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This is a contribution from *The Constitution of Visual Consciousness. Lessons from Binocular Rivalry*.

Edited by Steven M. Miller.

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The future of binocular rivalry research

Reaching through a window on consciousness

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Binocular rivalry is often considered an experimental window on the neural processes of consciousness. We propose three distinct approaches to exploit this window. First, one may look through the window, using binocular rivalry as a passive tool to dissociate unaltered sensory input from wavering perceptual output. Second, the mechanisms underlying binocular rivalry may yield detailed knowledge of the neuronal underpinnings of binocular vision and increase the value of rivalry as a tool to study consciousness. Finally, smart experimental manipulations allow experimenters to ‘reach through the window’ and interact with mechanisms of conscious visual perception. Within this distinction, we discuss the major open questions in binocular rivalry research and examine how recent technological developments may be incorporated in future studies.

1. Introduction

The integration of visual information from two eyes leads to perceptual advantages such as stereopsis and enhanced contrast sensitivity. Binocular integration is however not always beneficial and does not occur when the two retinal patterns are substantially different. In that case, rather than perceiving a mixture of the two patterns, observers typically report a stream of perceptual fluctuations in which each of the two patterns is perceived exclusively dominant for a few seconds, after which it fades from awareness and the other pattern becomes dominant. This phenomenon of perceptual fluctuations is called binocular rivalry because it resembles an ongoing competition for dominance between the visual patterns in the two eyes and their corresponding neuronal representations (Blake & Logothetis, 2002). In this chapter

* CK is supported by the NCU Focus and Mass program of Utrecht University. RvE is supported by a grant from the Flemish Methusalem program (METH/08/02). RvW and RvE are jointly supported by a Utrecht University High Potential grant.

we briefly summarize how scientific interest in the binocular rivalry phenomenon has developed and propose how recent technological advances and novel experimental results create opportunities for the future of binocular rivalry research.

1.1 A window on consciousness

The fluctuations in the content of perceptual awareness that arise during binocular rivalry despite the constant visual input into the eyes has advocated the use of this paradigm in studying the neuronal basis of conscious visual perception (Crick & Koch, 1990; Leopold & Logothetis, 1996). Visual processing starts as soon as photons hit the retina, but somewhere along the neuronal processing chain from stimulus to percept, the brain must ‘decide’ what the content of perceptual awareness is going to be. While this generic notion holds for all visual input, the mechanisms responsible for these perceptual choices are especially revealing when the same sensory input can evoke distinctly different conscious percepts. It is this characteristic of binocular rivalry that has earned it the qualification of ‘a window on consciousness’ (Logothetis, 1999). The realization that binocular rivalry can be used as a tool to study the neural correlates of consciousness is, however, a relatively recent development in the history of binocular rivalry research. Since the first systematic description of binocular rivalry appeared in the literature (Wheatstone, 1838), the paradigm has been used to investigate many different aspects of perceptual processing (Alais, 2012).

1.2 A brief history of binocular rivalry research

Before we unfold our ideas for future directions in binocular rivalry research, we will briefly summarize the history of binocular rivalry research. Because far more comprehensive overviews of the (early) history of binocular rivalry research can be found in this volume (see chapter by Wade & Ngo) and elsewhere (Alais, 2012), our summary will merely provide a coarse description of how the questions typically addressed with binocular rivalry experiments have evolved over the years. This coarse timeline will later function as the basis of our proposal to divide the field of binocular rivalry research into three distinct subfields, each with their own specific research aims and most suitable experimental approaches.

The invention of the mirror stereoscope by Charles Wheatstone in the 19th century marks the first significant boost in broad scientific interest for binocular rivalry (Wheatstone, 1838). In the decades that followed the introduction of the stereoscope, binocular rivalry was predominantly studied as a peculiar perceptual phenomenon. The main questions that were addressed in binocular rivalry

research in those days concerned the reason why binocular rivalry occurred in the first place and the phenomenon's relation to binocular fusion and stereoscopic depth perception (for a recent review, see Blake & Wilson, 2011). Some of the early observations describe aspects of binocular rivalry that are still present in contemporary binocular rivalry research, including the occurrence of piecemeal rivalry (Meenes, 1930; Wheatstone, 1838), the spatiotemporal profile of perceptual alternations (Wheatstone, 1838), the correlation between stimulus strength and predominance (Breese, 1899), and the extent to which perception is under an observer's voluntary control (Breese, 1899; Helmholtz, 1867; Wheatstone, 1838). During a revival of interest in binocular rivalry in the second half of the 20th century, researchers started using the phenomenon as a tool to study other psychological phenomena such as differences between the sexes (Kaufer & Riess, 1960), cultural differences between observers (Bagby, 1957; LoSciuto & Hartley, 1963), or personality aspects (Bokander & Radeborg, 1966; Kohn, 1960). In the meantime, the systematic investigation of binocular rivalry continued. Notable contributions in this area are the work of Fox on the suppression aspect of binocular rivalry (Fox, 1963), Levelt's studies on the relation between stimulus strength and predominance (Levelt, 1965), and Whittle's experiments on the effects of perceptual grouping (Whittle, 1963). Heavily influenced by Hubel and Wiesel's seminal series of publications on the anatomy and physiology of the visual cortex (for a review, see Hubel & Wiesel, 1998), this branch of research aimed to incorporate the newly discovered concepts of ocular dominance and binocular combination in their theories of binocular rivalry and stereopsis (e.g., Blake, 1989).

Research in the late nineties of the previous century challenged the early idea of binocular rivalry as a pure competition between eyes. Paradigms in which binocular rivalry images were rapidly switched between the eyes demonstrated that an additional level of pattern rivalry must exist at cortical processing stages where eye-of-origin information is lost (Logothetis, Leopold, & Sheinberg, 1996). While the debate as to what is actually rivaling in binocular rivalry and where in the brain the associated perceptual conflicts are resolved is still very much alive (see Blake & Wilson, 2011; Watanabe et al., 2011), there is now a broadly accepted consensus that binocular rivalry can involve different levels of processing depending on the precise stimulus characteristics (Blake & Logothetis, 2002; Ooi & He, 2003; Tong, Meng, & Blake 2006; van Boxtel & Koch, 2012).

The application of binocular rivalry as a tool to study other aspects of psychology took a noteworthy turn near the end of the 20th century when it was proposed as a potent method to study the neurobiological underpinnings of consciousness in general and visual awareness in particular (Crick & Koch, 1998; Koch & Braun, 1996). Interestingly, the publication of this proposition roughly coincided with the introduction of functional magnetic resonance imaging (fMRI) in the cognitive

neurosciences (Belliveau et al., 1991). With fMRI, researchers could now measure (a derivative of) neuronal activity in an entire brain, non-invasively and at relatively high spatial resolution. An overview of imaging studies on binocular rivalry is available elsewhere in this volume (see chapter by Sterzer, this volume), but it is clear that ever since its first appearance on the scene, functional neuroimaging has played a prominent role in binocular rivalry research, especially when researchers aimed to find neural concomitants of visual awareness.

Now, at the start of the 21st century, binocular rivalry has found its way into the clinic, demonstrating slower switching rates in patients with bipolar disorder (Krug, Brunskill, Scarna, Goodwin, & Parker, 2008; Miller et al., 2003; see chapter by Ngo, Barsdell, Law, & Miller, this volume). The future of binocular rivalry research is bright, with an ever-expanding number of studies (Baker, 2010) and numerous technological advances in the last few years that have opened up many potentially interesting pathways for future studies.

2. The future of binocular rivalry research

It is always difficult to predict the future of a research field in a context that evolves as rapidly as the neurosciences. Some technological developments, however, seem particularly suitable for application in binocular rivalry research. In the following sections we will discuss several of these advances and relate them to specific types of binocular rivalry research. Suggestions for future directions range from classic topics in binocular rivalry to more novel questions inspired by recent findings from both binocular rivalry and other fields of neuroscience.

2.1 A challenge on three fronts

The broad range of possibilities for future binocular rivalry research asks for a sound research strategy. In keeping with the metaphor of binocular rivalry as an experimental window on consciousness, we propose three distinct branches of binocular rivalry experiments (Figure 1). First, the most obvious function of a window is that it allows an observer to see what is happening on the other side of a wall. Because binocular rivalry allows the experimenter to ‘observe’ the neuronal mechanisms involved in converting sensory input into perceptual output, this is what earned the paradigm its qualification of a ‘window on consciousness’.

