

Caloric vestibular stimulation reveals discrete neural mechanisms for coherence rivalry and eye rivalry: A meta-rivalry model

Trung T. Ngo^{a,d,e,*}, Guang B. Liu^{a,b}, Andrew J. Tilley^c,
John D. Pettigrew^a, Steven M. Miller^{d,e,f}

^a Vision Touch and Hearing Research Centre, Research Road, School of Biomedical Sciences, University of Queensland, Brisbane, Qld 4072, Australia

^b Department of Biological and Physical Sciences, University of Southern Queensland, Toowoomba, Qld 4350, Australia

^c School of Psychology, McElwain Building 64A, University of Queensland, Brisbane, Qld 4072, Australia

^d Caulfield Pain Management and Research Centre, Caulfield General Medical Centre, Kooyong Road, Caulfield, Vic. 3162, Australia

^e Brain Stimulation Laboratory, Alfred Psychiatry Research Centre, The Alfred Hospital, Commercial Road, Melbourne, Vic. 3004, Australia

^f Department of Psychological Medicine, Monash University, Clayton Campus, Melbourne, Vic. 3800, Australia

Received 8 April 2006; received in revised form 27 February 2007

Abstract

Binocular rivalry is an extraordinary visual phenomenon that has engaged investigators for centuries. Since its first report, there has been vigorous debate over how the brain achieves the perceptual alternations that occur when conflicting images are presented simultaneously, one to each eye. Opposing high-level/stimulus-representation models and low-level/eye-based models have been proposed to explain the phenomenon, recently merging into an amalgam view. Here, we provide evidence that during viewing of Díaz-Caneja stimuli, coherence rivalry—in which aspects of each eye's presented image are perceptually regrouped into rivalling coherent images—and eye rivalry operate via discrete neural mechanisms. We demonstrate that high-level brain activation by unilateral caloric vestibular stimulation shifts the predominance of perceived coherent images (coherence rivalry) but not half-field images (eye rivalry). This finding suggests that coherence rivalry (like conventional rivalry according to our previous studies) is mediated by *interhemispheric* switching at a high level, while eye rivalry is mediated by *intra*hemispheric mechanisms, most likely at a low level. Based on the present data, we further propose that Díaz-Caneja stimuli induce '*meta-rivalry*' whereby the discrete high- and low-level competitive processes themselves rival for visual consciousness.

© 2007 Elsevier Ltd. All rights reserved.

Keywords: Binocular rivalry; Bottom-up versus top-down processing; Amalgam view; Interocular grouping; Multistability; Coherence rivalry; Caloric vestibular stimulation; Interhemispheric switching; Meta-rivalry; Visual consciousness

1. Introduction

In the past decade, there has been a rekindling of the perennial debate concerning the neural level at which binocular rivalry is resolved. Rivalry is characterized by perceptual alternations that occur every few seconds when

conflicting stimuli are dichoptically presented in corresponding retinal locations (Fig. 1a). Helmholtz (1867/1962), James (1890) and Sherrington (1906) considered that the brain achieved these striking changes in perception through the employment of attentional mechanisms. Hering (1879/1942), on the other hand, favored a bottom-up explanation for the phenomenon. This historical debate has continued to the present day with a wide range of psychophysical, electrophysiological, brain-imaging and brain-stimulation evidence supporting each side of the argument.

The most dramatic turn in recent theorizing about rivalry occurred when Logothetis and colleagues

* Corresponding author. Address: Caulfield Pain Management and Research Centre, Caulfield General Medical Centre, Kooyong Road, Caulfield, Vic. 3162, Australia.

E-mail addresses: trung.ngo@uq.edu.au (T.T. Ngo), steven.miller@med.monash.edu.au (S.M. Miller).

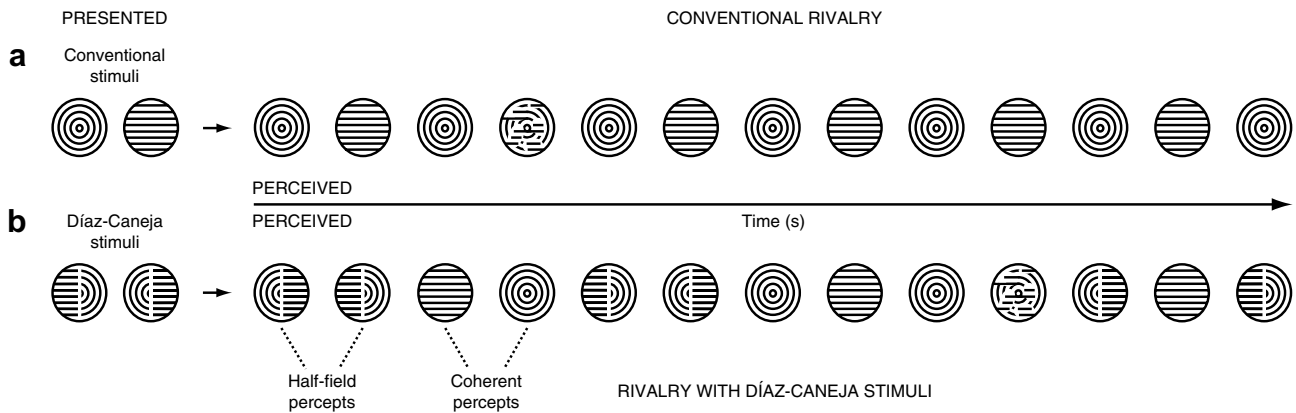


Fig. 1. Rivalry with conventional stimuli and Díaz-Caneja (DC) stimuli. (a) Dichoptic presentation of dissimilar stimuli yields alternating perception of each image, every few seconds. (b) Dichoptic presentation of DC stimuli (Díaz-Caneja, 1928) induces perception of interocularly regrouped images (coherent percepts) for around half the viewing time and perception of each eye's presented image (half-field percepts, given each is divided into two different halves) for the remaining time (Ngo et al., 2000). In both (a) and (b), brief periods of mixed/mosaic images are also depicted.

demonstrated that in alert macaque monkeys, the activity of low-level monocular neurones was not correlated with the monkey's rivaling perceptions (Leopold & Logothetis, 1996). This cast doubt upon Blake's (1989) monocular-channel reciprocal-inhibition model of rivalry which had been based on a large number of psychophysical studies. Logothetis' group found an increasing degree of perception-dependent neural activity as they progressed through the visual pathway, with around 90% of neurones at the high-level (inferotemporal cortex) exhibiting activity correlated with the monkey's perceptual reports (Sheinberg & Logothetis, 1997; reviewed in Logothetis, 1998). Following subsequent psychophysical and brain-imaging studies (Section 4.3) in favor of high- and low-level accounts of the phenomenon, Blake and Logothetis (2002) together proposed an amalgam view in which rivalry is conceived as a series of processes implemented by neural mechanisms at different levels of the visual hierarchy (see also multi-stage models by Freeman, 2005; Pearson & Clifford, 2005a; Wilson, 2003).

1.1. The interhemispheric switch model

Our group raised another issue, also rooted in opposing high- versus low-level interpretations, concerning whether activity between the two cerebral hemispheres during rivalry is synchronous, or rather independent and in alternation (asynchronous). We proposed a novel high-level mechanism for binocular rivalry (and for perceptual rivalry in general), according to which one cerebral hemisphere selects one image, the other hemisphere selects the rival image, and the perceptual alternations reflect an alternating pattern of relative hemispheric activation (i.e., interhemispheric switching; Miller et al., 2000).

The interhemispheric switch (IHS) model of rivalry arose from two intuitions. First, one of the authors (JDP) considered that a bistable oscillator could exist

in the human brain, inducing periodic switching between relative left- and right-hemispheric activation. There existed some evidence in the literature for such an inter-hemispheric switch in humans and other species (discussed in Miller et al., 2000). However, Pettigrew's intuition was based on comparative observations of the alternating eye movements of the sandlance (a small teleost; Pettigrew, Collin, & Ott, 1999), and on the logic emerging from the observations of Ramachandran (1994; see also Cappa, Sterzi, Vallar, & Bisiach, 1987) who considered that each cerebral hemisphere utilized a different cognitive style. Pettigrew reasoned that these complementary cognitive styles would not be engaged simultaneously, but rather in alternation.

The second intuition (that of author SMM) involved the conjunction of attentional notions of binocular rivalry, in particular as espoused by Helmholtz, with the finding of independent hemispheric attentional processing during visual search tasks (Luck, Hillyard, Mangun, & Gazzaniga, 1989; see also Alvarez & Cavanagh, 2005; Arguin et al., 2000; Kraft et al., 2005) and the reported capacity of a single cerebral hemisphere to sustain coherent visual perception (Bogen et al., 1998). Together, Pettigrew's and Miller's intuitions led to the proposal that the perceptual alternations of binocular rivalry are mediated by a process of interhemispheric switching. To test the model, Miller proposed the use of caloric vestibular stimulation (CVS), the same experimental technique that Ramachandran utilized in arguing for the existence of complementary cognitive styles of the cerebral hemispheres. It was reasoned that if one image is selected by one hemisphere and the rival image is selected by the opposite hemisphere, then activating a single hemisphere should increase rivalry predominance (the time spent perceiving one image relative to the other) in favor of that hemisphere's selected image.

CVS has traditionally been used as a diagnostic test to assess the integrity of the vestibular system (Bárány,

1906; Fife et al., 2000). We however, employed the technique to examine the IHS model because it induces unilateral hemisphere activation (see below) and has known effects on attentional processing. For example, *Silberpfennig* (1941) first reported that patients with unilateral attentional neglect following right-sided brain lesions can have their attentional deficit temporarily ameliorated by left-ear CVS (right-hemisphere activation), a finding that has been widely replicated (reviewed in *Rossetti & Rode*, 2002; *Vallar, Guariglia, & Rusconi*, 1997). Such effects of CVS usually last for around 10–15 min, though a related brain stimulation technique (neck muscle vibration; *Bottini et al.*, 2001) has been shown to induce long-lasting restoration of attentional function (*Johannsen, Akermann, & Karnath*, 2003; *Schindler, Kerkhoff, Karnath, Keller, & Goldenberg*, 2002).

Brain-imaging studies of CVS have revealed activation in contralateral temporo-parietal, anterior cingulate and insular cortices (*Bottini et al.*, 1994, 2001; *Indovina et al.*, 2005; *Vitte et al.*, 1996; *Wenzel et al.*, 1996). These areas have been consistently linked to attentional processing, including visual search and conflict resolution (*Botvinick, Cohen, & Carter*, 2004; *Corbetta & Shulman*, 2002; *Posner & DiGirolamo*, 2000; *Posner & Petersen*, 1990), and their disruption (almost exclusively on the right side) can cause unilateral attentional neglect (e.g., *Karnath, Berger, Küker, & Rorden*, 2004; *Leibovitch et al.*, 1998, 1999).

In accordance with the proposed IHS model, we demonstrated that CVS-induced unilateral activation of attentional structures did indeed significantly change predominance during binocular rivalry (*Miller et al.*, 2000). Our initial findings with horizontal/vertical gratings were replicated with orthogonal oblique gratings, thus excluding the possibility of the finding being due to residual eye movements (nystagmus) from CVS. In both experiments, only left-hemisphere activation induced a significant effect on predominance. Right-hemisphere activation (and the control condition) did not significantly affect predominance, a finding we interpreted on the basis of a previously reported transition-related right-sided frontoparietal network (*Lumer, Friston, & Rees*, 1998), or on the basis of known hemispheric asymmetries of spatial representation (discussed in *Miller*, 2001; indeed the same asymmetries that lead to unilateral attentional neglect following right- rather than left-sided brain lesions; *Beis et al.*, 2004; *Bowen, McKenna, & Tallis*, 1999).

