive. In a split-brain observer, rivalry has been demonstrated despite the fact that the conflicting stimuli were presented to a single hemifield, and were thus restricted to a single hemisphere (O'Shea and Corballis, 2000; O'Shea and Corballis, this issue). The authors argue that this demonstration challenges the interhemispheric switch hypothesis. However, the split-brain data does not challenge the hypothesis as forcefully as the authors suggest. While it is true that the absence of rivalry in split-brain observers with hemifield presentation could support the interhemispheric switch hypothesis, it is not true that the presence of rivalry in such observers argues against the hypothesis. It does not follow, for example, from the fact that a single hemisphere can sustain a coherent visual percept, that coherent visual perception is mediated (in the normal case) by one hemisphere alone. Similarly, it does not follow from the fact that a single hemisphere can perceive rivalry that this is how rivalry normally occurs (see Chalmers (2000) for a detailed discussion of the limitations inherent in extrapolating principles of normal brain function from cases of disrupted neuronal architecture). Thus the brain may utilize whatever resources it has available to it to achieve a particular function such as rivalry, and this may consist in within-hemisphere rivalry in split-brain subjects – perhaps hypercoloumn rivalry (O'Shea and Corballis, this issue) – and between-hemisphere rivalry in normal subjects. It is therefore not possible to make clear predictions of the perceptions of split-brain subjects (with hemifield presentation) based on the interhemispheric switch hypothesis.

Moreover, in the absence of an explanation for how each hemisphere could process rivalry at different rates – presuming these differences are not artefacts of hemispheric reporting styles (O'Shea and Corballis, this issue) – it is not readily apparent why the split-brain data supports low- rather than high-level models of rivalry. However, low-level hypercoloumn rivalry (O'Shea and Corballis, this issue), based on the mismatch of stimulus features viewed by each eye, might be occurring in the split-brain. This is quite possible, for example, for left hemisphere split-brain rivalry involving faces because the high-level face processing region, the fusiform face area, is usually lateralized to the right hemisphere (Kanwisher *et al.*, 1997; Tong *et al.*, 1998; see Tong, this issue). This could explain the observed differences in rivalry rates between the two hemispheres as the faster alternating right hemisphere might employ its specialized face-processing region while the left hemisphere can only employ non-specialized (low-level) regions. This explanation does not however, account for the existence of rate differences between the hemispheres in sine-wave grating split-brain experiments (O'Shea and Corballis, in preparation). Whatever explanation is invoked, it is noteworthy that rate differences between right and left hemifield presentations in normal subjects were not observed. This further underscores the difference between rivalry in split-brains and normal brains.

The split-brain data presents only a limited challenge to the interhemispheric switch hypothesis because it is what happens after each hemisphere receives the initial information about stimulus features that is pertinent to the neural mechanism of rivalry in the normal case. O'Shea and Corballis (this issue, pp. 115–124) conclude from the split-brain data that normal rivalry occurs at "low levels of the visual system at which each hemisphere carries out its own analysis of its half of visual space". However, this conclusion does not contend with the fact that in the non-split-brain case, the 90% of IT neurones whose activity is correlated with a monkey's perceptions during rivalry, have large receptive fields covering both sides of visual space (see note 20).

9. Perceptual Rivalry and Bipolar Disorder

Elsewhere, Jack Pettigrew and I have used our interhemispheric switch model of perceptual rivalry to help explain the pathophysiology of bipolar disorder (manic depression). This explanation was based on our finding that the rate of binocular rivalry in bipolar subjects (diagnosed according to DSM-III-R criteria) is significantly *slower* than in controls (Pettigrew and Miller, 1998). Figure 4 shows the rates of rivalry for 20 bipolar subjects and 63 controls viewing drifting, vertical and horizontal gratings of high spatial frequency (8cycles/degree).[28] The median

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[28] The majority of this data, along with details of diagnostic and other methods, were reported in Pettigrew and Miller (1998).