A second branch of binocular rivalry research involves the rivalry mechanism itself. To return to the window metaphor, the functionality of a window may be most efficiently exploited if the operator knows how the window works. While the

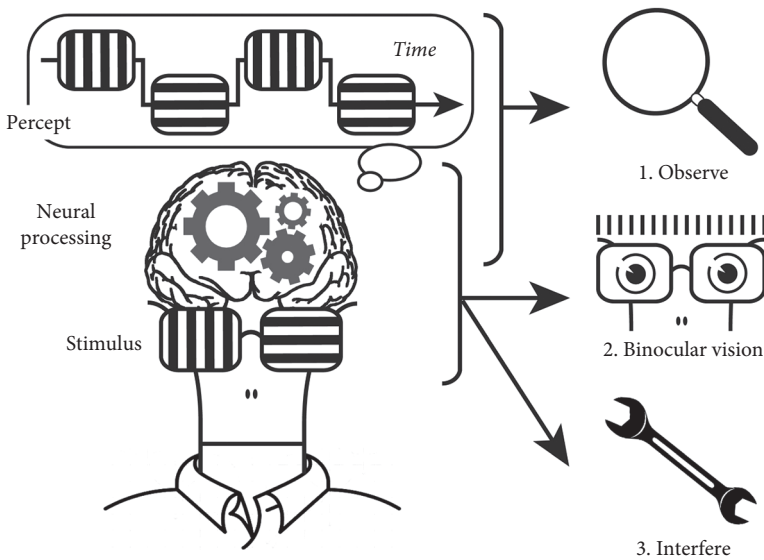


Figure 1. Three branches of binocular rivalry research. Binocular rivalry (left panel) involves a stimulus of incompatible images presented to the individual eyes (here horizontal and vertical line patterns). In the brain, complex neuronal processing converts the visual input into a conscious percept (indicated by the thought cloud). Over time, perception fluctuates between the two individual images. We propose the future of binocular rivalry research to focus on three intimately related areas (right panels). These areas are (1) the observation of perceptual and neuronal dynamics during fluctuations in awareness; (2) the binocular rivalry mechanism itself and its relation to other aspects of binocular vision; and (3) interference with neural processing, either via stimulus manipulations or by brain stimulation.

biological mechanisms involved in binocular rivalry are far more complex than the mechanistic properties of a window, the same principle applies and experimenters that study consciousness with binocular rivalry have much to gain from a deeper understanding of the binocular rivalry mechanism itself. Despite the long tradition in studying the neural underpinnings of the binocular rivalry phenomenon and the vast body of existing literature on the topic, there is still a lot that we do not know about the neural mechanisms and brain structures involved.

The third branch of binocular rivalry research takes elements of the first two and could be coarsely summarized as ‘interfering with the functional mechanisms of consciousness’. While the passive observation of a process has the advantage of encountering it in its most natural, unperturbed state, it also limits the amount of

information that can be derived about the underlying operational mechanisms. Alternatively, active interference with such a process will likely reveal much more information than can ever be inferred from mere observation. In terms of the window metaphor, one could imagine such an approach as actively reaching through the window to interfere with the ongoing mechanisms of consciousness rather than just observing them passively.

With these three branches of binocular rivalry research in mind we can now turn to some recent theoretical and technological developments in neuroscience and discuss their relevance for each of the proposed binocular rivalry approaches.

2.2 Observing streams of consciousness

Passive observation of the unperturbed mechanisms that shape visual awareness will yield most information if the recording techniques can measure activity in large portions of the brain simultaneously and with high spatiotemporal resolution. In the past, broad spatial focus and high measuring resolution have often been mutually exclusive, but improvements of existing, as well as the development of novel, imaging methods have greatly expanded these possibilities. In addition, some recent findings on the dynamic perceptual phenomenology of binocular rivalry may open the door to a whole new range of behavioral and imaging experiments.

2.2.1 *Transitions, traveling waves and nucleations*

Much of the existing binocular rivalry research treats the perceptual phenomenology of alternating percepts as a more or less binary process in which either one or the other percept is exclusively dominant at any time. While this approach has certainly revealed much about the perceptual dynamics involved in rivalry, its focus on dominance episodes overlooks the transition period as a fundamental property of binocular rivalry. It has been argued that the two hallmark features of binocular rivalry are *mutual exclusivity* and *reversibility* (Klink, van Wezel, & van Ee, 2012a; Leopold & Logothetis, 1999; Long & Toppino, 2004). Mutual exclusivity entails that observers perceive either one, or the other perceptual interpretation, but not both. Alternatively, one could say that exclusivity concerns the content of perception and thus deals with the episodes of temporary stable dominance (Klink et al., 2012a). The reversibility aspect, pertains to the occurrence of perceptual alternations, and thus to the transitions between episodes of exclusive dominance. These transitions seem especially interesting for questions about neural correlates of conscious perception because they mark the moment when ‘the brain changes its mind’ and constructs new conscious percepts from the same sensory input.

It has long been known that perceptual alternations in binocular rivalry are not instantaneous (Wheatstone, 1838). Instead, a currently dominant percept often appears to be ‘swept into suppression’ by a wave-like intrusion of the alternative percept. Systematic investigation of these traveling transition waves has only started recently (Wilson, Blake, & Lee, 2001), but has already resulted in valuable information about the neural correlates of perceptual alternations during binocular rivalry. Most notably, the perceptual experience of dominance-altering waves traveling through the visual field has been shown to coincide with similar waves of neural activity traveling over the retinotopic maps of early visual cortices (Lee, Blake, & Heeger, 2005, 2007). In addition, these cortical waves of activity were abolished by diverting attention away from the visual stimulus in V2 and V3, but remained present in V1 (Lee et al., 2007), lending support for the involvement of hierarchical stages of cortical processing involved in binocular rivalry (Blake & Logothetis, 2002; Wilson 2003). Two distinct aspects of transition waves will likely turn out to be informative about different aspects of their neuronal basis. First, the location within the visual field where the wave is instigated (Naber, Carter, & Verstraten, 2009; Paffen, Naber, & Verstraten, 2008; Stuit, Verstraten, & Paffen, 2010), or the ‘nucleation site’ (van Ee, 2011), may reflect important inhomogeneities in neuronal properties throughout retinotopic cortical areas. A thorough investigation of this aspect of binocular rivalry requires a focus on the initial moments of rivalry. Indeed, experimental paradigms aimed at explaining the onset of rivalry have strongly gained in popularity over recent years, albeit mostly for an entirely different reason (Carter & Cavanagh, 2007; Klink et al., 2008a; Leopold, Wilke, Maier, & Logothetis, 2002; Pearson & Brascamp, 2008) (see also Section 2.3.2). The second interesting aspect of perceptual transition waves is their spatiotemporal dynamics. The speed and directional pattern with which dominance waves propagate through visual space (Knapen, van Ee, & Blake, 2007; Wilson et al., 2001) combined with the fact that similar waves of activity can be observed in visual cortex (Lee et al., 2005) may reveal essential aspects of cortical connectivity.

Renewed interest in the properties of perceptual transitions may inspire a whole new range of psychophysical experiments and the paradigms developed in these behavioral studies will likely be fit for neuroimaging and neurophysiological experiments as well.

2.2.2 *fMRI*

In the few years that functional magnetic resonance imaging (fMRI) has been available to record brain activity, it has established itself as a force to reckon with in binocular rivalry research (Knapen, Brascamp, Pearson, van Ee, & Blake, 2011; Lee et al., 2007; Polonsky, Blake, Braun, & Heeger, 2000; Tong, Nakayama, Vaughan,

& Kanwisher, 1998; Wunderlich, Schneider, & Kastner, 2005). Both the technique itself and the associated data analysis procedures are, however, still under development. The first fMRI experiments typically used scanners with magnetic field strengths of 1.5 Tesla, allowing a resolution of about $2 \times 2 \times 2$ mm. With stronger magnetic fields, higher signal to noise ratios and better spatial resolutions can be obtained. While 3 Tesla scanners are now relatively common, the latest generation high field fMRI scanners even boost magnetic fields of 7 Tesla or more, resulting in spatial resolutions at the level of cortical columns (Yacoub, Shmuel, Logothetis, & Ugurbil, 2007). For binocular rivalry, these advanced resolutions seem especially promising because monocular neurons that represent input from only one eye are organized in ocular dominance columns based on their eye-of-preference (Horton & Hedley-Whyte, 1984; Hubel & Wiesel, 1969). It would provide a broad view of neural processing from stimulus to percept if activity patterns of monocular and binocular neurons could simultaneously be recorded throughout visual cortex and correlated with perception during binocular rivalry.