Pettigrew subsequently proposed that our significant CVS findings could be confirmed by applying a single pulse of transcranial magnetic stimulation (TMS) to the left temporo-parietal cortex during binocular rivalry, timed to occur on a subject's reported switch from horizontal to vertical or on the opposite transition. According to the IHS model, only one condition should result in perceptual disruption induced by the TMS. In other words, the model predicted that disrupting temporo-pari-

etal areas in one hemisphere, timed to occur on a perceptual switch to that hemisphere's selected image, would disrupt perception of the image. However, temporo-parietal disruption of the same hemisphere timed to occur on transition to the opposite hemisphere's selected image should have no perceptual effect. That is indeed what was found (*Miller et al.*, 2000).

The findings from the CVS and TMS experiments on binocular rivalry supported the IHS model and are difficult to explain on an account of rivalry that has competition occurring within, rather than between, the hemispheres (at any level). The IHS model was also extended to perceptual rivalry in general with the demonstration (by author TTN) of CVS-induced changes in predominance during viewing of an ambiguous figure—the Necker cube (*Miller et al.*, 2000; see also *Ngo, Liu, Tilley, Pettigrew, & Miller*, submitted for publication). Finally, various elements of the IHS model have been developed. *Pettigrew* (2001) elaborated on the notion of a subcortical oscillator driving the IHS process. *Miller* (2001) developed the model in the context of involuntary attention (proposing that interhemispheric switching involves alternating unihemispheric attentional selection) and discussed its relevance to the scientific study of visual consciousness.

1.2. Coherence rivalry

In the present study, we aimed to further test a specific aspect of the IHS model. *Miller et al.* (2000) suggested that the existence of coherence rivalry (*Kovács, Papathomas, Yang, & Feher*, 1996; *Ngo, Miller, Liu, & Pettigrew*, 2000) supported higher-order (stimulus-representation) interpretations of conventional rivalry. Coherence rivalry, reported by Emilio Díaz-Caneja in 1928 (translation in *Alais, O'Shea, Mesana-Alais, & Wilson*, 2000), occurs when aspects of each eye's presented image are perceptually regrouped into rivalling coherent images (*Fig. 1b*). Over half a century prior to Díaz-Caneja's description of the phenomenon, *Towne* (1863, 1864) had observed some degree of interocular grouping (*Wade, Ono, & Mapp*, 2006). However, it was Díaz-Caneja who asserted that the perception of components from both eyes' images at the same time reflected more than just rivalry between the eyes. *Ngo et al.* (2000) quantified Díaz-Caneja's early observations (see also *Kovács et al.*, 1996; *Sengpiel*, 1997; Section 4.1) and found that coherent percepts (coherence rivalry) occurred for around half the viewing time with the remaining half spent perceiving either eye's presented image (herein referred to as half-field images given each is divided into two different halves; *Fig. 1b*).

The present study employed the CVS technique during viewing of Díaz-Caneja (DC) stimuli to assess whether coherent and half-field perceptual periods are affected by unilateral hemisphere activation. This experiment addresses the issue of whether these different perceptual

periods are mediated by the same or discrete neural mechanisms, with implications for understanding the level of processing at which each rivalry type occurs. As originally proposed by Miller et al. (2000), the IHS model predicts that the predominance of at least the coherent percepts should be affected by unilateral CVS. Eye-rivalry models, being usually equated with low-level and within-hemisphere (*intrahemispheric*) mechanisms, predict that CVS should not affect the predominance of either the coherent or the half-field percepts.

2. Methods

2.1. Participants

Thirty-two healthy male volunteers (aged 18–35 years) who were right-handed (School of Psychology handedness questionnaire), were recruited from advertisements placed around the campus. All subjects had normal or corrected-to-normal vision and were screened for medical and psychiatric history with a brief questionnaire. Exclusion criteria were any psychiatric condition or significant medical disorder such as cardiovascular disease, epilepsy, vestibular or other neurological disorder. Participants were naïve to the experimental hypothesis and written, informed consent was obtained prior to each experimental session according to a protocol approved by the University of Queensland's Medical Research Ethics Committee and in keeping with the National Statement on Ethical Conduct in Research Involving Humans (1999) issued by the National Health and Medical Research Council of Australia. Subjects received a token financial remuneration for completing all three experimental sessions (see Section 2.3).

2.2. Rivalry stimuli

The DC stimuli were elliptical patches (subtending visual angle of 2.8° [height] \times 2.1° [width]; s.f. = 8.7 cycles/degree; contrast = 0.9) presented dichoptically using a PC-compatible VisionWorks™ package (Vision

Research Graphics, Inc., Durham, NH, USA) on a monochrome 53-cm computer monitor (green, P46 phosphor, persistence = 500 ns) with NuVision 60GX® stereoscopic wireless LCD glasses (MacNaughton, Inc., Beaverton, OR, USA). These goggles allowed dichoptic presentation without the need for training in fixation. All subjects spontaneously perceived all four possible stable percepts (Fig. 1b) during familiarization with the task. The stimuli used in the present study were the same as those used by Ngo et al. (2000) and were similarly devoid of colour cues (cf. original stimuli used by Díaz-Caneja, 1928).

2.3. Recording procedure

Sixteen subjects reported their coherent percepts and another sixteen subjects reported their half-field percepts. In the coherence rivalry group, observers responded with one key to indicate the perception of concentric circles and another key to indicate coherent horizontal lines. A third response option (space bar) was used to indicate mixed/mosaic states (Fig. 1b), errors or either of the half-field percepts. In the half-field rivalry group, subjects pressed one key to indicate the perception of one half-field percept and another key to indicate the other half-field percept. A third response option (space bar) was used to indicate mixed/mosaic states, errors or either of the coherent percepts. Within each group, percept-key response options and hand used were counterbalanced across subjects and the third response option was excluded before data analysis. Participants sat upright and were instructed to record what they passively observed and not to preferentially respond to any of the percepts.

All subjects underwent three 1-hr rivalry sessions consisting of two half-hour data collection periods, each divided into three blocks (separated by 2-min breaks; Fig. 2a) of four 100-s trials (separated by 30-s breaks; Fig. 2b). Thus each block consisted of around 7 min of rivalry viewing. The first (control) experimental session involved no CVS (5 min rest) after half an hour of baseline recording. The second and third sessions involved CVS (Fig. 2c) of either the right ear (left hemisphere) or left ear (right hemisphere), counterbalanced across subjects within each rivalry group. In these experimental sessions, CVS was administered approximately 1 min after the end of baseline rivalry recording (Fig. 2a and c). All data collection was conducted in a quiet, completely darkened room except for a single incandescent light source (25–40 W bulb) in a corner directed upwards

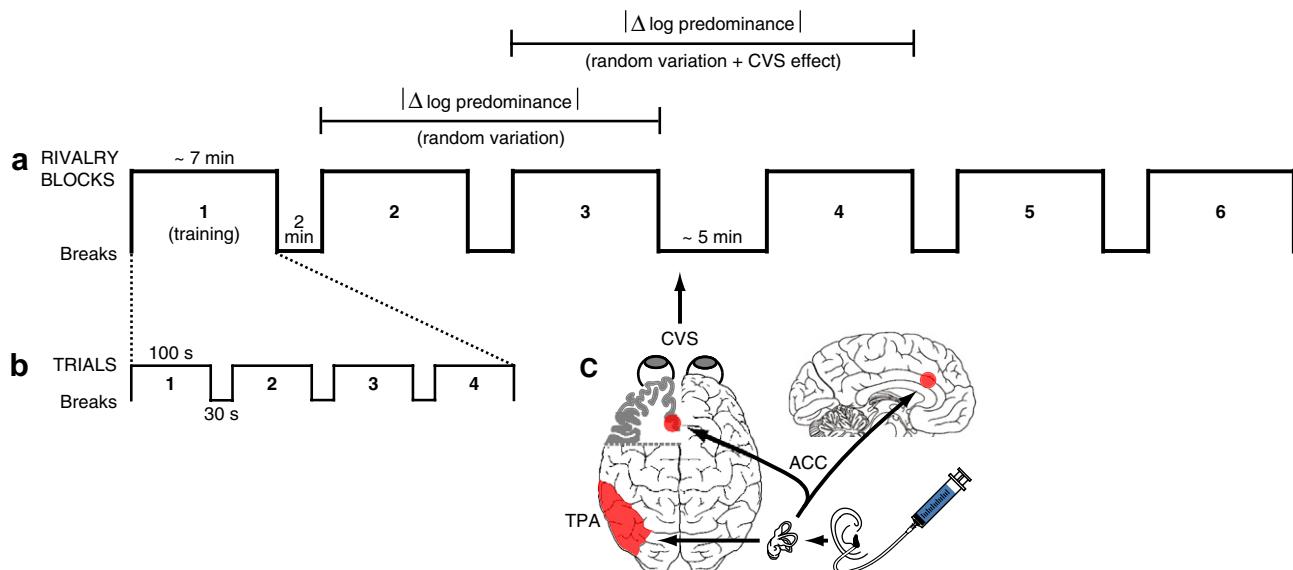


Fig. 2. Experimental protocol and the CVS technique. Subjects recorded their rivalry responses in three separate experimental sessions, one of which is represented in (a). After three blocks of data collection (one block is represented in b), in the first (control) session they had 5 min rest while for the second and third sessions, they underwent the right-ear (left-hemisphere) and left-ear (right-hemisphere) CVS intervention which was counterbalanced across subjects within each of the coherence rivalry and half-field rivalry groups. (c) The CVS technique involves cold-water irrigation of (in this case) the right ear, which via the semicircular canals, activates high-level cortical regions in the contralateral hemisphere (TPA, temporo-parietal areas, and ACC, anterior cingulate cortex; e.g., Bottini et al., 1994, 2001; insular cortex activation not indicated).

and away from the monitor and participant. Both the PC-compatible online rivalry recording and offline analysis programs were generated with MATLAB software (The MathWorks, Inc., Natick, MA, USA).

2.4. Caloric vestibular stimulation technique

All subjects were otoscopically examined by a medical officer for any signs of ear disease or cerumen impaction prior to CVS. Participants were reminded of the CVS procedure (having been initially informed via an information sheet), and were instructed to report the onset of the anticipated signs of the stimulation (see below). With the subject maintaining a vertical mid-sagittal plane, head orientation was kept at 30° from the horizontal plane thereby placing the lateral (horizontal) semicircular canal into the vertical plane for maximal stimulation (Coats & Smith, 1967). Cold (iced) water was similarly used to provide maximal stimulation (Schmäl, Lübber, Weiberg, & Stoll, 2005) and was slowly injected into the external auditory canal using a 50-ml plastic syringe with a short piece of soft silastic tubing attached and positioned near the tympanum. Irrigation stopped usually after around 20–30 ml when the subject reported vertigo and the experimenter observed nystagmus (slow-phase direction ipsilateral to the ear stimulated).

The reflux water from the external auditory canal was recovered in a plastic container rested on the subject's shoulder underneath the irrigated ear. When there were no signs of ongoing nystagmus and the subject had reported that their vertigo had ceased (usually 2–3 min following their onset), they resumed the upright position and started the second half-hour of rivalry recording. This sequence meant there was the least likelihood of residual nystagmus and vertigo during data collection but ensured that subjects started post-stimulation rivalry recording within the reported 10-min maximal effect window following CVS. The approximate duration of the period between the end of pre-stimulation rivalry recording and the beginning of post-stimulation rivalry recording was 5 min (Fig. 2a and c).