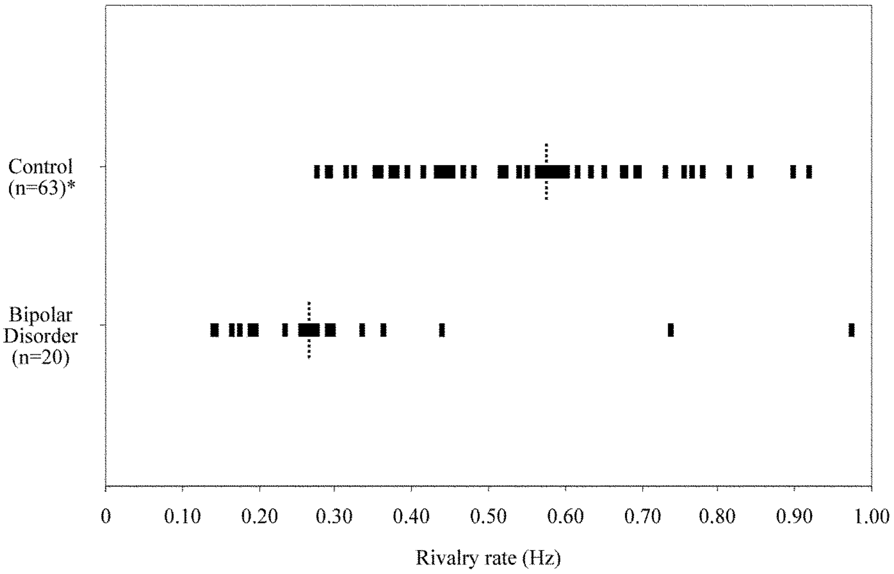

Figure 4. Rivalry rates (Hz) in subjects with bipolar disorder and control subjects, viewing drifting horizontal and vertical gratings of high spatial frequency (8cycles/degree). The bipolar subjects have significantly slower rates of rivalry than controls (see also Hunt and Guilford, 1933; Miller *et al.*, submitted; Pettigrew and Miller, 1998). Slow binocular rivalry is therefore a candidate biological marker for bipolar disorder (see text). Dotted lines depict median rivalry rates for each group. *Four control outliers not shown (rates = 1.11Hz, 1.11Hz, 1.19Hz and 1.48Hz).

rivalry rate for the bipolar group was 0.26Hz (i.e., a perceptual switch roughly every 3.8 seconds), significantly slower (Mann-Whitney test, $p < 0.001$) than that for control subjects (median rate = 0.58Hz; i.e., a perceptual switch roughly every 1.7 seconds). Several bipolar subjects experienced intervals as long as 10 to 15 seconds. The bipolar subjects were neither manic nor depressed at the time of testing and slow rivalry rate was observed in both medicated and unmedicated subjects. Our findings suggested that slow binocular rivalry might be a biological marker for bipolar disorder (Pettigrew and Miller, 1998).[29]

We have since replicated our original finding in a different population of subjects (Miller, Gynther, Heslop, Liu, Mitchell, Ngo, Pettigrew and Geffen, submitted). Thirty bipolar subjects, 30 control subjects, 18 subjects with schizophrenia and 18 subjects with major depression viewed stationary, vertical and horizontal gratings of low spatial frequency (4 cycles/degree). Bipolar subjects (mean rate = 0.28Hz) were again significantly slower than controls (mean rate = 0.40Hz; t-test, $p < 0.001$) though the separation between groups was less than

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[29] Other authors have demonstrated individual variation in rivalry rates in controls (e.g. Aafjes *et al.*, 1966), including wide variation demonstrated using optkinetic nystagmus to measure rivalry rate (Enoksson *et al.*, 1963).