The development of robust analysis methods to deal with the large amounts of data generated with fMRI is perhaps an even more important objective than the technical improvement of scanning resolution (Logothetis, 2008; Poldrack, 2012). Fundamentally flawed conclusions drawn from inadequate statistical data analysis or circular reasoning are a widespread problem in cognitive neuroimaging and appropriate solutions are now being suggested to resolve this issue (Bennett, Baird, Miller, & Wolford, 2010; Poldrack, 2012). Furthermore, if fMRI is used in combination with binocular rivalry to investigate how the evolution of neural activity throughout the brain correlates with the dynamics of perception, it does not suffice to limit data analysis to what is sometimes called 'blobology' (Poldrack, 2012); finding a brain area where average activity fluctuations correlate with perception and call it 'a neural correlate'. Instead, it would be more interesting to take patterns of activation into account. While global patterns may reveal aspects of functional connectivity (Ramsey et al., 2010), patterns on a more local scale have been shown to encode information that cannot be extracted from averaged activity alone (Kriegeskorte, Goebel, & Bandettini, 2006).

Functional near-infrared spectroscopy (fNIRS) is relatively new technique that, like fMRI, measures brain oxygenation (Izzetoglu et al., 2005). It does so by detecting the absorption of near-infrared light noninvasively directed at the brain. fNIRS has lower spatial resolution than fMRI, but a better temporal resolution. More importantly however, it offers a cheap, portable and relatively motion-resistant method to detect hemodynamic responses that may in the future become a viable alternative for fMRI in studying, for instance, developmental aspects of binocular rivalry in children.

2.2.3 MEG/EEG

Whereas fMRI is the most broadly used brain imaging technique, it has a rather low temporal resolution. This is perhaps the primary reason why magnetoencephalography (MEG) is rapidly gaining popularity as a temporally sensitive functional neuroimaging tool. Unlike fMRI, which measures changes in blood flow or blood oxygenation as an indirect measure of neural activity, MEG registers the weak magnetic fields induced by the actual electrical signals within populations of neurons. This allows sub-millisecond temporal resolution, but comes at the cost of spatial resolution. Moreover, MEG can only record brain activity at the scalp surface, and while spatial resolutions in the order of millimeters can be obtained with post-hoc dipole analysis, the signal will always remain superficial.

Recent binocular rivalry MEG studies have reported early spatial and temporal aspects of neural activity during perceptual alternations (e.g., Kamphuisen, Bauer, & van Ee, 2008). In the future though, a combination of data obtained from the same observers with fMRI and MEG under the same experimental conditions promises to offer a spectacularly detailed record of the spatiotemporal dynamics of neural activity throughout the brain (Horwitz & Poeppel, 2002).

A similar exciting combination of techniques that we may expect to see more of in the future is the combination of fMRI and electroencephalography (EEG). Like MEG, EEG has excellent temporal resolution at the cost of poor spatial performance. Unlike MEG however, EEG does not require big machines to register brain activity which means that EEG signals can in fact be recorded inside the MRI scanner (Ritter & Villringer, 2006). This approach allows the simultaneous monitoring of the neural processes involved in rivalry with both high spatial and high temporal resolution. The particular advantage of having the EEG signal in addition to the whole brain scans from the fMRI lies in the possibility to employ so-called frequency-tagging paradigms (that are possible with MEG) in which each eye's stimulus is flickering at a different frequency. Fluctuation in the power of these stimulus-specific frequencies in the EEG-signal recorded from occipitally placed electrodes reflects the perceptual dominance cycles evoked by the rivalry (Brown & Norcia, 1997; Lansing, 1964; Lawwill & Biersdorf, 1968). As such, the EEG signal thus represents an objective measure of the subjective process of perception that can be correlated with the spatial information from the fMRI signal to unravel the neural correlates of conscious visual perception.

In addition to the value of MEG and EEG in combination with fMRI, there are some topics in rivalry where these methods by themselves may be the appropriate experimental tools. While fMRI research has demonstrated the involvement of a hierarchical set of brain areas in binocular rivalry (e.g., Lee et al., 2007), EEG and MEG may pinpoint the temporal characteristics of the dynamic neural information processing in networks of areas throughout the brain.

2.2.4 *Electrophysiology*

It is currently not possible to directly measure single neuron activity non-invasively. Single neuron activity in humans can occasionally be recorded in patients equipped with intracranial electrode grids in preparation of brain surgery (Kreiman, Fried, & Koch, 2002), but these opportunities are relatively rare and the location of electrodes is on such occasions optimized for the pending surgical procedure, not for a rivalry experiment. For this reason, single-unit activity during binocular rivalry is generally recorded in animals, preferably non-human primates, because their brains (and in particular their visual cortices) closely resemble those of humans.

While recording the activity of a single neuron provides a remarkably detailed insight in the dynamic response properties of that particular cell (Logothetis, 1998), it omits the responses of many other potentially relevant neurons. The classic way to overcome this constraint is to repeat the experiment many times and record from a large population of different neurons (Logothetis & Schall, 1989). However, with the increased availability of computational resources it is now becoming more common to record activity with large multi-electrode grids rather than with single electrodes. Elaborate spike-sorting algorithms can split up signals according to individual source neurons. This approach not only saves the experimenter time by measuring activity from many neurons at once, it also allows an evaluation of interneuronal activity relations (Gail, Brinksmeyer, & Eckhorn, 2004; Wilke, Logothetis, & Leopold, 2006). In the specific case of binocular rivalry it would, for instance, be very interesting to see how the activity of individual cells in primary visual cortex relates to the activity of cells in later cortical areas. The progression of activity over cortex associated with perceptual traveling waves of dominance discussed in Section 2.2.1 would also be an excellent topic to investigate with large multi-electrode grids to allow the detection of neural activity in a direct way rather than the indirect approach of fMRI.

On a side-note, it is not yet clear at all how the different measures of neural activity like spikes, local field potentials, and fMRI responses correspond to one another (Logothetis, 2003; Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001). There is an urgent need for multimodal recording approaches, both to establish this relation and to decipher how information is encoded in different forms of neural activity.

2.2.5 *Two-photon imaging*

Two-photon excited microscopy is a relatively new, but rapidly developing, method to simultaneously record the activity of populations of neurons with single cell resolution or better (Svoboda & Yasuda, 2006). By recording the

amount of light that is emitted by neurons labeled with calcium concentration or voltage-sensitive fluorescent dyes and excited with laser-light, neuronal activity can be measured up to a depth of one millimeter. Furthermore, the choice of marker allows a distinction between excitatory and inhibitory cells (Hofer et al., 2011). At the moment, the technique is predominantly used with smaller animals like mice (Stosiek, Garaschuk, Holthoff, & Konnerth, 2003), rats (Kerr, Greenberg, & Helmchen, 2005), zebra finches (Roberts, Tschida, Klein, & Mooney, 2010), or ferrets (Li, van Hooser, Mazurek, White, & Fitzpatrick, 2008) because they easily fit under a microscope, but solutions for two-photon imaging in monkeys are being developed as well (Heider, Nathanson, Isacoff, Calaway, & Siegel, 2010). Ocular dominance plasticity is a popular topic for two-photon imaging studies in mice (Hofer, Mrcic-Flogel, Bonnhoeffer, & Hübener, 2006). Binocular rivalry research may benefit from advances in this field and apply similar imaging techniques to obtain spatiotemporally detailed recordings from populations of tens of neurons located in multiple cortical layers. These studies may complement existing work with optical imaging of intrinsic signals (Sengpiel, Freeman, Bonnhoeffer, & Blakemore, 2001) and voltage-sensitive dyes (Wen & Zhang, 2009) that have related the characteristics of binocular rivalry to the dynamic activation patterns in large ensembles of cortical neurons. In addition to being capable of imaging detailed activity fluctuations in large cell ensembles, two-photon microscopy also has a high enough spatial resolution to visualize axons, dendrites and even the location of synapses (Holtmaat & Svoboda, 2009). Combining structural information with high-resolution activity patterns may eventually become valuable in revealing the neuronal mechanism of visual awareness.

2.3 Mechanisms of binocular rivalry: How the window works

With the increasing use of binocular rivalry as a convenient tool to study the neural mechanisms of consciousness, some of the fundamental questions about the binocular rivalry mechanism itself may have moved into the background. It is however conceivable that the answers to several of these questions will be essential for the interpretation of any neural correlate of consciousness revealed with binocular rivalry. We therefore argue that a second branch of binocular rivalry research should dedicate itself to the investigation of binocular rivalry as an under-defined perceptual phenomenon and attempt to unravel its basic functional and neuronal properties. In the next few paragraphs, a number of longstanding questions as well as several novel findings will be discussed as potentially fruitful topics of interest for this branch of research.