3. Results

The first of the six blocks of rivalry recording in each experimental session was used for training and was thus not included in the analysis (Fig. 2a). The total time (seconds) spent perceiving one image (e.g., coherent concentric circles) was divided by the total time (seconds) spent perceiving the other image (e.g., coherent horizontal lines), excluding mixed percepts. This provided the predominance ratio for each rivalry block. The ratios were then log-transformed to account for the disproportionate numerical representation in predominance (i.e., >1 for one image cf. <1 for the other). The absolute magnitude of difference (i.e., regardless of the direction of change) between two pre-CVS blocks of rivalry (blocks 2 and 3) was then calculated in order to assess baseline (random) fluctuations in predominance. This difference measure was referred to as $|\Delta \log \text{predominance}|$ and was again calculated for changes in predominance between the blocks immediately before and after CVS (blocks 3 and 4). The latter calculation was a measure of random fluctuation plus the experimental effect (if indeed there was any to be discerned).

In order to show an experimental effect, the $|\Delta \log \text{predominance}|$ of blocks 3–4 had to be significantly larger than the $|\Delta \log \text{predominance}|$ of blocks 2–3. In other words, a significantly greater predominance change across blocks 3–4 than across blocks 2–3 would indicate an effect from CVS over and above baseline predominance fluctuations (Fig. 2a). These predominance change values are shown

for the left-hemisphere stimulation condition in Fig. 3b (coherence rivalry) and d (half-field rivalry). The difference between predominance changes of blocks 3–4 and blocks 2–3, for all three experimental conditions, is presented in Fig. 3a (coherence rivalry) and c (half-field rivalry) and referred to as Δ ($|\Delta \log \text{predominance}|$).

All within-group statistical analyses employed two-tailed Wilcoxon signed-ranks test ($\alpha = 0.05$) for magnitude of difference (i.e., $|\Delta \log \text{predominance}|$) comparisons and for rate comparisons (below). The summary statistics of $|\Delta \log \text{predominance}|$ analyses are reported in Table 1 and were based on $n = 15$ due to the exclusion of one outlier from each of the coherence and half-field rivalry groups (outliers are not shown in Fig. 3 and were subjects who had a baseline predominance value that was greater than $\pm 3SD$ of the corresponding Mean $|\Delta \log \text{predominance}|$ for blocks 2–3 in any of the three experimental conditions). All other statistical analyses (below) were also based on the same $n = 15$ from each group.

The main finding is that left-hemisphere stimulation significantly changed the predominance of rivalling coherent percepts but not half-field percepts. For both coherence rivalry and half-field rivalry, the right-hemisphere stimulation and control conditions were not significant. The direction of the significant predominance shifts during coherence rivalry was determined (following Miller et al., 2000) by examining individual data from the twelve subjects with the highest Δ ($|\Delta \log \text{predominance}|$). Around half of these subjects (five) favored the coherent concentric circles after stimulation, while the other half (seven) favored the coherent horizontal lines.

To assess rivalling tendency in both types of rivalry, for each subject the frequency of rivalry response strings was tallied from blocks 2 and 3 of their control condition. Fig. 4 presents the total frequency of single rivalry responses (i.e., one or the other coherent percept in the coherence rivalry group, and one or the other half-field percept in the half-field rivalry group) prior to a space bar response. Similarly, the total frequency of strings of 2, 3, 4 and ≥ 5 alternating rivalry responses prior to a space bar response is also presented. It can be observed from the frequency histogram that coherent percepts tend to rival with each other more often than do half-field percepts. Despite this tendency, the substantial frequency of strings of 2 or more half-field percepts prior to a space bar response indicates that the two half-field percepts nevertheless do engage in periods of rivalling with each other during DC stimuli viewing.

The mean alternation rate for each rivalry type (i.e., the rate at which coherent percepts rivalled with each other, and at which half-field percepts rivalled with each other) was calculated by averaging the rate across blocks 2 and 3 for each subject in their control condition and then averaging the obtained values for each rivalry group. It was found that coherent percepts rivalled with each other significantly faster than did half-field percepts (0.49 and 0.32 Hz, respectively; two-tailed Mann–Whitney test, $U = 56$, $p < 0.05$). Finally, to assess whether CVS caused

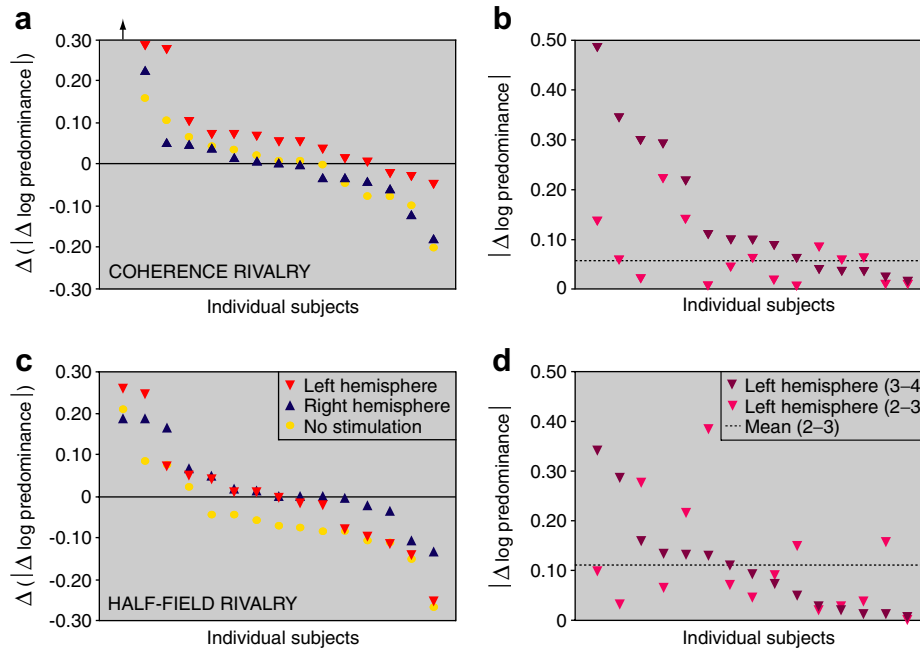


Fig. 3. CVS significantly changes predominance during coherence rivalry but not half-field rivalry. The pattern of greater predominance change following CVS than in baseline rivalry viewing can be observed in (b) which shows the significant left-hemisphere effect on the coherent perceptual periods. Each pair of points corresponds to the same individual subject and was ordered according to the block 3–4 values (similarly for the non-significant half-field rivalry data; d). Subtraction of the block 2–3 value from the block 3–4 value removes baseline predominance variation (Fig. 2a), and is represented by $\Delta(|\Delta \log \text{predominance}|)$ and shown for all experimental conditions in the coherence rivalry (a) and half-field rivalry (c) groups. Thus the points above zero in (a) and (c) represent individuals who showed larger predominance shifts following CVS than in baseline rivalry viewing. The subjects in (a) and (c) were arranged in descending order of magnitude, separately for each condition, and therefore do not necessarily correspond to the data points representing individual subjects in (b) and (d), respectively. Data points not shown but included in statistical analyses are 0.35 (left-hemisphere stimulation), 0.59 (right-hemisphere stimulation) and 0.84 (no stimulation) and are indicated by \uparrow for subjects in (a). Outliers are also not shown but were excluded from the predominance analyses (and all other analyses; see Section 3).

Table 1
Summary statistics of CVS effects on rivalry with Díaz-Caneja stimuli

Type of rivalry and conditions	n	Mean $ \Delta \log \text{predominance} $		W^*	p
		Blocks 2–3	Blocks 3–4		
<i>Coherence rivalry</i>					
Left hemisphere	15	0.057	0.145	–94	<0.01
Right hemisphere	15	0.077	0.114	–10	0.80
Control	15	0.133	0.184	–16	0.68
<i>Half-field rivalry</i>					
Left hemisphere	15	0.111	0.105	16	0.68
Right hemisphere	15	0.104	0.128	–25	0.41
Control	15	0.145	0.096	62	0.08

* Sum of signed ranks (Wilcoxon signed-ranks test).

any effect on rivalry rate, statistical analyses were performed on block 3 (immediately pre-stimulation) rivalry rates versus block 4 (immediately post-stimulation) rivalry rates. No significant effect was found for either coherence rivalry (left-hemisphere stimulation condition: mean rate of blocks 3 and 4, respectively = 0.65 and 0.68 Hz, $W = -36$, $p = 0.27$; right-hemisphere stimulation condition: mean rate of blocks 3 and 4, respectively = 0.66 and 0.69 Hz, $W = -53$, $p = 0.10$) or half-field rivalry (left-hemisphere stimulation condition: mean rate of blocks 3 and 4, respectively = 0.35 and 0.36 Hz, $W = -8$, $p = 0.79$; right-hemisphere stimulation condition: mean rate of blocks 3 and 4, respectively = 0.33 and 0.33 Hz, $W = 7$, $p = 0.84$).

4. Discussion

The demonstrated effect of CVS on predominance of coherent perceptual periods during rivalry with DC stimuli confirms our earlier prediction (Miller et al., 2000) that interhemispheric switching mediates these perceptual alternations. This adds to our original CVS finding for conventional rivalry (Fig. 5a). The present results thus support the notion that rivalry between coherent perceptual periods is indeed occurring at a high level of visual processing given the fact that CVS activates high-level cortical regions. However, the results also show that half-field rivalry during viewing of DC stimuli is not mediated by a process of

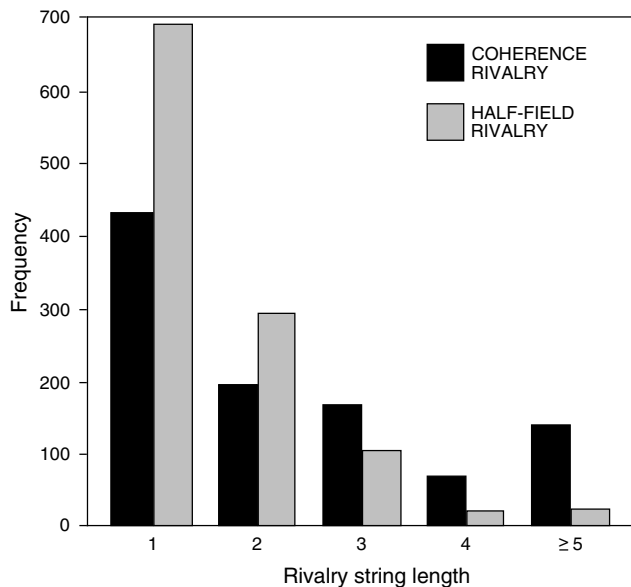


Fig. 4. Frequency histogram of rivalry string-lengths for coherent percepts and half-field percepts. The total frequency of string-lengths for coherence rivalry (black bars) and half-field rivalry (grey bars) represents the tendency of the two coherent percepts to rival with each other and the two half-field percepts to rival with each other, respectively. It can be seen that coherent percepts tend to rival more often with each other than do half-field percepts, i.e., compared with half-field percepts, coherent percepts demonstrate a lower frequency of string-lengths of 1 (690 and 430, respectively), and a higher frequency of string-lengths of 2 or more alternating percepts (total of 438 and 564, respectively). Despite this difference between the two types of rivalry, it is evident that half-field percepts nevertheless do rival with each other as shown by their substantial frequency of string-lengths of 2 or more. Nevertheless, the difference between the two rivalry types in rivalling tendency suggests that high-level coherence rivalry is a 'higher-strength' type of rivalry than low-level half-field rivalry, i.e., the high-level coherence (interhemispheric) rivalry more readily overcomes the suppression exerted by the low-level half-field (intra-hemispheric) rivalry, than occurs vice versa (see Section 4.1).

interhemispheric switching. Activation of a single hemisphere by CVS did not alter the predominance of these perceptual periods, suggesting they are mediated by intrahemispheric processes. The findings therefore demonstrate that coherence rivalry and half-field rivalry operate via discrete neural mechanisms. In accordance with our other CVS experiments (Miller et al., 2000; Ngo et al., submitted for publication), there was no significant effect of right-hemisphere stimulation (see Section 1.1). Furthermore, the direction of predominance shifts indicate that either coherent percept can be selected by either hemisphere, a finding consistent with experiments using conventional rivalry stimuli, designed specifically to assess the issue of percept-to-hemisphere selection (reported in a separate paper in preparation).