that with higher strength stimuli as used in the earlier study.[30] The schizophrenia group (mean rate = 0.39Hz) and major depression group (mean rate = 0.36Hz) were not significantly different from controls ($p > 0.05$, respectively), but were significantly different from the bipolar group ($p < 0.05$, respectively).[31] However, some individuals in the schizophrenia and major depression groups exhibited slow rates of rivalry. Predominance values did not differ between groups, and in all groups the perceptual intervals were well described by a gamma distribution (Fox and Herrmann, 1967; Levelt, 1965; Logothetis *et al.*, 1996; Walker, 1978).[32]

The rivalry rate findings are in accordance with those of Hunt and Guilford (1933) who assessed Necker cube rivalry rates in bipolar disorder, schizophrenia (dementia praecox) and control groups. In this study, only the bipolar group was significantly different, four times slower than the other two groups during passive viewing and six times slower during voluntary inhibition of reversals. The concordance of this study with our study further suggests that binocular rivalry and Necker cube rivalry share a similar neural mechanism (see above).[33] While these empirical observations have potentially important clinical and research implications in their own right, they also enable a link to be made between the interhemispheric switch hypothesis of rivalry and the many demonstrations of hemispheric asymmetries of mood and mood disorders (Miller *et al.*, submitted; Pettigrew and Miller, 1998).

10. The Correlates and Constitution of Visual Consciousness

Recall Crick and Koch's core issue for the scientific study of consciousness: "It is probable that at any moment some active neuronal processes in your head correlate with consciousness, while others do not; *what is the difference between them?*" (1998, p. 97, original italics). As discussed in section 1, recent developments in binocular rivalry research support Crick and Koch's premise and answer, to some extent, the question they pose.

Summarizing the neuronal correlation findings for binocular rivalry, the activity of nearly all high-level visual processing neurones in macaque monkeys increases

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[30] The cause of the decreased separation between groups in the stationary grating study was due to the effect of lower stimulus strength on control rivalry rates, with little effect on bipolar rates. Thus it may be that bipolar disorder is associated with robustly slow rivalry, relatively insensitive to stimulus characteristics. We are currently assessing this using a within-subject design.

[31] There were suggestions of medication and clinical state effects on rivalry rate however these require testing using a within-subject design (Miller *et al.*, submitted).

[32] Predominance values did not vary according to the clinical state or medication of subjects in any group, though this too requires assessment using a within-subject design (Miller *et al.*, submitted).

[33] The finding of normal rivalry rates in schizophrenia in our study (Miller *et al.*, submitted) and in Hunt and Guilford's (1933) study can be compared with the findings of Keil *et al.* (1998). The latter study demonstrated normal perceptual alternation rates associated with schizophrenia when viewing Schröder's staircase, a perspective-reversal ambiguous figure similar to the Necker cube. However when viewing Rubin's vase (a figure-ground ambiguous figure), schizophrenia subjects exhibited *faster* than normal alternation rates.

and decreases according to perceptual dominance and suppression, respectively (Sheinberg and Logothetis, 1997). On the other hand, the activity of monocular neurones in early visual processing regions is not correlated with the monkeys' perceptual states (Leopold and Logothetis, 1996). These results, together with the finding of perception-dependent fMRI activity in specific extrastriate brain regions in humans undergoing rivalry (Tong *et al.*, 1998), demonstrate convincingly the principle that only a subset of neuronal activity is correlated with visual consciousness during rivalry. Furthermore, these studies demonstrate (to some extent) *which* neurones are, and which are not, perception-dependent.