2.3.1 *Stereopsis*

While the ‘rivalry’ aspect in binocular rivalry may attract most interest in the phenomenon, the ‘binocular’ aspect may actually be more interesting from a functional point of view. The question how stereopsis and rivalry can coexist in a single neuronal organization of binocular vision has been a prominent issue ever since the discovery of binocular rivalry (Andrews & Purves, 1997; Blake, Yang, & Wilson, 1991; Grossberg, Yazdanbakhsh, Cao, & Swaminathan, 2008; Livingstone, 1996; Wolfe, 1986). Striking observations of binocular rivalry in the absence of binocular conflict due to a temporal separation of the rival images (O’Shea & Crassini, 1984; van Boxtel, Alais, Erkelens, & van Ee, 2008), and binocular fusion of stimuli that would generally instigate rivalry (Yang, Rose, & Blake, 1992) suggest an intricate relation between fusion and rivalry. Even though our knowledge of the complex neurophysiological mechanisms of stereopsis has increased tremendously over the past few years (Blake & Wilson, 2011), binocular rivalry and non-rivaling binocular vision are still predominantly studied in relative isolation, with only a limited number of studies directly addressing the issue (Andrews & Lotto, 2004; Andrews & Purves, 1997; Blake & Camisa, 1978; Blake et al., 1991; Buckthought & Mendola, 2011; Buckthought & Wilson, 2007; Treisman, 1962). We believe that both research fields may greatly benefit from each other’s progress and that, especially with novel imaging techniques, chances are now better than ever to pinpoint how the brain decides whether to fuse information from two eyes or engage in binocular rivalry.

2.3.2 *Computational modeling*

One area of research where mechanisms of stereopsis and binocular vision are already being combined on a regular basis is computational modeling. A solid tradition of model-driven experimental work in binocular rivalry research has resulted in a plethora of binocular rivalry models that explain (parts of) the phenomenon at a wide range of conceptual levels (Freeman, 2005; Kalarickal & Marshall, 2000; Lehky, 1988; Mueller, 1990; Noest et al., 2007; Seely & Chow, 2011; Stollenwerk & Bode, 2003; Wilson, 2007). We do not foresee a definitive, universally accepted, computational model of binocular vision or binocular rivalry anytime soon, but experience with existing models teaches that, on many occasions, (counterintuitive) model predictions can be instrumental in getting to understand functional and physiological mechanisms.

Recently, so-called ‘percept-choice’ or ‘onset-rivalry’ models have yielded important novel insights in the formation of the initial percept at the onset of binocular rivalry (Carter & Cavanagh, 2007; Noest et al., 2007). We have made the distinction between the *reversibility* and *mutual exclusivity* aspects of binocular rivalry (see Section 2.2.1) and argued that reversibility may be the most interesting

feature when studying fluctuations in visual awareness. Mutual exclusivity, on the other hand, may be probed best at the onset of rivalry, when the brain ‘chooses’ a dominant percept. This choice process can be studied with sequences of briefly interrupted stimuli in which stimulus onsets are repeated many times (Leopold et al., 2002). The percept-choice paradigm has already been instrumental in demonstrating forms of perceptual memory and spatial relations in binocular rivalry (Brascamp et al., 2008; Brascamp, Pearson, Blake, & van den Berg, 2009; de Jong, Knapen, & van Ee, 2012; Klink et al., 2008a; Klink, Noest, Holten, van den Berg, & van Wezel, 2009; Knapen, Brascamp, Adams, & Graf, 2009; Pastukhov & Braun, 2008) and the underlying neurophysiology (Klink, Oleksiak, Lankheet, & van Wezel, 2012b), but in the future it may also reveal information about more generic questions of visual decision-making.

An overview of the role of computational evidence in binocular rivalry research can be found in the chapter by Wilson (this volume). We are confident that computational studies will remain crucial in providing testable predictions about the functional mechanisms and neural substrates of binocular rivalry in the future.

2.3.3 *Plasticity*

Functional conceptualizations and computational models of binocular rivalry generally contribute fluctuations in awareness to a combination of the effects of adaptation, inhibition and neural noise (Seely & Chow, 2011; van Ee, 2009). Without going into too much detail, these explanations usually assume that neuronal populations coding for conflicting stimulus features engage in a competition for conscious representation in which they actively inhibit the activity of their rival populations while their own noisy activity levels are subject to neuronal fatigue that reduces their responsiveness. While the effective strength of mutual inhibition in such a mechanism will be the product of the driving activity and the inhibitory efficacy, the gain of the proposed inhibitory connectivity is often (implicitly) assumed to be constant. Recent findings, however, demonstrate a form of plasticity in the binocular rivalry mechanism that implies a recalibration of inhibitory efficacy based on recent perceptual history (Klink, Brascamp, Blake, & van Wezel, 2010).

In this study, researchers explicitly focused on the transition periods between periods of exclusive percepts. As we noted before, these transitions are often erroneously classified as instantaneous switches from one dominant percept to the other. In reality, transition periods can however have significant durations and take a range of qualitatively different forms that are all mixtures of the two exclusive percepts (Blake, O’Shea, & Mueller, 1992; Hollins, 1980; Klink et al., 2010; Yang, Rose, & Blake, 1992). The occurrence and duration of mixture percept transition

periods can be regarded as an indication of the inhibitory efficacy between the neuron populations that represent these exclusive percepts (Hollins, 1980). When binocular rivalry exposure was prolonged to more than half an hour, considerably longer than typically used presentation durations of several minutes, the mixture periods became progressively longer, indicating a decrease in inhibitory efficacy (Klink et al., 2010). Additional experiments revealed that this apparent loss of inhibition was highly selective to the eye-of-origin and to the stimulus features. It also showed that it could not be attributed to straightforward fatigue because it required selective exposure to binocularly matching stimuli to recover to baseline values rather than that it recovered passively.

Other forms of plasticity in binocular rivalry affect the rate at which percepts fluctuate in dominance (Lack, 1969; Suzuki & Grabowecky, 2007; van Ee, 2005), the relative dominance of visual information presented to a previously deprived eye (Lunghi, Burr, & Morrone, 2011), or even the ability to experience binocular rivalry altogether (Lack, 1978). Together, these plasticity phenomena demonstrate the dynamic nature of the binocular visual system, a feature that may be important for interocular contrast-gain control during binocular summation and the coexistence of binocular rivalry and stereopsis. A focus on visual plasticity may furthermore be helpful for the study of adult brain plasticity, the same way research on ocular dominance has been helpful for the field of neuronal development (Katz & Crowley, 2002).

2.3.4 *Genetics*

The temporal dynamics of binocular rivalry have been vigorously investigated and it has long been known that the rate of perceptual fluctuations, while relatively stable within observers, can differ greatly between observers (Aafjes, Hueting, & Visser, 1966). Inspired by the observation that alternation rates are generally slower in patients with bipolar disorder (Krug et al., 2008; Miller et al., 2003; Pettigrew & Miller, 1998), a heritable mental disorder, a recent study aimed to find out whether there could be a genetic component to the individual differences in alternation rate (Miller et al., 2010). When alternation rates were measured in a large sample of monozygotic and dizygotic twins they indeed revealed a substantial genetic contribution, a finding that was later confirmed with a broader range of rivalry stimuli (Shannon, Patrick, Jiang, Bernat, & He, 2011), and complemented by a demonstrated correlation between brain structure and alternation rate (Kanai, Bahrami, & Rees, 2010). Not only do these findings open up possibilities to use binocular rivalry alternation rates as a diagnostic endophenotype for bipolar disorder, they also suggest that important determinants of the specific neuronal machinery of binocular rivalry are encoded in our DNA. This notion asks for the introduction of molecular biology

in binocular rivalry research. Animal models like *Drosophila melanogaster* that are easily accessible to genetic manipulations and for which evidence of rivalry characteristics has repeatedly been shown, will likely become fruitful tools in this direction of research (Miller, Ngo, & van Swinderen, 2012). Such a completely novel experimental approach may reveal many previously unexplained aspects of binocular rivalry in the future. Elsewhere in this volume the genetic contribution to rivalry is discussed in more detail (see chapters by Ngo et al. and Bressler, Denison, & Silver, this volume).

2.4 Reaching through a window on consciousness

For the third branch of binocular rivalry research, we return to the use of rivalry as a window on the neural processes of visual awareness. This time, however, we ask for a more experimentally proactive approach. Instead of passively observing these processes, we propose to interfere with them and investigate how closely controlled experimental manipulations may alter perceptual experience and neural processing during binocular rivalry. Such manipulations can range from simple stimulus variations to invasive interference with specific aspects of neural processing. Each of these perturbations and the corresponding consequences may potentially help in determining whether certain processes are merely correlates of consciousness or whether they are essential for its constitution (Miller, 2007).