4.1. Levels and mechanisms of rivalry with conventional stimuli and DC stimuli

The results of the present study bear directly upon the perennial debate concerning at what level rivalry takes

place in the brain. In the years preceding Blake and Logothetis' (2002) amalgam view, Blake's (1989) interpretation of a wealth of psychophysical experiments led him to defend a neurophysiological mechanism in which rivalry was mediated by reciprocal inhibition between neurones in the separate monocular channels responsive to each eye. This model however, gained no support from Logothetis and colleagues' direct electrophysiological measurement of neural activity at various levels of visual processing during rivalry (see Section 1). Nevertheless, there remained psychophysical evidence in support of eye rivalry (and more recently, brain-imaging evidence—Section 4.3). The demonstration of non-selective suppression of visual test probes during rivalry (Wales & Fox, 1970), for example, suggested that what rivals are regions of an eye rather than particular stimulus features within those regions. However, the regrouping of stimulus features from each eye into coherent percepts during viewing of DC stimuli (and other interocular-grouping stimuli) argues against this interpretation. Such observations suggest that high-level grouping principles dictate which regions of an eye are suppressed at which time. Clearly such grouping takes place by virtue of particular stimulus features (Miller, 2001), and as Blake (2001, pp. 13–14) put it, "perhaps attention is providing part of the neural glue".¹

Furthermore, Logothetis' group demonstrated that rapidly swapping stimuli between the eyes at 3 Hz did not induce rapidly alternating perceptions, but rather, smooth and slow perceptual transitions every few seconds (Logothetis, Leopold, & Sheinberg, 1996). This suggested rivalry occurs between stimulus representations high in the visual hierarchy rather than between the eyes. They further demonstrated that the temporal dynamics of stimulus-representation rivalry were similar to those of conventional rivalry, thus equating the two rivalry types. However, Blake's group showed that stimulus-representation rivalry with the rapid eye-swap method required very specific viewing conditions for its induction (Lee & Blake, 1999). These investigators therefore argued that such conditions override the neural events underlying conventional rivalry and in doing so, reveal a high-level form of rivalry (Lee & Blake, 2004; see also Wilson, 2003; Wolfe, 1996). Thus, in contrast to Logothetis et al. (1996), Lee and Blake (2004) equate conventional rivalry with eye rivalry and suggest that high-level stimulus-representation rivalry is the exception rather than the norm.

Returning to the findings of the present study, while it is evident that rivalry between coherent perceptual periods is occurring at a high level on an interhemispheric basis, it is difficult to determine from the data at what level the intra-hemispheric competition during half-field rivalry is occurring. Although high-level intrahemispheric rivalry for

¹ Lee and Blake (2004) and Alais and Melcher (2007) consider that interocular grouping may still be consistent with notions of early local interactions, although with global high-level feedback projections guiding these low-level local processes.

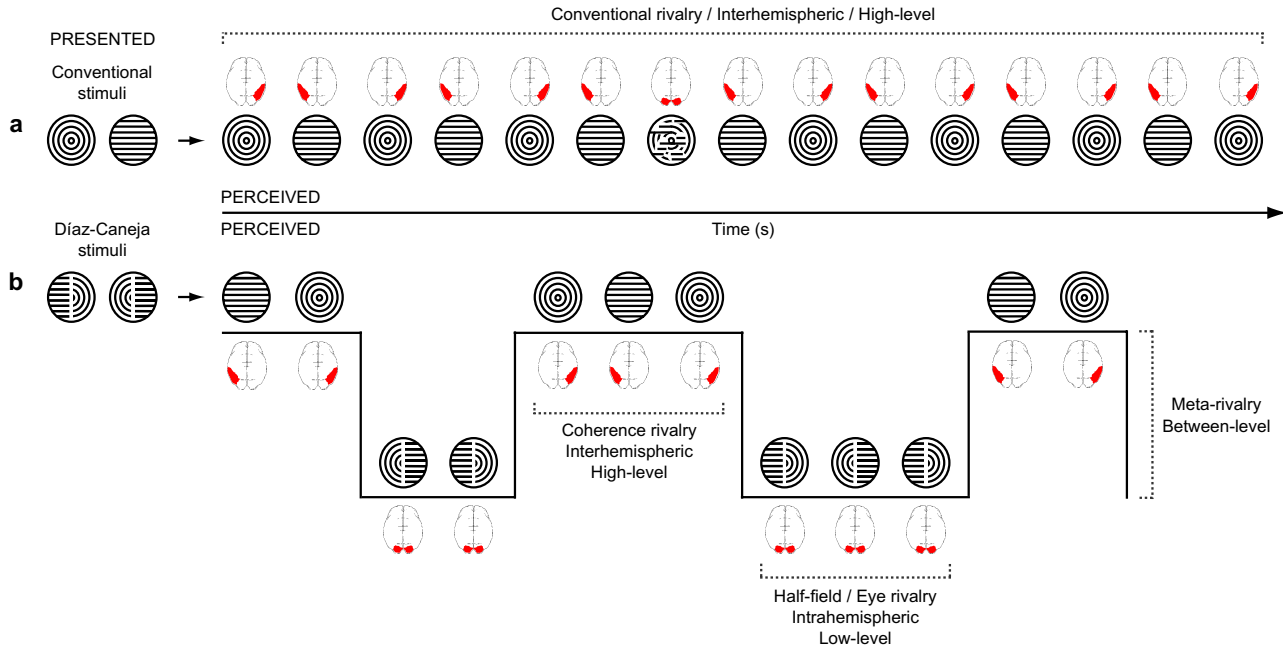


Fig. 5. Models and levels of rivalry with conventional stimuli and DC stimuli. (a) Our previous CVS experiments with conventional stimuli demonstrated that *interhemispheric* switching at a high level of visual processing mediates this type of rivalry (Miller et al., 2000). (b) In the present study, the finding that CVS significantly changes predominance of coherent percepts during viewing of DC stimuli (Fig. 3a and b, Table 1) demonstrates that high-level *interhemispheric* switching also mediates coherence rivalry. However, the data further show that half-field rivalry predominance with these stimuli is not significantly affected by CVS (Fig. 3c and d, Table 1), suggesting that the rivaling half-field percepts are mediated by *intrahemispheric* mechanisms at a low-level of visual processing (eye rivalry). The present findings therefore reveal discrete neural mechanisms for coherence rivalry and eye rivalry. In addition, we propose that these discrete high- and low-level rivalries themselves rival for visual consciousness (*meta-rivalry*).

these periods is not incompatible with our results, we suggest that rivalry between half-field perceptual periods occurs at a low-level of visual processing, consistent with other evidence for eye rivalry (see above). If this is the case, DC stimuli can be considered to induce an alternation between high-level and low-level processes within a given viewing period (along with a corresponding alternation between *interhemispheric* and *intrahemispheric* rivalry). Moreover, we propose this alternation occurs via a *third* rivalry mechanism between these high and low levels, accounting for the fact that the viewer perceives coherent and half-field perceptual periods each for around half the given viewing time (as quantified by Ngo et al., 2000). Thus, according to this interpretation, what rivals during viewing of DC stimuli is (i) the two coherent percepts at a high level (*interhemispheric*), (ii) the two half-field percepts at a low level (*intrahemispheric*), and (iii) a between-level rivalry or '*meta-rivalry*'² (i.e., high- versus low-level). These three processes are illustrated in Fig. 5b.

For this view to hold it should be the case that high-level coherent percepts rival with each other and low-level half-field percepts rival with each other, rather than the four distinct percepts being perceived randomly during DC stimuli viewing. Suzuki and Grabowecy (2002) have indirectly assessed such issues but they combined data obtained from DC stimuli viewing with data obtained from DC conventional

rivalry (the latter with concentric circles presented to one eye and horizontal lines to the other). Despite this methodological issue, they suggested (using an estimated probability level) that the coherent percepts tended to rival with each other while the half-field percepts did not. Our data support the notion that coherent percepts tend to rival together *more often* than do half-field percepts, but in contrast to the findings of Suzuki and Grabowecy, the data also show a substantial frequency of strings of alternating half-field percepts (this is consistent with Suzuki and Grabowecy's finding using other interocular-grouping stimuli, that non-grouped percepts tend to rival with each other). Nevertheless from our data it does seem that during DC stimuli viewing, the 'strength' of coherence (*interhemispheric*) rivalry is greater than that of half-field (*intrahemispheric*) rivalry given the capacity of the high-level process to more easily disrupt the suppression exerted by the low-level process, than vice versa.

This interpretation is also supported by our finding that the rate of coherence rivalry is faster than that of half-field rivalry. This is consistent with the data of Suzuki and Grabowecy using DC stimuli (noting the methodological issue above), and of Kovács et al. (1996) who used other interocular-grouping stimuli (see also Alais, Lorenceau, Arrighi, & Cass, 2006). Thus, not only does high-level coherence rivalry more readily overcome the suppression exerted by low-level half-field rivalry, but also once initiated, one coherent percept more readily overcomes the suppression exerted by the other coherent percept (compared with rivalry between

² We thank Anthony Hannan for suggesting the term '*meta-rivalry*' as an alternative to '*between-level rivalry*'.

the two half-field percepts). This ‘endogenous’ determination of greater rivalry strength is similar to exogenous stimulus parameters known to influence the strength of rivalry (including rate-determining parameters such as contrast, motion and spatial frequency; Alexander, 1951; Alexander & Bricker, 1952; Blake, Yu, Lokey, & Norman, 1998; Fahle, 1982a, 1982b, 1983; Norman, Norman, & Bilotta, 2000; Schor, 1977; Wade, de Weert, & Swanston, 1984; Whittle, 1965; see also Miller et al., 2003).

The meta-rivalry model we have proposed could extend to other stimuli that induce interocular grouping such as dichoptic complementary patchwork images (Kovács et al., 1996). Our model may also shed light on the fact that, depending on the experimental conditions, rapidly swapping each eye’s presented image during rivalry sometimes leads to high-level stimulus-representation rivalry and sometimes to low-level eye-based rivalry. Indeed, it is evident from the data of Bonneh, Sagi, and Karni (2001) that the rapid eye-swap protocol also induces an alternation between these two rivalry types within the same viewing period. Hence we suggest the perceptions during the rapid-eye swap protocol could similarly be explained by meta-rivalry between high- and low-level competitive processes. For both the rapid eye-swap protocol and rivalry with interocular-grouping stimuli, investigation is already underway into the factors determining the relative time spent perceiving the high-level and low-level processes.³

³ Bonneh et al. (2001) investigated the stimulus parameters determining the relative percentage of smooth-slow rivalry and rapid eye-rivalry, and notably in the current context, they interpreted their data with reference to competition at different levels of visual processing. Indeed, consistent with our present data, they also found using the rapid eye-swap protocol that the greater the coherence of the stimuli, the faster the rivalry rate. Furthermore, they reported the (simultaneous) coexistence of smooth-slow rivalry and rapid eye-rivalry. In the case of Lee & Blake’s (1999) experiments, it is not clear whether smooth-slow rivalry alternated with rapid eye-rivalry within a given viewing period. They reported the percentage of trials during which subjects perceived one or the other rivalry type. Moreover, their use of short (10 s) trials, rather than longer trials as employed by Bonneh et al. (2001), may have made it difficult to demonstrate meta-rivalry and to quantify the percentage of time spent perceiving each rivalry type. Similarly, Logothetis et al. (1996) referred to conditions for optimal stimulus-representation rivalry (333 ms swapping) but did not report whether the less effective conditions (222 and 444 ms) induced meta-rivalry with smooth-slow alternations competing against rapid alternations for conscious perception. In a more recent study, Silver and Logothetis (2007) used temporal tagging of either the eye or the stimuli to respectively enhance fast regular perceptions (consistent with eye rivalry) and slow irregular perceptions (consistent with stimulus-representation rivalry). Using DC stimuli, Knapen, Paffen, Kanai, and van Ee (2007) found synchronous and counterphase flicker to respectively increase and decrease the proportion of time that coherence rivalry is observed. These authors argue that such stimulus manipulations place coherence rivalry high in the visual pathway and half-field rivalry at the low level, an interpretation consistent with our current data. Investigators have also quantified the predominance of interocularly grouped and non-grouped perceptions, and the factors influencing this, with the use of dichoptic images other than DC stimuli (de Weert, Snoeren, & Koning, 2005; Ooi & He, 2003; Pappathomas, Kovács, & Conway, 2005; Pappathomas, Kovács, Feher, & Julesz, 1999; Wong & Freeman, 1999; cf. Pearson & Clifford, 2005b).