Despite this success, the scientific study of visual consciousness faces a serious problem. Not every neuronal correlate of an experienced visual state will be *constitutive* of that state. As Revonsuo notes (2000, p. 60, original italics), "What is the relation between the neural *correlates* of consciousness and the actual neural *constituents* of consciousness?" Consider optokinetic nystagmus (OKN) accompanying motion rivalry (Enoksson *et al.*, 1963; Fox *et al.*, 1975; Wei and Sun, 1998). The eyes follow perceived alternations in motion direction and thus exhibit alternating patterns of OKN. The nucleus of the optic tract and the dorsal terminal nucleus of the accessory optic tract are implicated in such oculomotor activity (Cohen *et al.*, 1992; Fuchs *et al.*, 1992) and are lateralized.[34] It is likely therefore, that these structures would demonstrate activity correlated with the subject's perceptual alternations during motion rivalry. Yet *this* correlated activity is unlikely to play a constitutive role in the rivalling visual states.[35] It is therefore the neuronal *constitution*, rather than the neuronal correlates, of visual consciousness that we seek to understand.[36]

But on this view we are faced with the difficult issue of how a science of visual consciousness could distinguish correlated from constitutive neuronal activity. While it may be reasonable to surmise that oculomotor neuronal processes are not good candidates for constitutive neuronal activity with respect to visual consciousness (Baars, 1997),[37] the problem runs deeper in the case of cortical neurons in different visual processing areas. Do all perception-dependent neurons (binocular neurons in V1, V4, MT, IT and STS; monocular neurons in the blind-spot repre-

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[34] Single units on one side prefer stimuli moving in the ipsilateral direction, and trains of electrical stimuli on one side induce optokinetic nystagmus with an ipsilaterally directed slow-phase (Fuchs *et al.*, 1992).

[35] This may be too corticocentric and could be relaxed without losing the point by distinguishing subcortical neural activity driving OKN and subcortical neural activity underlying visual drive to such oculomotor activity which may or may not be constitutive of visual consciousness.

[36] Objections to the 'neural correlates' terminology have also been raised on philosophical grounds. Smart's (1959) concern was that you cannot correlate something with itself and given that consciousness and (the relevant) brain processes refer to the same thing, you cannot have neural correlates of consciousness. For a related objection, see Mahner and Bunge (1997). Place (1990) on the other hand, draws on Boring (1933), holding that a perfect correlation is identity.

[37] Notwithstanding the close relationship between mechanisms of attention and eye-movement control (Chelazzi and Corbetta, 2000).

sentation) play a constitutive role during rivalry (or during normal vision for that matter) or only those in specific visual (or even non-visual) regions or circuits? Logothetis (1998b, p. 541) asks, "Do neurons responding only when a stimulus is perceived actually mediate the conscious experience of this stimulus?" He answers, "The current data, although they favour such an interpretation, cannot prove it unequivocally". The same question is raised by Crick (1994, p. 218; see also, Crick and Koch, 1998) in terms that illustrate the advantage of distinguishing the neural correlates and constitution of visual consciousness:

> ... although the behavior of the neurons in cortical area MT appears to be correlated with the monkey's discrimination, and therefore probably with its visual awareness, it does not follow that these particular neurons are the real seat of awareness. They may, by their firing, influence other neurons, perhaps elsewhere in the visual hierarchy, that are the true correlates of awareness.[38]

The interhemispheric switch hypothesis further illustrates the correlation/ constitution distinction. Interhemispheric switching predicts alternating hemispheric activity correlated with a subject's perceptual alternations during rivalry. This raises the possibility that visual consciousness of rivalling stimuli is unihemispheric at any one time (Miller *et al.*, 2000). However, as discussed in the present paper, interhemispheric switching may involve alternating unihemispheric attentional selection and the relationship between processes of attentional selection and visual consciousness is not clear. If the neuronal processes constitutive of attentional selection are distinct from those constitutive of visual consciousness (Baars, 1997; Newman and Baars, 1993; Posner, 1994), interhemispheric switching could mediate perceptual rivalry whether visual consciousness of rivalling stimuli is uni- or *bi*hemispheric. Bihemispheric consciousness during rivalry, for example, could occur at the *sites* of attentional selection (areas affected by attentional selection – presuming such areas are indeed constitutive of visual consciousness) despite the *source(s)* of attention being unihemispheric (Posner and DiGirolamo, 2000). Alternatively, the constitutive neuronal circuitry of visual consciousness during rivalry might involve (uni- or bihemispheric) brain regions outside those of the sites and source(s) of attentional selection. The difficulty encountered in determining whether visual consciousness of rivalling stimuli is indeed uni- or bihemispheric is a special case of the major empirical obstacle facing the scientific study of consciousness – the correlation/constitution distinction.