2.4.1 *Human psychophysics*

With the availability of modern imaging possibilities, there is a danger of underappreciating the value of human psychophysical tools in binocular rivalry research. Even though one cannot directly measure brain activity with psychophysics, psychophysical experiments can teach us much about the mechanisms of perception, especially when they are combined with computational modeling and thorough knowledge of neurophysiology and neuroanatomy. Psychophysical experiments systematically investigate the relation between stimulus and perception or behavior. They thus look at processes from a functional point of view, which is the only viewpoint relevant to the observing organism. In addition, many inventive experimental paradigms in binocular rivalry research were originally developed in a psychophysical setting, but have later been used in imaging experiments. A detailed overview of psychophysical techniques can be found in the chapter by Brascamp and Baker (this volume), accompanied by a discussion of general pitfalls and possibilities. Here, we merely stress the importance of 'simple' psychophysics for the technologically advanced future of binocular rivalry research and point out some of the most promising novel approaches.

In psychophysics, binocular rivalry stimuli are typically presented to an observer in a dark and quiet room, isolated from any form of context. With this situation as a starting point, any additional context can be regarded as a manipulation of the pathway from stimulus to awareness. An extensive overview of studies that have shown how the brain uses spatial, temporal, and crossmodal contexts, or even ‘internal states’ like emotional or attentional load to interpret perceptual ambiguities is available elsewhere (Klink et al., 2012a; see chapter by Bressler et al., this volume). Here we will only briefly touch upon some of the most promising approaches. The temporal characteristics of binocular rivalry are not only being exploited in the onset paradigms mentioned in Section 2.3.2 and the frequency tagging approach discussed in Section 2.2.2, but they may also reveal sequential processing steps in rivalry resolution and possibly the involvement of feedback connectivity (e.g., Bartels & Logothetis, 2010; van Boxtel, Knapen, Erkelens, & van Ee, 2008). Explorations in multimodal interactions have also began to make their way into binocular rivalry research (Blake, Sobel, & James, 2004; Conrad, Bartels, Kleiner, & Noppeney, 2010; Lunghi, Binda, & Morrone, 2010; van Ee, van Boxtel, Parker, & Alais, 2009; Zhou, Jiang, He, & Chen, 2010) and we expect a lot from these approaches in unraveling general processes of perceptual selection and binding. Spatial context effects on the other hand have been investigated in binocular rivalry for quite some time (e.g., Fukuda & Blake, 1992; Sobel & Blake, 2002), but the relatively new nucleation and traveling wave approaches mentioned in Section 2.2.1 can provide important new insights in the spatial instigation and progression of perceptual fluctuation.

A whole new class of experiments have started to use binocular rivalry as a tool to investigate the unconscious processing of sensory information (Lin & He, 2008) and the interaction between attention and awareness (Brascamp, van Boxtel, Knapen, & Blake, 2010; Koch & Tsuchiya, 2007; Lamme, 2003; van Boxtel, Tsuchiya, & Koch, 2010). Such studies frequently use a form of rivalry dubbed continuous flash suppression (Tsuchiya & Koch, 2005), where one eye is presented with a highly salient, rapidly changing, stimulus that suppresses a far less salient image in the other eye for minutes at a time (Figure 2a), much longer than the typical suppression duration in conventional binocular rivalry. As research interest in this field of unconscious perceptual processing is rapidly growing, there is increasing demand for binocular rivalry as a tool to manipulate which sensory input is consciously perceived. However, as we argued in Section 2.1, such instrumental use of binocular rivalry can only benefit from a better understanding of the binocular rivalry mechanism itself.

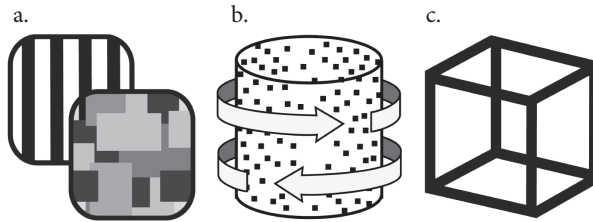


Figure 2. Other rivalry stimuli. (a) Continuous flash suppression is a special case of binocular rivalry where a highly salient, dynamic, image in one eye (e.g., a dynamic Mondrian pattern), suppresses a static image in the other eye for much longer periods than is the case with equally salient stimuli. (b) In ambiguously rotating structure-from-motion cylinders, the impression of a three-dimensional object arises from a two-dimensional projection of dots moving as if they are located on the surface of a rotating transparent cylinder. Lacking depth information, the rotation direction is ambiguous. (c) A Necker cube lacks depth cues, rendering its three-dimensional orientation ambiguous.

2.4.2 *Transcranial magnetic stimulation*

Instead of interfering with the processes of conscious perception by manipulating stimulus conditions, one may also try to directly influence the activity of the involved neurons. One way of doing this is with transcranial magnetic stimulation (TMS; see chapter by Thomson & Fitzgerald, this volume). With this technique, a locally applied, rapidly changing, magnetic field induces weak electrical currents in the brain that can cause neurons to become active or silent, depending on the precise stimulation paradigm. A comprehensive review of recent brain stimulation experiments during rivalry can be found in the chapter by Ngo et al. (this volume), but for the future of binocular rivalry research, TMS and related non-invasive stimulation techniques will be most informative if some aspects of the technique can be improved. One basic problem is the rather coarse spatial specificity of the stimulation that disrupts processing in relatively large patches of cortex. Another issue is that there is no detailed understanding of the physiological consequences of TMS (Bestmann, 2008). This may however not be a deal-breaker. A minimal functional interpretation of TMS as interfering with ongoing neural processing is enough to make TMS a valuable research tool. Besides, the combination of TMS with fMRI (another technique for which the physiological underpinnings are not entirely resolved, see Section 2.2.3) or EEG, provides a powerful non-invasive approach to study causal relations between activity patterns in different areas of the brain (Driver, Blankenburg, Bestmann, Vanduffel, & Ruff, 2009). TMS thus has the potential of becoming an important tool in unraveling both the necessity and sufficiency of specific neural processes in visual perception and binocular rivalry.

2.4.3 *Microstimulation*

Invasive forms of brain stimulation like electrical microstimulation can be used in animal models and the occasional human patient (Bak et al., 1990). Binocular rivalry essentially confronts the brain with a perceptual conflict in which it eventually ‘chooses’ a dominant percept. Similar perceptual decisions between options with equal or close to equal sensory support have been shown to be highly susceptible to the influence of microstimulation (Cohen & Newsome, 2004). Stimulating only a very limited number of neurons has been shown to alter perceived motion direction (Salzman, Murasugi, Britten, & Newsome, 1992), heading direction (Britten & van Wezel, 1998), and depth perception (DeAngelis, Cumming, & Newsome, 1998). If the subjective appearance of such basic features can be altered with microstimulation, it should also be possible to influence the perceptual choices between two competing binocular rivalry stimuli by subtly stimulating subsets of neurons. If microstimulation is combined with additional imaging techniques, it may reveal the complex recurrent connectivity within and between functional brain networks.

2.4.4 *Photostimulation*

In addition to electrical stimulation, recent advances have promoted a rapid growth in popularity of photostimulation as a novel neuronal interference technique. Photostimulation is used in animal models, both *in vitro* and *in vivo*, and allows precisely targeted neuronal stimulation. The variant that is most likely to be useful for binocular rivalry in the near future is optogenetics, Nature magazine’s ‘Method of the Year 2010’ (Deisseroth, 2010). In optogenetics, light sensitive ion channels are genetically built into the membranes of a specific class of neurons. If these channels are illuminated with precisely controlled light of a specific wavelength and flicker frequency, these ion channels open or close, depending on their protein compounds. With operational control over ion channels, an experimenter can effectively switch a neuron on or off with the flick of a light switch. While initial studies were limited to rodents, the method has now also been applied to non-human primates (Han et al., 2009), opening up possibilities of combining it with behavioral paradigms in which awake behaving monkeys are exposed to binocular rivalry while the activity of specific groups of neurons, either in visual cortex or elsewhere, are experimentally controlled.

3. Concluding remarks

Binocular rivalry is a popular tool in the scientific study of consciousness because it dissociates stable, unchanged, visual stimulation from fluctuations in visual awareness. Other types of visual ambiguities exhibit a similar behavior without the need to present conflicting information to the two eyes (Leopold & Logothetis, 1999). Stimuli like the Necker cube, or ambiguously rotating structure-from-motion cylinders embody a competition between mutually exclusive, three-dimensional perceptual interpretations based on two-dimensional projections that lack explicit depth information (Figure 2b and 2c). It has been argued, that while different types of visual ambiguities are likely resolved by different cortical neurons and at different cognitive levels, the operational principles may to a certain extent be comparable (Klink, van Ee, & van Wezel, 2008b).