An immediate further question is raised by the present findings: if coherence rivalry occurs at a high level and half-field rivalry occurs at a low level, at what level is conventional rivalry mediated? Upon initial consideration, it may seem that it occurs at the same level as half-field rivalry with DC stimuli (and rapid perceptual alternations with rapid eye-swap protocols), given that in all cases the perceived images match what is presented to the eyes. Indeed as previously mentioned, Lee and Blake (1999, 2004) consider high-level stimulus-representation rivalry to be the exception, with conventional rivalry at a low level (eye rivalry) being the norm. On the contrary however, the CVS data of the present study, together with our previous CVS findings (Miller et al., 2000), argue for exactly the opposite view. Thus the fact that predominance of both coherence rivalry and conventional rivalry is susceptible to influence by CVS, while that of half-field/eye rivalry is not, demonstrates that high-level resolution is the norm, with low-level/eye rivalry being the exception. We therefore postulate that low-level/eye rivalry occurs only when stimuli are of the sort that can induce meta-rivalry. In the case of DC stimuli, along with other interocular-grouping stimuli and rapid eye-swap protocols, there is indeed meta-rivalry (as we have postulated) and thus eye rivalry competes with high-level rivalry for perceptual dominance. However, with conventional rivalry, there is no meta-rivalry and thus no eye rivalry. In this case, high-level resolution automatically prevails.⁴

4.2. Rivalry, visual consciousness and attention

At this point, it is difficult to ignore an explicit discussion of what level-based theories of rivalry imply with respect to visual consciousness. It is clear that proposals for low- or high-level mechanisms of a particular rivalry type entail some neural activity at the respective level that is critical to the contents of visual consciousness. What is less clear is whether this critical neural activity (at which-

⁴ Our view does not entirely exclude low-level processing during conventional rivalry. Indeed some monocular signal is likely to be retained at the low level, presumably accounting for the non-selective suppression data that supports eye-rivalry explanations (notably obtained with conventional stimuli, e.g., Wales & Fox, 1970). Another issue that may seem unclear upon initial consideration is whether separate hemifield representation is relevant to our use of DC stimuli. In the original presentation of the IHS model (Miller et al., 2000), we pointed out that the postulated high-level interhemispheric activity involved neurones with large, *bilateral* receptive fields such as those in inferotemporal cortex (Gross, Rodman, Gochin, & Colombo, 1993), in keeping with the single-unit data of Sheinberg and Logothetis (1997). The exclusive representation of the contralateral visual hemifield in each hemisphere was therefore considered irrelevant to the IHS model given this exclusivity occurs only at the V1 level. In relation to DC stimuli, although they may appear to be hemifield stimuli (given each is divided along the vertical meridian into two halves; Fig. 1b), it must be noted that the central 1° of vision is represented in both hemispheres, even in V1 (Stone, 1966; Stone, Leicester, & Sherman, 1973; cf. Lavidor & Walsh, 2004; Lefé, 2004). True hemifield presentation therefore does not occupy this foveal overlap and as such, centrally presented DC stimuli cannot be considered hemifield stimuli.

ever level is being considered) is a direct constituent of the conscious visual states. Indeed it has been proposed that distinguishing actual constituents from mere correlates of consciousness is the major obstacle facing the scientific study of consciousness (Miller, 2001, 2007). Bearing in mind this empirical problem, it is postulated that during coherence rivalry, there is critical neural activity occurring at a high level that (i) is a constituent of one or the other coherent percept, and/or (ii) sends signals to constitutive neural circuitry. The same can be said of half-field/eye rivalry, whereby there is critical neural activity occurring at a low level that (i) is a constituent of one or the other half-field percept, and/or (ii) sends signals to constitutive neural circuitry (see also Bonneuh et al., 2001 for the notion of a multi-level allocation of awareness). In the case of conventional rivalry, we suggest visual consciousness bypasses the low-level entirely and instead is constituted by, or receives critical neural signals from, the high-level only.⁵

Another concern for the scientific study of consciousness and for the present discussion is to what degree the neural circuitry constitutive of visual consciousness overlaps with, or is distinct from, that of attentional selection (discussed in Miller, 2001). This is a special case of the correlation/constitution distinction problem and, as with the general case, there is not yet a clear approach strategy. Nevertheless, the role of attention during rivalry was a key component of proposing the IHS model and assessing it with the CVS technique. Notions of voluntary and involuntary attention during rivalry have a long history (Breese, 1899; Helmholtz, 1867/1962; James, 1890; Lack, 1978; McDougall, 1903, 1906; Sherrington, 1906; see also Walker, 1978) and have been further addressed in recent years.⁶ Miller (2001) discussed potential mechanisms of attentional selection and modulation during rivalry. Based on the notion that mechanisms of consciousness and mechanisms of attentional selection may indeed be distinct (recently reviewed by Koch & Tsuchiya, 2007), he further argued that visual consciousness during conventional rivalry (and during coherence rivalry) could be either unihemispheric or bihemispheric. Alternating unihemispheric visual consciousness during rivalry is a straightforward corollary of the IHS model, whereas bihemispheric visual consciousness was invoked as a possibility if it was attentional selection rather than visual consciousness that occurred independently in each hemisphere. On this latter

view, interhemispheric switching was proposed to involve alternating unihemispheric attentional selection.

Whichever way consciousness is conceptualized, it is inescapable that our CVS experiments provide evidence for a functional role of (involuntary) attention during rivalry.⁷ The brain regions activated by CVS are known to be involved in attention and attentional selection (Section 1.1), and our finding that CVS affects rivalry predominance clearly implicates such brain regions in the mechanisms of rivalry. For reasons that are not apparent to us, investigators interested in the role of attention during rivalry commonly overlook the evidence for just such a role provided by our CVS experiments. We point out that on the contrary, many recent studies of attentional mechanisms of rivalry (particularly those addressing involuntary attention) could be expanded upon by using CVS as the intervention, and the IHS model as the exploratory framework.

Furthermore, we argue that CVS is a generally underutilized tool in the cognitive neurosciences, the clinical neurosciences, and the scientific study of consciousness (Miller & Ngo, 2007) given its often dramatic effects on phenomena that are of legitimate interest to such investigation, including (i) binocular rivalry and ambiguous figure reversals (as our own work has demonstrated); (ii) verbal- and spatial-memory performance (Bächtold et al., 2001); (iii) unilateral attentional neglect (Section 1.1); (iv) motor neglect (Rode, Perenin, Honoré, & Boisson, 1998); (v) hemianesthesia (Bottini et al., 2005); (vi) anosognosia (denial of disease; Cappa et al., 1987; Ramachandran, 1994); (vii) somatoparaphrenias (such as bizarre beliefs that one's hemiplegic limb belongs to someone else; Rode et al., 1992); (viii) mood (see next section); and (ix) phantom limb perception, phantom limb pain and other pain states (André, Martinet, Paysant, Beis, & Le Chapelain, 2001; Le Chapelain, Beis, Paysant, & André, 2001).

4.3. Further testing the IHS and meta-rivalry models

Despite some limitations with respect to the scientific study of visual consciousness, correlative approaches can nevertheless provide evidence in support of, or against, the IHS model of rivalry. Before considering such strategies, and the methodological issues they entail, we first discuss the challenge to our model from experiments with split-brain subjects. O'Shea and Corballis (2001, 2003, 2005) reported that a single hemisphere can perceive conventional rivalry, and coherence rivalry with DC stimuli, and suggested these findings pose a major problem for

⁵ This conception is not intended to address or take a stance on specific mechanistic models of visual consciousness (such as recurrent neural processing; Lamme, 2006; Tononi & Edelman, 1998), though clearly we are taking a stance on a specific mechanistic model of rivalry.

⁶ See Bonneuh, Pavlovskaya, Ring, and Soroker (2004), Chong and Blake (2006), Chong, Tadin, and Blake (2005), Hancock and Andrews (2007), Leopold and Logothetis (1999), Meng and Tong (2004), Mitchell, Stoner, and Reynolds (2004), Ooi and He (1999, 2005), Paffen, Alais, and Verstraten (2006), Sasaki and Gyoba (2002), van Dam and van Ee (2006), van Ee, Noest, Brascamp, and van den Berg (2006), van Ee, van Dam, and Brouwer (2005).

⁷ Our body of CVS findings relate more readily to notions of involuntary attention because voluntary attention mechanisms, initiated when observers are instructed to increase/decrease the duration of a particular percept or to speed up/slow down the rate of rivalry, do not feature in our experimental methodology. Such effects of voluntary attention have been shown to be limited and it is well-known that observers cannot voluntarily prevent perceptual alternations (e.g., Breese, 1899, 1909; Meng & Tong, 2004; van Ee et al., 2005).

the IHS model. However, their rejection of the model on this basis is premature for at least two reasons.

First, it is not clear whether non-callosal transfer of visual information from one hemisphere to the other may have confounded their experiments. In relation to this, it is emphasized that the site of an interhemispheric switch in rivalry is postulated to be subcortical rather than callosal (Miller et al., 2000; Pettigrew, 2001), with our prediction that conventional rivalry would survive callosotomy (Miller et al., 2000) made well in advance of their initial studies (O'Shea and Corballis, 2001, 2003). Furthermore, given that here we have argued for equating conventional rivalry with coherence rivalry, it is not surprising that O'Shea and Corballis (2005) subsequently demonstrated that coherence rivalry also survives callosotomy. Second, even if the presented visual information does indeed remain unihemispheric in their split-brain observers, extrapolation from the split-brain case to the callosally-intact case may not be reliable (Miller, 2001). In other words, the mechanism of rivalry in the split-brain may not be the same as that in the normal brain. Moreover, O'Shea and Corballis (2001, 2003, 2005) strongly embrace the notion of low-level, eye-based rivalry yet offer no convincing explanation for why rivalry predominance should be affected by unilateral hemisphere stimulation or disruption of high-level cortical regions. Our current findings with respect to half-field rivalry may support their low-level, eye-based preference, however those for coherence rivalry and our previous work with conventional rivalry, do not support their view.

In contrast to the work of O'Shea and Corballis, we have found support for the IHS model from the pathological domain. Pettigrew and Miller (1998) used their finding of slow binocular rivalry rate in bipolar disorder (manic depression; Miller et al., 2003), the IHS model of perceptual rivalry, and evidence for hemispheric asymmetries of mood and mood disorders, to propose a novel pathophysiological model of bipolar disorder. One aspect of their model was the explicit prediction that right-hemisphere activation (with left-ear CVS) would reduce the signs and symptoms of acute mania, by restoring to normal the left-over-right hemispheric activation asymmetry evident in mania (e.g., in anterior cingulate cortex; Blumberg et al., 2000). This specific prediction was remarkably confirmed by Dodson (2004). Although requiring replication in a larger sample, along with testing of the converse prediction (i.e., left-hemisphere activation with right-ear CVS will reduce the signs and symptoms of depression), this finding directly supports the pathophysiological model of bipolar disorder proposed by Pettigrew and Miller (1998), and indirectly supports the IHS model of perceptual rivalry on which it relies.