If the current data cannot unequivocally distinguish the correlates and constitution of visual consciousness, will future data do so? Revonsuo (2000), having noted the distinction, outlines the limitations of current methodologies in the cognitive

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[38] Chalmers (see Atkinson *et al.*, 2000, p. 373; see also Chalmers, 2000) avoids this confusion of 'correlates' and 'true correlates' by defining a neural correlate of consciousness as, "... a minimal neural system such that there is a mapping of states of that system to states of consciousness, where a given state of the neural system is sufficient, under certain conditions, for the corresponding state of consciousness." Chalmers (2000) also refers to 'direct' and 'core' (minimally sufficient) correlates (see also Kanwisher, 2001).

neurosciences and suggests that none of these methods can be expected to reveal organization at the phenomenal level in the brain.[39] He goes on, "can we even imagine any possible future method that could?" (p. 72). The problem here is that even in possession of methodologies that could capture the intricate details of all neural correlates of consciousness, the correlation/constitution remains. Though it may be possible to propose hypotheses for the neuronal constitution of consciousness, it is not obvious how such hypotheses could be assessed? For binocular rivalry, we *currently* possess details of correlated neuronal processes in cortical regions that are equally likely to play a role in visual consciousness, yet there are simply no clear strategies for determining which are indeed constitutive processes.[40,41] Similarly, it is not clear how to identify constitutive subcortical processes, amongst those exhibiting correlated *and non-correlated*[42] activity. Correlational approaches, it must be clearly stated, at least narrow the range of plausible candidates for the neuronal constitution of visual consciousness. However, it remains a major challenge for science to overcome the problem posed by the correlation/constitution distinction.

Acknowledgements

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[39] The correlation/constitution distinction extends beyond notions of visual consciousness to phenomenal consciousness in all modalities. This adds to other epistemic limitations associated with the scientific study of neural systems with subjectivity (Miller, 1999; in preparation).

[40,] It is worth remembering that binocular rivalry is not normal vision and though the activity of V1 monocular neurones does not appear to be constitutive of rivalling visual states, such activity may play a constitutive role in normal vision. Kosslyn *et al.* (1999) for example, has shown that V1 is activated during visual imagery (with no direct visual stimulation). Crick and Koch (1995; see also 1998 on visual imagery) on the other hand contend that V1 activity is unlikely to be constitutive of visual consciousness because it lacks the direct connections to the frontal cortex that would be needed for reasoning and decision-making in the control of behavior. Though see Block (1996).

[41] Perhaps strategies will emerge to overcome these limitations, however we may be forced to accept indirect and inferential evidence. The suggestion by Crick and Koch (1998) that new methods in molecular biology may enable the precise inactivation of particular neuronal circuits is intriguing, but even this evidence will be inferential. Simply because the brain can sustain consciousness while particular circuits are inactivated does not prove that such circuits do not play a constitutive role in normal consciousness. Similarly, a change in consciousness following the inactivation (or stimulation) of particular circuits might suggest but cannot prove a constitutive role for those circuits during normal consciousness.

[42] Aside from perception-dependent visually responsive neurons that may or may not be constitutive of visual consciousness during rivalry, there is presumably also a class of neurones (e.g. brainstem and/or other subcortical neurons) whose activity is not correlated with the alternating visual states but is nevertheless constitutive of those states. Such neurons may be constitutive of visual consciousness by virtue of being constitutive of *all* conscious states (i.e., involved in states of waking consciousness generally).

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