The primary difference between these perceptual rivalry stimuli and binocular rivalry is that the same phenomenological experience of alternating perception emerges without involving of the complex neuronal organization of binocular vision. It thus avoids the issue of interocular interactions and focuses purely on the (cortical) perceptual conflict between competing interpretations of the stimulus. It is, however, unclear whether suppressing (part of) a visual stimulus from awareness, as is the case in binocular rivalry, is the same as suppressing a perceptual interpretation while still using all the available visual information. In addition, the techniques that most effectively suppress visual input from awareness, like continuous flash suppression, actually exploit the binocular visual system. Clearly, perceptual rivalry and binocular rivalry both have their advantages and disadvantages in studying the neural underpinnings of conscious visual perception and the choice of stimuli and experimental paradigm will ultimately depend on the specific research question that is to be addressed. Both types of rivalry will however continue to be valuable tools in studying the neuronal basis of visual awareness. The similarities and differences between them, complemented by the increasing knowledge of the neuronal underpinnings of binocular vision and object perception, may in fact prove to be highly informative about the brain mechanisms that shape visual awareness.

The technological developments discussed in this chapter make it possible to register neuronal activity at many different processing levels. Each method comes with its own advantages and disadvantages, making it increasingly prudent to combine techniques and explore multimodal recording possibilities. Care should however be taken that all these exciting new technological possibilities do not distract us from the fact that the binocular rivalry mechanism itself remains poorly understood. We therefore proposed a distinction between three intimately

related branches of binocular rivalry research that each offer specific possibilities for future research (Box 1). Novel imaging techniques will further promote the use of binocular rivalry as a window on the processes of visual awareness, while ongoing efforts aimed at understanding the mechanisms of binocular rivalry itself and its relation to stereopsis will continue to advance our understanding of visual processing. Finally, we invite binocular rivalry researchers to reach through the window on consciousness, interact with the underlying neuronal processes, and learn the neuronal language of consciousness.

Box 1. Major opportunities on three fronts

While we propose a wide range of possibilities for future binocular rivalry research throughout this chapter, here we tentatively select one topic for each branch of research that we currently believe to have most potential.

1. New animal models and optical imaging techniques

The rapid rise in studying visual perception with optical imaging techniques in rodents (Grewe & Helmchen, 2009) offers great opportunities for the ‘observation’ of binocular rivalry processes. While it may be more difficult to obtain perceptual reports from these animals (it is currently not known if they even experience binocular rivalry), the amount of detail that can potentially be obtained about patterns of activity and involved neural structures is unprecedented. In addition, this line of research can provide a lot of information about the stereopsis vs rivalry issue as basic (binocular) vision experiments are already quite common in this field. Expanding the technique to non-human primates and combining imaging with stimulation paradigms allows this approach to be useful for all three branches of binocular rivalry research.

2. Plasticity and inhibition link binocular rivalry and stereopsis

The observation of plasticity in inhibitory efficacy during binocular rivalry (Klink et al., 2010) may move interest in binocular rivalry towards the transition periods. On the computational side, it urges new models to incorporate more adaptive neuronal interactions that may bridge the gap between stereopsis and rivalry. The focus on neuronal processes that mediate perceptual alternations and correlating those with perceptual experience may also inspire new psychophysical, physiological and imaging experiments.

3. Multisensory context as interference on the stimulus side

A straightforward way of interfering with binocular rivalry processing is to add context to the stimulus. Because we live in a multimodal world, the brain employs mechanisms of multimodal integration to establish rich perceptual experiences (Ernst & Bühlhoff, 2004). These mechanisms can be exploited in binocular rivalry to reveal the functional mechanisms of perceptual awareness. Such endeavors have recently started to appear in the literature (e.g., Conrad et al., 2010; Lunghi et al., 2010; van Ee et al., 2009; Zhou et al., 2010), but we expect more revealing findings to emerge from this field in the future.

References

- Aafjes, M., Hueting, J.E., & Visser, P. (1966). Individual and interindividual differences in binocular retinal rivalry in man. *Psychophysiology*, 3(1), 18–22.
- Alais, D. (2012). Binocular rivalry: Competition and inhibition in visual perception. *Wiley Interdisciplinary Reviews: Cognitive Science*, 3(1), 87–103.
- Andrews, T. J., & Lotto, R. B. (2004). Fusion and rivalry are dependent on the perceptual meaning of visual stimuli. *Current Biology*, 14(5), 418–423.
- Andrews, T. J., & Purves, D. (1997). Similarities in normal and binocularly rivalrous viewing. *Proceedings of the National Academy of Sciences USA*, 94(18), 9905–9908.
- Bagby, J. W. (1957). A cross-cultural study of perceptual predominance in binocular rivalry. *Journal of Abnormal and Social Psychology*, 54(3), 331–334.
- Bak, M., Girvin, J. P., Hambrecht, F. T., Kufta, C. V., Loeb, G. E., & Schmidt, E. M. (1990). Visual sensations produced by intracortical microstimulation of the human occipital cortex. *Medical & Biological Engineering & Computing*, 28(3), 257–259.
- Baker, D. H. (2010). Visual consciousness: The binocular rivalry explosion. *Current Biology*, 20(15), R644–R646.
- Bartels, A., & Logothetis, N. K. (2010). Binocular rivalry: A time dependence of eye and stimulus contributions. *Journal of Vision*, 10(12), 3. doi:10.1167/10.12.3
- Belliveau, J. W., Kennedy, D. N., McKinstry, R. C., Buchbinder, B. R., Weisskoff, R. M., Cohen, M. S. et al. (1991). Functional mapping of the human visual cortex by magnetic resonance imaging. *Science*, 254(5032), 716–719.
- Bennett, C. M., Baird, A. A., Miller, M. B., & Wolford, G. L. (2010). Neural correlates of interspecies perspective taking in the post-mortem Atlantic Salmon: An argument for proper multiple comparisons correction. *Journal of Serendipitous and Unexpected Results*, 1(1), 1–5.
- Bestmann, S. (2008). The physiological basis of transcranial magnetic stimulation. *Trends in Cognitive Sciences*, 12(3), 81–83.
- Blake, R. (1989). A neural theory of binocular rivalry. *Psychological Review*, 96(1), 145–167.
- Blake, R., & Camisa, J. (1978). Is binocular vision always monocular? *Science*, 200(4349), 1497–1499.
- Blake, R., & Logothetis, N. K. (2002). Visual competition. *Nature Reviews Neuroscience*, 3(1), 13–21.
- Blake, R., O'Shea, R. P., & Mueller, T. J. (1992). Spatial zones of binocular rivalry in central and peripheral vision. *Visual Neurosciences*, 8(5), 469–478.
- Blake, R., Sobel, K. V., & James, T. W. (2004). Neural synergy between kinetic vision and touch. *Psychological Science*, 15(6), 397–402.
- Blake, R., & Wilson, H. (2011). Binocular vision. *Vision Research*, 51(7), 754–770.
- Blake, R., Yang, Y. D., & Wilson, H. R. (1991). On the coexistence of stereopsis and binocular rivalry. *Vision Research*, 31(7–8), 1191–1203.
- Bokander, I., & Radeborg, K. (1966). The solution of perceptual conflict between stereoscopically presented facial photographs. *Psychological Research Bulletin*, 6(3), 1–10.
- Brascamp, J. W., van Boxtel, J. J. A., Knapen, T. H. J., & Blake, R. (2010). A dissociation of attention and awareness in phase-sensitive but not phase-insensitive visual channels. *Journal of Cognitive Neuroscience*, 22(10), 2326–2344.