As mentioned above, to directly corroborate our CVS and TMS findings in support of the IHS model, correlations will need to be sought that show perception-dependent hemispheric asynchrony. This could occur via simultaneous bilateral single- or multi-unit electrophysiological recordings, via non-invasive electrophysiological

approaches (electroencephalography and event-related potentials), or via magnetoencephalography and functional magnetic resonance imaging studies (or combinations thereof). The brain-imaging data on rivalry have shown perception-dependent activation at both high and low levels of visual processing (Haynes, Deichmann, & Rees, 2005; Haynes & Rees, 2005; Lee & Blake, 2002; Polonsky, Blake, Braun, & Heeger, 2000; Tong & Engel, 2001; Tong, Nakayama, Vaughan, & Kanwisher, 1998; Williams, Morris, McGlone, Abbott, & Mattingley, 2004; Wunderlich, Schneider, & Kastner, 2005; see also Wilke, Logothetis, & Leopold, 2006) but no studies have specifically examined the IHS model. To adequately do so with brain-imaging techniques, we point out that data must be analysed separately for each individual and for each direction of perceptual switch. Furthermore, regions of interest should focus on high-level structures. This could include both the sites and sources of attentional selection (Miller, 2001; Posner & DiGirolamo, 2000; see also Grossmann & Dobbins, 2006), as well as areas activated by CVS (noting some overlap of these regions). Imaging studies should also take into account evidence for a right-lateralized network that may subservise the transitions during rivalry (Lumer et al., 1998).

Our suggestion that coherence rivalry and eye rivalry are mediated by discrete high- and low-level mechanisms, respectively, can similarly be assessed with these experimental methodologies by adding a low-level focus during half-field rivalry with DC stimuli and with other interocular-grouping stimuli. TMS studies with this approach may also be particularly revealing. Furthermore, psychophysical experiments, such as those measuring detection thresholds of test probes, could compare the nature of suppression with half-field percepts and coherent percepts during rivalry with DC stimuli (Miller, 2001), and correspondingly for other interocular-grouping stimuli and the rapid eye-swap protocol.⁸ In addition, further studies comparing the temporal properties of the high- and low-level processes can be performed (such as rivalry rate and strength differences between the two rivalry types; see Section 4.1).

Specifically addressing the meta-rivalry notion is a more complex issue. It could be argued that rivalry with DC stimuli, and with other interocular-grouping stimuli, merely involves the alternating success and failure of perceptual grouping mechanisms, rather than the existence of a between-level competitive process in addition to the high- and low-level competitive processes. However the perceptual predominance of high- versus low-level processes does vary with stimulus parameters (Section 4.1), reflecting a well-known feature of rivalry. It cannot be assumed though, that the characteristics of meta-rivalry will match those commonly associated with rivalry in all respects (given that it involves a four-percept multi-level

⁸ Investigations of our present findings could also consider the possibility mentioned earlier (but not explored), that half-field rivalry with DC stimuli is mediated by *high-level intrahemispheric* mechanisms.

phenomenon). Therefore it is not clear, for example, whether the temporal dynamics of meta-rivalry would entail stochastic independence of successive intervals and be well described by a gamma distribution (as typically shown for conventional rivalry; Blake, Fox, & McIntyre, 1971; Fox & Herrmann, 1967; Levelt, 1967; Logothetis et al., 1996; Murata, Matsui, Miyauchi, Kakita, & Yanagida, 2003).⁹

Finally, what can be said of the current data and the IHS and meta-rivalry models in the context of Blake and Logothetis' (2002) amalgam view? As we have stated throughout the discussion, the present CVS data demonstrate discrete neural mechanisms for coherence rivalry and eye rivalry during viewing of DC stimuli. Blake and Logothetis' (2002) amalgam view invokes a series of processes at different levels of the visual pathway. Our present findings are consistent with this conception however our findings also suggest an interpretation that differs from this amalgam view.

Consider Blake and colleagues' latest model (Tong, Meng, & Blake, 2006) that specifies a variety of feedforward, feedback and lateral excitatory and inhibitory connections between low-level eye-selective neurones and high-level stimulus-selective (pattern-selective) neurones. The authors proposed that these connections could account for a variety of phenomena associated with rivalry. The IHS model, on the other hand, suggests that rather than focussing on connections between either eye-selective or stimulus-selective neurones, it is the independent attentional selection mechanisms in each cerebral hemisphere, and a subsequent switching between relative hemispheric activation, that mediates the perceptual alternations of conventional rivalry and coherence rivalry. That said, the local interactions in Blake and colleagues' recent model may indeed be the mechanism of intrahemispheric half-field rivalry.

Blake and colleagues' model also includes postulated between-level interactions, but these were proposed to account for interocular grouping (among other functions) and thus the coherent perceptual periods during viewing of DC stimuli. Such interactions were not specifically postulated to account for the fact that coherence rivalry occurs for half the viewing time while eye rivalry occurs for the remaining half. Our present meta-rivalry model instead

focuses on this observation and postulates that the competition for visual consciousness, between eye rivalry and coherence rivalry, is itself a third rivalry mechanism between these low- and high-level processes. Thus our version of an amalgam view (cf. Blake & Logothetis, 2002) is a meta-rivalry model that entails a rivalry between processing levels under certain stimulus conditions. Our view further holds, again in contrast to Blake and Logothetis (2002), and especially in contrast to Lee and Blake (2004), that rivalry with conventional stimuli is mediated high in the visual pathway.

5. Conclusions

Several centuries since the first report of binocular rivalry, a detailed neural mechanism of the phenomenon has yet to be conclusively identified. Indeed, specific neurophysiological models are relatively uncommon. In a series of six separate experiments, each with different rivalry stimuli (including three previous studies, the present study, and two studies to be published), we have demonstrated that unilateral (left) hemisphere activation by CVS significantly changes rivalry predominance, thus supporting an IHS model of perceptual rivalry. There have been no alternative explanations proffered for our empirical CVS (and TMS) data, and despite its tangible and readily testable nature, there has only been a single attempt (in addition to our own) to falsify the model. We welcome further such attempts and have outlined methodological strategies to this end. The present study has provided evidence using CVS that discrete neural mechanisms mediate coherence rivalry and eye rivalry during viewing of DC stimuli. In addition, we have proposed the notion of meta-rivalry during viewing of DC stimuli and other interocular-grouping stimuli (along with the rapid eye-swap protocol) in which the separate high- and low-level competitive processes themselves rival for visual consciousness. Clearly, further experimental work is also required to verify or falsify these new proposals.

Acknowledgments

We thank Randolph Blake for comments on the original submission. We also thank the anonymous reviewers and all experimental subjects. The authors declare that they have no conflicts of interest.

References

- Alais, D., Lorenceau, J., Arrighi, R., & Cass, J. (2006). Contour interactions between pairs of Gabors engaged in binocular rivalry reveal a map of the association field. *Vision Research*, *46*(8–9), 1473–1487.
- Alais, D., & Melcher, D. (2007). Strength and coherence of binocular rivalry depends on shared stimulus complexity. *Vision Research*, *47*(2), 269–279.
- Alais, D., O'Shea, R. P., Mesana-Alais, C., & Wilson, I. G. (2000). On binocular alternation. *Perception*, *29*(12), 1437–1445.

⁹ In fact, the meta-rivalry notion can be assessed using DC stimuli and CVS in the following way. In addition to unilateral high-level brain activation (see Section 1), CVS has also been shown to induce deactivation in V1 (Bottini et al., 2001; Wenzel et al., 1996). However, such deactivation was bilateral and therefore cannot offer grounds for an alternative explanation for our findings of significant CVS-induced predominance shifts. Nevertheless, bilateral deactivation at a low level may bear upon the meta-rivalry notion. Thus it could be hypothesized that CVS will decrease the relative time spent perceiving half-field percepts versus coherent percepts due to deactivation of low-level processing mechanisms. Such an analysis could not be performed with the protocol used in the present study. It would instead require a four-choice response protocol or that employed by Ngo et al. (2000).