- Brascamp, J. W., Knapen, T. H. J., Kanai, R., Noest, A. J., van Ee, R., & van den Berg, A. V. (2008). Multi-timescale perceptual history resolves visual ambiguity. *PLoS ONE*, 3(1), e1497. doi: 10.1371/journal.pone.0001497
- Brascamp, J. W., Pearson, J., Blake, R., & van den Berg, A. V. (2009). Intermittent ambiguous stimuli: Implicit memory causes periodic perceptual alternations. *Journal of Vision*, 9(3), 3. doi: 10.1167/9.3.3
- Breese, B. B. (1899). On inhibition. *Psychological Monographs*, 3(1), 1–65.
- Britten, K. H., & van Wezel, R. J. A. (1998). Electrical microstimulation of cortical area MST biases heading perception in monkeys. *Nature Neuroscience*, 1(1), 59–63.
- Brown, R. J., & Norcia, A. M. (1997). A method for investigating binocular rivalry in real-time with the steady-state VEP. *Vision Research*, 37(17), 2401–2408.
- Buckthrought, A., & Mendola, J. D. (2011). A matched comparison of binocular rivalry and depth perception with fMRI. *Journal of Vision*, 11(6), 3. doi: 10.1167/11.6.3
- Buckthrought, A., & Wilson, H. R. (2007). Interaction between binocular rivalry and depth in plaid patterns. *Vision Research*, 47(19), 2543–2556.
- Carter, O. L., & Cavanagh, P. (2007). Onset rivalry: Brief presentation isolates an early independent phase of perceptual competition. *PLoS ONE*, 2, e343. doi: 10.1371/journal.pone.0000343
- Cohen, M. R., & Newsome, W. T. (2004). What electrical microstimulation has revealed about the neural basis of cognition. *Current Opinion in Neurobiology*, 14(2), 169–177.
- Conrad, V., Bartels, A., Kleiner, M., & Noppeney, U. (2010). Audiovisual interactions in binocular rivalry. *Journal of Vision*, 10(10), 27. doi: 10.1167/10.10.27
- Crick, F., & Koch, C. (1990). Towards a neurobiological theory of consciousness. *Seminars in the Neurosciences*, 2, 263–275.
- Crick, F., & Koch, C. (1998). Consciousness and neuroscience. *Cerebral Cortex*, 8(2), 97–107.
- DeAngelis, G. C., Cumming, B. G., & Newsome, W. T. (1998). Cortical area MT and the perception of stereoscopic depth. *Nature*, 394(6694), 677–680.
- Deisseroth, K. (2010). Optogenetics. *Nature Methods*, 8(1), 26–29.
- de Jong, M. C., Knapen, T., & van Ee, R. (2012). Opposite influence of perceptual memory on initial and prolonged perception of sensory ambiguity. *PLoS ONE*, 7(1), e30595. doi: 10.1371/journal.pone.0030595
- Driver, J., Blankenburg, F., Bestmann, S., Vanduffel, W., & Ruff, C. C. (2009). Concurrent brain-stimulation and neuroimaging for studies of cognition. *Trends in Cognitive Sciences*, 13(7), 319–327.
- Ernst, M. O., & Bühlhoff, H. H. (2004). Merging the senses into a robust percept. *Trends in Cognitive Sciences*, 8(4), 162–169.
- Fox, R. (1963). *An analysis of the suppression mechanism in binocular rivalry*. (Doctoral dissertation, University of Cincinnati, 1963).
- Freeman, A. W. (2005). Multistage model for binocular rivalry. *Journal of Neurophysiology*, 94(6), 4412–4420.
- Fukuda, H., & Blake, R. (1992). Spatial interactions in binocular rivalry. *Journal of Experimental Psychology: Human Perception and Performance*, 18(2), 362–370.
- Gail, A., Brinksmeyer, H., & Eckhorn, R. (2004). Perception-related modulations of local field potential power and coherence in primary visual cortex of awake monkey during binocular rivalry. *Cerebral Cortex*, 14(3), 300–313.
- Grewe, B. F., & Helmchen, F. (2009). Optical probing of neuronal ensemble activity. *Current Opinion in Neurobiology*, 19(5), 520–529.

- Grossberg, S., Yazdanbakhsh, A., Cao, Y., & Swaminathan, G. (2008). How does binocular rivalry emerge from cortical mechanisms of 3-D vision? *Vision Research*, 48(21), 2232–2250.
- Han, X., Qian, X., Bernstein, J. G., Zhou, H.-H., Franzesi, G. T., Stern, P. et al. (2009). Millisecond-timescale optical control of neural dynamics in the nonhuman primate brain. *Neuron*, 62(2), 191–198.
- Heider, B., Nathanson, J. L., Isacoff, E. Y., Callaway, E. M., & Siegel, R. M. (2010). Two-photon imaging of calcium in virally transfected striate cortical neurons of behaving monkey. *PLoS ONE*, 5(11), e13829. doi: 10.1371/journal.pone.0013829
- Helmholtz, H. (1867). *Handbuch der physiologischen Optik*, Leipzig: Voss. J. P. C. Southall, 1962 (Trans.), *Helmholtz's treatise on physiological optics*, Vol 3. New York: Dover Publications Inc.
- Hofer, S. B., Ko, H., Pichler, B., Vogelstein, J., Ros, H., Zeng, H. et al. (2011). Differential connectivity and response dynamics of excitatory and inhibitory neurons in visual cortex. *Nature Neuroscience*, 14(8), 1045–1052.
- Hofer, S. B., Mrsic-Flogel, Th. D., Bonhoeffer, T., & Hübener, M. (2006). Lifelong learning: Ocular dominance plasticity in mouse visual cortex. *Current Opinion in Neurobiology*, 16(4), 451–459.
- Hollins, M. (1980). The effect of contrast on the completeness of binocular rivalry suppression. *Perception & Psychophysics*, 27(6), 550–556.
- Holtmaat, A., & Svoboda, K. (2009). Experience-dependent structural synaptic plasticity in the mammalian brain. *Nature Reviews Neuroscience*, 10(9), 647–658.
- Horton, J. C., & Hedley-Whyte, E. T. (1984). Mapping of cytochrome oxidase patches and ocular dominance columns in human visual cortex. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 304(1119), 255–272.
- Horwitz, B., & Poeppel, D. (2002). How can EEG/MEG and fMRI/PET data be combined? *Human Brain Mapping*, 17(1), 1–3.
- Hubel, D. H., & Wiesel, T. N. (1969). Visual area of the lateral suprasylvian gyrus (Clare-Bishop area) of the cat. *Journal of Physiology*, 202(1), 251–260.
- Hubel, D. H., & Wiesel, T. N. (1998). Early exploration of the visual cortex. *Neuron*, 20(3), 401–412.
- Izzetoglu, M., Izzetoglu, K., Bunce, S., Ayaz, H., Devaraj, A., Onaral, B. et al. (2005). Functional near-infrared neuroimaging. *IEEE Transactions on Neural Systems and Rehabilitation Engineering*, 13(2), 153–159.
- Kalarickal, G. J., & Marshall, J. A. (2000). Neural model of temporal and stochastic properties of binocular rivalry. *Neurocomputing*, 32–33, 843–853.
- Kamphuisen, A., Bauer, M., & van Ee, R. (2008). No evidence for widespread synchronized networks in binocular rivalry: MEG frequency tagging entrains primarily early visual cortex. *Journal of Vision*, 8(5), 4. doi: 10.1167/8.5.4
- Kanai, R., Bahrami, B., & Rees, G. (2010). Human parietal cortex structure predicts individual differences in perceptual rivalry. *Current Biology*, 20(18), 1626–1630.
- Katz, L. C., & Crowley, J. C. (2002). Development of cortical circuits: Lessons from ocular dominance columns. *Nature Reviews Neuroscience*, 3(1), 34–42.
- Kaufer, G., & Riess, B. F. (1960). Stereoscopic perception as a tool in psychotherapeutic research. *Perceptual and Motor Skills*, 10(3), 241.
- Kerr, J. N. D., Greenberg, D., & Helmchen, F. (2005). Imaging input and output of neocortical networks in vivo. *Proceedings of the National Academy of Sciences USA*, 102(39), 14063–14068.