- Alexander, L. T. (1951). The influence of figure-ground relationships in binocular rivalry. *Journal of Experimental Psychology*, 41(5), 376–381.
- Alexander, L. T., & Bricker, P. (1952). Figure-ground contrast and binocular rivalry. *Journal of Experimental Psychology*, 44(6), 452–454.
- Alvarez, G. A., & Cavanagh, P. (2005). Independent resources for attentional tracking in the left and right visual hemifields. *Psychological Science*, 16(8), 637–643.
- André, J.-M., Martinet, N., Paysant, J., Beis, J.-M., & Le Chapelain, L. (2001). Temporary phantom limbs evoked by vestibular caloric stimulation in amputees. *Neuropsychiatry, Neuropsychology, and Behavioral Neurology*, 14(3), 190–196.
- Arguin, M., Lassonde, M., Quattrini, A., Del Pesce, M., Foschi, N., & Papo, I. (2000). Divided visuo-spatial attention systems with total and anterior callosotomy. *Neuropsychologia*, 38(3), 283–291.
- Bächtold, D., Baumann, T., Sándor, P. S., Kritos, M., Regard, M., & Brugger, P. (2001). Spatial- and verbal-memory improvement by cold-water caloric stimulation in healthy subjects. *Experimental Brain Research*, 136(1), 128–132.
- Bárány, R. (1906). Untersuchungen über den vom Vestibularapparat des Ohres reflektorisch ausgelösten rhythmischen Nystagmus und seine Begleiterscheinungen. *Monatsschrift für Ohrenheilkunde*, 40, 193–297.
- Beis, J.-M., Keller, C., Morin, N., Bartolomeo, P., Bernati, T., Chokron, S., et al., French Collaborative Study Group on Assessment of Unilateral Neglect (GEREN/GRECO) (2004). Right spatial neglect after left hemisphere stroke: Qualitative and quantitative study. *Neurology*, 63(9), 1600–1605.
- Blake, R. (1989). A neural theory of binocular rivalry. *Psychological Review*, 96(1), 145–167.
- Blake, R. (2001). A primer on binocular rivalry, including current controversies. *Brain and Mind*, 2(1), 5–38.
- Blake, R., Fox, R., & McIntyre, C. (1971). Stochastic properties of stabilized-image binocular rivalry alternations. *Journal of Experimental Psychology*, 88(3), 327–332.
- Blake, R., & Logothetis, N. K. (2002). Visual competition. *Nature Reviews Neuroscience*, 3(1), 13–21.
- Blake, R., Yu, K., Lokey, M., & Norman, H. (1998). Binocular rivalry and motion perception. *Journal of Cognitive Neuroscience*, 10(1), 46–60.
- Blumberg, H. P., Stern, E., Martinez, D., Ricketts, S., de Asis, J., White, T., et al. (2000). Increased anterior cingulate and caudate activity in bipolar mania. *Biological Psychiatry*, 48(11), 1045–1052.
- Bogen, J., Berker, E., Van Lancker, D., Sudia, S., Lipstad, B., Sadun, A., et al. (1998). Left hemisectomy: Vision, olfaction and mentation 45 years later. Proceedings of the 28th Annual Meeting of the Society for Neuroscience, *Society for Neuroscience Abstracts*, 24, 173 (Abstract).
- Bonneh, Y. S., Pavlovskaya, M., Ring, H., & Soroker, N. (2004). Abnormal binocular rivalry in unilateral neglect: Evidence for a non-spatial mechanism of extinction. *Neuroreport*, 15(3), 473–477.
- Bonneh, Y., Sagi, D., & Karni, A. (2001). A transition between eye and object rivalry determined by stimulus coherence. *Vision Research*, 41(8), 981–989.
- Bottini, G., Karnath, H.-O., Vallar, G., Sterzi, R., Frith, C. D., Frackowiak, R. S. J., et al. (2001). Cerebral representations for egocentric space. Functional-anatomical evidence from caloric vestibular stimulation and neck vibration. *Brain*, 124(6), 1182–1196.
- Bottini, G., Paulesu, E., Gandola, M., Loffredo, S., Scarpa, P., Sterzi, R., et al. (2005). Left caloric vestibular stimulation ameliorates right hemianesthesia. *Neurology*, 65(8), 1278–1283.
- Bottini, G., Sterzi, R., Paulesu, E., Vallar, G., Cappa, S. F., Erminio, F., et al. (1994). Identification of the central vestibular projections in man: A positron emission tomography activation study. *Experimental Brain Research*, 99(1), 164–169.
- Botvinick, M. M., Cohen, J. D., & Carter, C. S. (2004). Conflict monitoring and anterior cingulate cortex: An update. *Trends in Cognitive Sciences*, 8(12), 539–546.
- Bowen, A., McKenna, K., & Tallis, R. C. (1999). Reasons for variability in the reported rate of occurrence of unilateral spatial neglect after stroke. *Stroke*, 30(6), 1196–1202.
- Breese, B. B. (1899). On inhibition. *Psychological Monographs*, 3(1), 1–65.
- Breese, B. B. (1909). Can binocular rivalry be suppressed by practise? *Journal of Philosophy, Psychology and Scientific Methods*, 6(25), 686–687.
- Cappa, S., Sterzi, R., Vallar, G., & Bisiach, E. (1987). Remission of hemineglect and anosognosia during vestibular stimulation. *Neuropsychologia*, 25(5), 775–782.
- Chong, S. C., & Blake, R. (2006). Exogenous attention and endogenous attention influence initial dominance in binocular rivalry. *Vision Research*, 46(11), 1794–1803.
- Chong, S. C., Tadin, D., & Blake, R. (2005). Endogenous attention prolongs dominance durations in binocular rivalry. *Journal of Vision*, 5(11), 1004–1012, <http://journalofvision.org/5/11/6/>, doi:10.1167/5.11.6.
- Coats, A. C., & Smith, S. Y. (1967). Body position and the intensity of caloric nystagmus. *Acta Otolaryngologica (Stockholm)*, 63(6), 515–532.
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, 3(3), 201–215.
- de Weert, C. M. M., Snoeren, P. R., & Koning, A. (2005). Interactions between binocular rivalry and Gestalt formation. *Vision Research*, 45(19), 2571–2579.
- Díaz-Caneja, E. (1928). Sur l'alternance binoculaire. *Annales D'Oculistique*, 165, 721–731.
- Dodson, M. J. (2004). Vestibular stimulation in mania: A case report. *Journal of Neurology, Neurosurgery and Psychiatry*, 75(1), 168–169.
- Fahle, M. (1982a). Cooperation between different spatial frequencies in binocular rivalry. *Biological Cybernetics*, 44(1), 27–29.
- Fahle, M. (1982b). Binocular rivalry: Suppression depends on orientation and spatial frequency. *Vision Research*, 22(7), 787–800.
- Fahle, M. (1983). Non-fusible stimuli and the role of binocular inhibition in normal and pathologic vision, especially strabismus. *Documenta Ophthalmologica*, 55(4), 323–340.
- Fife, T. D., Tusa, R. J., Furman, J. M., Zee, D. S., Frohman, E., Baloh, R. W., et al. (2000). Assessment: Vestibular testing techniques in adults and children. Report of the Therapeutics and Technology Assessment Subcommittee of the American Academy of Neurology. *Neurology*, 55(10), 1431–1441.
- Fox, R., & Herrmann, J. (1967). Stochastic properties of binocular rivalry alternations. *Perception and Psychophysics*, 2(9), 432–436.
- Freeman, A. W. (2005). Multistage model for binocular rivalry. *Journal of Neurophysiology*, 94(6), 4412–4420.
- Gross, C. G., Rodman, H. R., Gochin, P. M., & Colombo, M. W. (1993). Inferior temporal cortex as a pattern recognition device. In E. B. Baum (Ed.), *Computational learning and cognition: Proceedings of the third NEC research symposium* (pp. 44–73). Philadelphia, PA: SIAM.
- Grossmann, J. K., & Dobbins, A. C. (2006). Competition in bistable vision is attribute-specific. *Vision Research*, 46(3), 285–292.
- Hancock, S., & Andrews, T. J. (2007). The role of voluntary and involuntary attention in selecting perceptual dominance during binocular rivalry. *Perception*, 36(2), 288–298.
- Haynes, J.-D., Deichmann, R., & Rees, G. (2005). Eye-specific effects of binocular rivalry in the human lateral geniculate nucleus. *Nature*, 438(7067), 496–499.
- Haynes, J.-D., & Rees, G. (2005). Predicting the stream of consciousness from activity in human visual cortex. *Current Biology*, 15(14), 1301–1307.
- Helmholtz, H. von. (1867/1962). *Handbuch der physiologischen Optik* (Leipzig: Voss). *Treatise on physiological optics* Vol. III, J. P. C. Southall (New York: Dover, 1962), trans 3rd German edition (Hamburg: Voss, 1910).
- Hering, E. (1879/1942). Der Raumsinn und die Bewegungen des Auges, In L. Hermann (Ed.), *Handbuch der Physiologie*, III (1879), pp. 343–601,

- Leipzig: Vogel). *Spatial sense and movements of the eye*, C. A. Radde, trans (Baltimore, MD: American Academy of Optometry, 1942).
- Indovina, I., Maffei, V., Bosco, G., Zago, M., Macaluso, E., & Lacquaniti, F. (2005). Representation of visual gravitational motion in the human vestibular cortex. *Science*, *308*(5720), 416–419.
- James, W. (1890). *The principles of psychology*. London: Macmillan.
- Johannsen, L., Akermann, H., & Karnath, H.-O. (2003). Lasting amelioration of spatial neglect by treatment with neck muscle vibration even without concurrent training. *Journal of Rehabilitation Medicine*, *35*(6), 249–253.
- Karnath, H.-O., Berger, M. F., Küker, W., & Rorden, C. (2004). The anatomy of spatial neglect based on voxelwise statistical analysis: A study of 140 patients. *Cerebral Cortex*, *14*(10), 1164–1172.
- Knapen, T., Paffen, C., Kanai, R., & van Ee, R. (2007). Stimulus flicker alters interocular grouping during binocular rivalry. *Vision Research*, *47*(1), 1–7.
- Koch, C., & Tsuchiya, N. (2007). Attention and consciousness: Two distinct brain processes. *Trends in Cognitive Sciences*, *11*(1), 16–22.
- Kovács, I., Papathomas, T. V., Yang, M., & Feher, A. (1996). When the brain changes its mind: Interocular grouping during binocular rivalry. *Proceedings of the National Academy of Sciences of the United States of America*, *93*(26), 15508–15511.
- Kraft, A., Müller, N. G., Hagendorf, H., Schira, M. M., Dick, S., Fendrich, R. M., et al. (2005). Interactions between task difficulty and hemispheric distribution of attended locations: Implications for the splitting attention debate. *Cognitive Brain Research*, *24*(1), 19–32.
- Lack, L. (1978). *Selective attention and the control of binocular rivalry*. Mouton: The Hague.
- Lamme, V. A. F. (2006). Towards a true neural stance on consciousness. *Trends in Cognitive Sciences*, *10*(11), 494–501.
- Lavidor, M., & Walsh, V. (2004). The nature of foveal representation. *Nature Reviews Neuroscience*, *5*(9), 729–735.
- Le Chapelain, L., Beis, J.-M., Paysant, J., & André, J.-M. (2001). Vestibular caloric stimulation evokes phantom limb illusions in patients with paraplegia. *Spinal Cord*, *39*(2), 85–87.
- Lee, S.-H., & Blake, R. (1999). Rival ideas about binocular rivalry. *Vision Research*, *39*(8), 1447–1454.
- Lee, S.-H., & Blake, R. (2002). V1 activity is reduced during binocular rivalry. *Journal of Vision*, *2*(9), 618–626, <http://journalofvision.org/2/9/4/>, doi:10.1167/2.9.4.
- Lee, S.-H., & Blake, R. (2004). A fresh look at interocular grouping during binocular rivalry. *Vision Research*, *44*(10), 983–991.
- Leff, A. (2004). A historical review of the representation of the visual field in primary visual cortex with special reference to the neural mechanisms underlying macular sparing. *Brain and Language*, *88*(3), 268–278.
- Leibovitch, F. S., Black, S. E., Caldwell, C. B., Ebert, P. L., Ehrlich, L. E., & Szalai, J. P. (1998). Brain–behavior correlations in hemispatial neglect using CT and SPECT: The Sunnybrook Stroke Study. *Neurology*, *50*(4), 901–908.
- Leibovitch, F. S., Black, S. E., Caldwell, C. B., McIntosh, A. R., Ehrlich, L. E., & Szalai, J. P. (1999). Brain SPECT imaging and left hemispatial neglect covaried using partial least squares: The Sunnybrook Stroke Study. *Human Brain Mapping*, *7*(4), 244–253.
- Leopold, D. A., & Logothetis, N. K. (1996). Activity changes in early visual cortex reflect monkeys' percepts during binocular rivalry. *Nature*, *379*(6565), 549–553.
- Leopold, D. A., & Logothetis, N. K. (1999). Multistable phenomena: Changing views in perception. *Trends in Cognitive Sciences*, *3*(7), 254–264.
- Levelt, W. J. M. (1967). Note on the distribution of dominance times in binocular rivalry. *British Journal of Psychology*, *58*(1–2), 143–145.
- Logothetis, N. K. (1998). Single units and conscious vision. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *353*(1377), 1801–1818.
- Logothetis, N. K., Leopold, D. A., & Sheinberg, D. L. (1996). What is rivalling during binocular rivalry? *Nature*, *380*(6575), 621–624.
- Luck, S. J., Hillyard, S. A., Mangun, G. R., & Gazzaniga, M. S. (1989). Independent hemispheric attentional systems mediate visual search in split-brain patients. *Nature*, *342*(6249), 543–545.
- Lumer, E. D., Friston, K. J., & Rees, G. (1998). Neural correlates of perceptual rivalry in the human brain. *Science*, *280*(5371), 1930–1934.
- McDougall, W. (1903). III.—The physiological factors of the attention-process (III.). *Mind*, *12*(48), 473–488.
- McDougall, W. (1906). III.—Physiological factors of the attention-process (IV.). *Mind*, *15*(59), 329–359.
- Meng, M., & Tong, F. (2004). Can attention selectively bias bistable perception? Differences between binocular rivalry and ambiguous figures. *Journal of Vision*, *4*(7), 539–551, <http://journalofvision.org/4/7/2/>, doi:10.1167/4.7.2.
- Miller, S. M. (2001). Binocular rivalry and the cerebral hemispheres: With a note on the correlates and constitution of visual consciousness. *Brain and Mind*, *2*(1), 119–149.
- Miller, S. M., Gynther, B. D., Heslop, K. R., Liu, G. B., Mitchell, P. B., Ngo, T. T., et al. (2003). Slow binocular rivalry in bipolar disorder. *Psychological Medicine*, *33*(4), 683–692.
- Miller, S. M., Liu, G. B., Ngo, T. T., Hooper, G., Riek, S., Carson, R. G., et al. (2000). Interhemispheric switching mediates perceptual rivalry. *Current Biology*, *10*(7), 383–392.
- Miller, S. M. (2007). On the correlation/constitution distinction problem (and other hard problems) in the scientific study of consciousness. *Acta Neuropsychiatrica*, *19*(3), 159–176.
- Miller, S. M., & Ngo, T. T. (2007). Studies of caloric vestibular stimulation: Implications for the cognitive neurosciences, the clinical neurosciences and neurophilosophy. *Acta Neuropsychiatrica*, *19*(3), 183–203.
- Mitchell, J. F., Stoner, G. R., & Reynolds, J. H. (2004). Object-based attention determines dominance in binocular rivalry. *Nature*, *429*(6990), 410–413.
- Murata, T., Matsui, N., Miyauchi, S., Kakita, Y., & Yanagida, T. (2003). Discrete stochastic process underlying perceptual rivalry. *Neuroreport*, *14*(10), 1347–1352.
- Ngo, T. T., Miller, S. M., Liu, G. B., & Pettigrew, J. D. (2000). Binocular rivalry and perceptual coherence. *Current Biology*, *10*(4), R134–R136.
- Norman, H. F., Norman, J. F., & Bilotta, J. (2000). The temporal course of suppression during binocular rivalry. *Perception*, *29*(7), 831–841.
- Ooi, T. L., & He, Z. J. (1999). Binocular rivalry and visual awareness: The role of attention. *Perception*, *28*(5), 551–574.
- Ooi, T. L., & He, Z. J. (2003). A distributed interocular processing of binocular rivalry: Psychophysical evidence. *Perception*, *32*(2), 155–166.
- Ooi, T. L., & He, Z. J. (2005). Surface representation and attention modulation mechanisms in binocular rivalry. In D. Alais & R. Blake (Eds.), *Binocular rivalry* (pp. 117–135). Cambridge, MA: MIT Press.
- O'Shea, R. P., & Corballis, P. M. (2001). Binocular rivalry between complex stimuli in split-brain observers. *Brain and Mind*, *2*(1), 151–160.
- O'Shea, R. P., & Corballis, P. M. (2003). Binocular rivalry in split-brain observers. *Journal of Vision*, *3*(10), 610–615, <http://journalofvision.org/3/10/3/>, doi:10.1167/3.10.3.
- O'Shea, R. P., & Corballis, P. M. (2005). Visual grouping on binocular rivalry in a split-brain observer. *Vision Research*, *45*(2), 247–261.
- Paffen, C. L. E., Alais, D., & Verstraten, F. A. J. (2006). Attention speeds binocular rivalry. *Psychological Science*, *17*(9), 752–756.
- Papathomas, T. V., Kovács, I., & Conway, T. (2005). Interocular grouping in binocular rivalry: Basic attributes and combinations. In D. Alais & R. Blake (Eds.), *Binocular rivalry* (pp. 155–168). Cambridge, MA: MIT Press.
- Papathomas, T. V., Kovács, I., Feher, A., & Julesz, B. (1999). Visual dilemmas: Competition between eyes and between percepts in binocular rivalry. In E. Lepore & Z. Pylyshyn (Eds.), *What is cognitive science?* (pp. 263–294). Malden, MA: Blackwell Publishing.
- Pearson, J., & Clifford, C. W. G. (2005a). Suppressed patterns alter vision during binocular rivalry. *Current Biology*, *15*(23), 2142–2148.
- Pearson, J., & Clifford, C. W. G. (2005b). When your brain decides what you see: Grouping across monocular, binocular, and stimulus rivalry. *Psychological Science*, *16*(7), 516–519.

- Pettigrew, J. D. (2001). Searching for the switch: Neural bases for perceptual rivalry alternations. *Brain and Mind*, 2(1), 85–118.
- Pettigrew, J. D., Collin, S. P., & Ott, M. (1999). Convergence of highly-specialised behaviour, eye movements and visual optics in the sandlance (Teleostei) and the chameleon (Reptilia). *Current Biology*, 9(8), 421–424.
- Pettigrew, J. D., & Miller, S. M. (1998). A ‘sticky’ interhemispheric switch in bipolar disorder? *Proceedings of the Royal Society of London Series B: Biological Sciences*, 265(1411), 2141–2148.
- Polonsky, A., Blake, R., Braun, J., & Heeger, D. J. (2000). Neuronal activity in human primary visual cortex correlates with perception during binocular rivalry. *Nature Neuroscience*, 3(11), 1153–1159.
- Posner, M. I., & DiGirolamo, G. J. (2000). Attention in cognitive neuroscience: An overview. In M. S. Gazzaniga (Ed.), *The new cognitive neurosciences* (pp. 623–631). Cambridge, MA: MIT Press.
- Posner, M. I., & Petersen, S. E. (1990). The attention system of the human brain. *Annual Review of Neuroscience*, 13, 25–42.
- Ramachandran, V. S. (1994). Phantom limbs, neglect syndromes and Freudian psychology. *International Review of Neurobiology*, 37, 291–333.
- Rode, G., Charles, N., Perenin, M.-T., Vighetto, A., Trillet, M., & Aimard, G. (1992). Partial remission of hemiplegia and somatoparaphrenia through vestibular stimulation in a case of unilateral neglect. *Cortex*, 28(2), 203–208.
- Rode, G., Perenin, M.-T., Honoré, J., & Boisson, D. (1998). Improvement of the motor deficit of neglect patients through vestibular stimulation: Evidence for a motor neglect component. *Cortex*, 34(2), 253–261.
- Rossetti, Y., & Rode, G. (2002). Reducing spatial neglect by visual and other sensory manipulations: Noncognitive (physiological) routes to the rehabilitation of a cognitive disorder. In H.-O. Karnath, D. Milner, & G. Vallarm (Eds.), *The cognitive and neural bases of spatial neglect* (pp. 375–396). Oxford: Oxford University Press.
- Sasaki, H., & Gyoba, J. (2002). Selective attention to stimulus features modulates interocular suppression. *Perception*, 31(4), 409–419.
- Schindler, I., Kerkhoff, G., Karnath, H.-O., Keller, I., & Goldenberg, G. (2002). Neck muscle vibration induces lasting recovery in spatial neglect. *Journal of Neurology, Neurosurgery and Psychiatry*, 73(4), 412–419.
- Schmal, F., Lübken, B., Weiberg, K., & Stoll, W. (2005). The minimal ice water caloric test compared with established vestibular caloric test procedures. *Journal of Vestibular Research*, 15(4), 215–224.
- Schor, C. M. (1977). Visual stimuli for strabismic suppression. *Perception*, 6(5), 583–593.
- Sengpiel, F. (1997). Binocular rivalry: Ambiguities resolved. *Current Biology*, 7(7), R447–R450.
- Sheinberg, D. L., & Logothetis, N. K. (1997). The role of temporal cortical areas in perceptual organization. *Proceedings of the National Academy of Sciences of the United States of America*, 94(7), 3408–3413.
- Sherrington, C. S. (1906). *Integrative action of the nervous system*. New Haven: Yale University Press.
- Silberpfennig, J. (1941). Contributions to the problem of eye movements. III. Disturbances of ocular movements with pseudo-hemianopsia in frontal lobe tumors. *Confinia Neurologica*, 4(1–2), 1–13.
- Silver, M. A., & Logothetis, N. K. (2007). Temporal frequency and contrast tagging bias the type of competition in interocular switch rivalry. *Vision Research*, 47(4), 532–543.
- Stone, J. (1966). The naso-temporal division of the cat’s retina. *Journal of Comparative Neurology*, 126(4), 585–600.
- Stone, J., Leicester, J., & Sherman, S. M. (1973). The naso-temporal division of the monkey’s retina. *Journal of Comparative Neurology*, 150(3), 333–348.
- Suzuki, S., & Grabowecy, M. (2002). Evidence for perceptual “trapping” and adaptation in multistable binocular rivalry. *Neuron*, 36(1), 143–157.
- Tong, F., & Engel, S. (2001). Interocular rivalry revealed in the human cortical blind-spot representation. *Nature*, 411(6834), 195–199.
- Tong, F., Meng, M., & Blake, R. (2006). Neural bases of binocular rivalry. *Trends in Cognitive Sciences*, 10(11), 502–511.
- Tong, F., Nakayama, K., Vaughan, J. T., & Kanwisher, N. (1998). Binocular rivalry and visual awareness in human extrastriate cortex. *Neuron*, 21(4), 753–759.
- Tononi, G., & Edelman, G. M. (1998). Consciousness and complexity. *Science*, 282(5395), 1846–1851.
- Towne, J. (1863). The stereoscope, and stereoscopic results—Section III. *Guy’s Hospital Reports*, 9, 102–125.
- Towne, J. (1864). The stereoscope, and stereoscopic results—Section V. *Guy’s Hospital Reports*, 10, 125–141.
- Vallar, G., Guariglia, C., & Rusconi, M. L. (1997). Modulation of the neglect syndrome by sensory stimulation. In P. Their & H.-O. Karnath (Eds.), *Parietal lobe contributions to orientation in 3D Space* (pp. 555–578). Berlin: Springer-Verlag.
- van Dam, L. C., & van Ee, R. (2006). The role of saccades in exerting voluntary control in perceptual and binocular rivalry. *Vision Research*, 46(6–7), 787–799.
- van Ee, R., Noest, A. J., Brascamp, J. W., & van den Berg, A. V. (2006). Attentional control over either of the two competing percepts of ambiguous stimuli revealed by a two-parameter analysis: Means do not make the difference. *Vision Research*, 46(19), 3129–3141.
- van Ee, R., van Dam, L. C., & Brouwer, G. J. (2005). Voluntary control and the dynamics of perceptual bi-stability. *Vision Research*, 45(1), 41–55.
- Vitte, E., Derosier, C., Caritu, Y., Berthoz, A., Hasboun, D., & Soulié, S. (1996). Activation of the hippocampal formation by vestibular stimulation: A functional magnetic resonance imaging study. *Experimental Brain Research*, 112(3), 523–526.
- Wade, N. J., de Weert, C. M. M., & Swanson, M. T. (1984). Binocular rivalry with moving patterns. *Perception and Psychophysics*, 35(2), 111–122.
- Wade, N. J., Ono, H., & Mapp, A. P. (2006). The lost direction in binocular vision: The neglected signs posted by Wells, Towne, and LeConte. *Journal of the History of Behavioral Sciences*, 42(1), 61–86.
- Wales, R., & Fox, R. (1970). Increment detection thresholds during binocular rivalry suppression. *Perception and Psychophysics*, 8(2), 90–94.
- Walker, P. (1978). Binocular rivalry: Central or peripheral selective processes? *Psychological Bulletin*, 85(2), 376–389.
- Wenzel, R., Bartenstein, P., Dieterich, M., Danek, A., Weindl, A., Minoshima, S., et al. (1996). Deactivation of human visual cortex during involuntary ocular oscillations. A PET activation study. *Brain*, 119(1), 101–110.
- Whittle, P. (1965). Binocular rivalry and the contrast at contours. *Quarterly Journal of Experimental Psychology*, 17(3), 217–226.
- Williams, M. A., Morris, A. P., McGlone, F., Abbott, D. F., & Mattingley, J. B. (2004). Amygdala responses to fearful and happy facial expressions under conditions of binocular suppression. *Journal of Neuroscience*, 24(12), 2898–2904.
- Wilke, M., Logothetis, N. K., & Leopold, D. A. (2006). Local field potential reflects perceptual suppression in monkey visual cortex. *Proceedings of the National Academy of Sciences of the United States of America*, 103(46), 17507–17512.
- Wilson, H. R. (2003). Computational evidence for a rivalry hierarchy in vision. *Proceedings of the National Academy of Sciences of the United States of America*, 100(24), 14499–144503.
- Wolfe, J. (1996). Resolving perceptual ambiguity. *Nature*, 380(6575), 587–588.
- Wong, E. M., & Freeman, A. W. (1999). Colour but not form patterns combine between the eyes. *Australian and New Zealand Journal of Ophthalmology*, 27(3–4), 275–277.
- Wunderlich, K., Schneider, K. A., & Kastner, S. (2005). Neural correlates of binocular rivalry in the human lateral geniculate nucleus. *Nature Neuroscience*, 8(11), 1595–1602.