- Klink, P. C., Brascamp, J. W., Blake, R., & van Wezel, R. J. A. (2010). Experience-driven plasticity in binocular vision. *Current Biology*, 20(16), 1464–1469.
- Klink, P. C., van Ee, R., Nijs, M. M., Brouwer, G. J., Noest, A. J., & van Wezel, R. J. A. (2008a). Early interactions between neuronal adaptation and voluntary control determine perceptual choices in bistable vision. *Journal of Vision*, 8(5), 16. doi:10.1167/8.5.16
- Klink, P. C., van Ee, R., & van Wezel, R. J. A. (2008b). General validity of levelt's propositions reveals common computational mechanisms for visual rivalry. *PLoS ONE*, 3(10), e3473. doi:10.1371/journal.pone.0003473
- Klink, P. C., Noest, A. J., Holten, V., van den Berg, A. V., & van Wezel, R. J. A. (2009). Occlusion-related lateral connections stabilize kinetic depth stimuli through perceptual coupling. *Journal of Vision*, 9(10), 20. doi:10.1167/9.10.20
- Klink, P. C., Oleksiak, A., Lankheet, M. J. M., & van Wezel, R. J. A. (2012b). Intermittent stimulus presentation stabilizes neuronal responses in macaque area MT. *Journal of Neurophysiology*, 108(8), 2101–2114.
- Klink, P. C., van Wezel, R. J. A., & van Ee, R. (2012a). United we sense, divided we fail: Context-driven perception of ambiguous visual stimuli. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 367(1591), 932–941.
- Knapen, T., Brascamp, J., Adams, W. J., & Graf, E. W. (2009). The spatial scale of perceptual memory in ambiguous figure perception. *Journal of Vision*, 9(13), 16. doi:10.1167/9.13.16
- Knapen, T., Brascamp, J., Pearson, J., van Ee, R., & Blake, R. (2011). The role of frontal and parietal brain areas in bistable perception. *Journal of Neuroscience*, 31(28), 10293–10301.
- Knapen, T., van Ee, R., & Blake, R. (2007). Stimulus motion propels traveling waves in binocular rivalry. *PLoS ONE*, 2(1), e739. doi:10.1371/journal.pone.0000739
- Koch, C., & Braun, J. (1996). Towards the neuronal correlate of visual awareness. *Current Opinion in Neurobiology*, 6(2), 158–164.
- Koch, C., & Tsuchiya, N. (2007). Attention and consciousness: Two distinct brain processes. *Trends in Cognitive Sciences*, 11(1), 16–22.
- Kohn, H. (1960). Some personality variables associated with binocular rivalry. *Psychological Record*, 10, 9–13.
- Kreiman, G., Fried, I., & Koch, C. (2002). Single-neuron correlates of subjective vision in the human medial temporal lobe. *Proceedings of the National Academy of Sciences USA*, 99(12), 8378–8383.
- Kriegeskorte, N., Goebel, R., & Bandettini, P. (2006). Information-based functional brain mapping. *Proceedings of the National Academy of Sciences USA*, 103(10), 3863–3868.
- Krug, K., Brunskill, E., Scarna, A., Goodwin, G. M., & Parker, A. J. (2008). Perceptual switch rates with ambiguous structure-from-motion figures in bipolar disorder. *Proceedings of the Royal Society of London B: Biological Sciences*, 275(1645), 1839–1848.
- Lack, L. C. (1969). The effect of practice on binocular rivalry control. *Perception & Psychophysics*, 6(6B), 397–400.
- Lack, L. C. (1978). *Selective attention and the control of binocular rivalry*. Mouton, The Hague.
- Lamme, V. A. F. (2003). Why visual attention and awareness are different. *Trends in Cognitive Sciences*, 7(1), 12–18.
- Lansing, R. W. (1964). Electroencephalographic correlates of binocular rivalry in man. *Science*, 146(3649), 1325–1327.
- Lawwill, T., & Biersdorf, W. R. (1968). Binocular rivalry and visual evoked responses. *Investigative Ophthalmology*, 7(4), 378–385.

- Lee, S.-H., Blake, R., & Heeger, D. J. (2005). Traveling waves of activity in primary visual cortex during binocular rivalry. *Nature Neuroscience*, 8(1), 22–23.
- Lee, S.-H., Blake, R., & Heeger, D. J. (2007). Hierarchy of cortical responses underlying binocular rivalry. *Nature Neuroscience*, 10(8), 1048–1054.
- Lehky, S. R. (1988). An astable multivibrator model of binocular rivalry. *Perception*, 17(2), 215–228.
- 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.
- Leopold, D. A., Wilke, M., Maier, A., & Logothetis, N. K. (2002). Stable perception of visually ambiguous patterns. *Nature Neuroscience*, 5(6), 605–609.
- Levelt, W. J. M. (1965). On binocular rivalry. (Doctoral dissertation, University of Leiden, 1965).
- Li, Y., van Hooser, S. D., Mazurek, M., White, L. E., & Fitzpatrick, D. (2008). Experience with moving visual stimuli drives the early development of cortical direction selectivity. *Nature*, 456(7224), 952–956.
- Lin, Z., & He, S. (2008). Seeing the invisible: The scope and limits of unconscious processing in binocular rivalry. *Progress in Neurobiology*, 87(4), 195–211.
- Livingstone, M. S. (1996). Differences between stereopsis, interocular correlation and binocular-ity. *Vision Research*, 36(8), 1127–1140.
- LoSciuto, L. A., & Hartley, E. L. (1963). Religious affiliation and open-mindedness in binocular resolution. *Perceptual and Motor Skills*, 17(2), 427–430.
- 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. (1999). Vision: A window on consciousness. *Scientific American*, 281(5), 69–75.
- Logothetis, N. K. (2003). The underpinnings of the BOLD functional magnetic resonance imaging signal. *Journal of Neuroscience*, 23(10), 3963–3971.
- Logothetis, N. K. (2008). What we can and what we cannot do with fMRI. *Nature*, 453(7197), 869–878.
- Logothetis, N. K., Leopold, D. A., & Sheinberg, D. L. (1996). What is rivalling during binocular rivalry? *Nature*, 380(6575), 621–624.
- Logothetis, N. K., Pauls, J., Augath, M. A., Trinath, T., & Oeltermann, A. (2001). Neurophysiological investigation of the basis of the fMRI signal. *Nature*, 412(6843), 150–157.
- Logothetis, N. K., & Schall, J. D. (1989). Neuronal correlates of subjective visual perception. *Science*, 245(4919), 761–763.
- Long, G. M., & Toppino, T. C. (2004). Enduring interest in perceptual ambiguity: Alternating views of reversible figures. *Psychological Bulletin*, 130(5), 748–768.
- Lunghi, C., Binda, P., & Morrone, M. C. (2010). Touch disambiguates rivalrous perception at early stages of visual analysis. *Current Biology*, 20(4), R143–R144.
- Lunghi, C., Burr, D. C., & Morrone, C. (2011). Brief periods of monocular deprivation disrupt ocular balance in human adult visual cortex. *Current Biology*, 21(14), R538–R539.
- Meenes, M. (1930). A phenomenological description of retinal rivalry. *American Journal of Psychology*, 42(2), 260–269.
- 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., 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., Hansell, N. K., Ngo, T. T., Liu, G. B., Pettigrew, J. D., Martin, N. G. et al. (2010). Genetic contribution to individual variation in binocular rivalry rate. *Proceedings of the National Academy of Sciences USA*, 107(6), 2664–2668.
- Miller, S. M., Ngo, T. T., & van Swinderen, B. (2012). Attentional switching in humans and flies: Rivalry in large and miniature brains. *Frontiers in Human Neuroscience*, 5, 188. doi: 10.3389/fnhum.2011.00188
- Mueller, T. J. (1990). A physiological model of binocular rivalry. *Visual Neurosciences*, 4(1), 63–73.
- Naber, M., Carter, O. L., & Verstraten, F. A. J. (2009). Suppression wave dynamics: Visual field anisotropies and inducer strength. *Vision Research*, 49(14), 1805–1813.
- Noest, A. J., van Ee, R., Nijs, M. M., & van Wezel, R. J. A. (2007). Percept-choice sequences driven by interrupted ambiguous stimuli: A low-level neural model. *Journal of Vision*, 7(8), 10. doi: 10.1167/7.8.10
- Ooi, T. L., & He, Z. J. (2003). A distributed intercortical processing of binocular rivalry: Psychophysical evidence. *Perception*, 32(2), 155–166.
- O’Shea, R. P., & Crassini, B. (1984). Binocular rivalry occurs without simultaneous presentation of rival stimuli. *Perception & Psychophysics*, 36(3), 266–276.
- Paffen, C. L. E., Naber, M., & Verstraten, F. A. J. (2008). The spatial origin of a perceptual transition in binocular rivalry. *PLoS ONE*, 3(6), e2311. doi: 10.1371/journal.pone.0002311
- Pastukhov, A., & Braun, J. (2008). A short-term memory of multi-stable perception. *Journal of Vision*, 8(13), 7. doi: 10.1167/8.13.7
- Pearson, J., & Brascamp, J. W. (2008). Sensory memory for ambiguous vision. *Trends in Cognitive Sciences*, 12(9), 334–341.
- Pettigrew, J. D., & Miller, S. M. (1998). A “sticky” interhemispheric switch in bipolar disorder? *Proceedings of the Royal Society of London B: Biological Sciences*, 265(1411), 2141–2148.
- Poldrack, R. A. (2012). The future of fMRI in cognitive neuroscience. *Neuroimage*, 62(2), 1216–1220.
- 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.
- Ramsey, J. D., Hanson, S. J., Hanson, C., Halchenko, Y. O., Poldrack, R. A., & Glymour, C. (2010). Six problems for causal inference from fMRI. *Neuroimage*, 49(2), 1545–1558.
- Ritter, P., & Villringer, A. (2006). Simultaneous EEG-fMRI. *Neuroscience & Biobehavioral Reviews*, 30(6), 823–838.
- Roberts, T. F., Tschida, K. A., Klein, M. E., & Mooney, R. (2010). Rapid spine stabilization and synaptic enhancement at the onset of behavioural learning. *Nature*, 463(7283), 948–952.
- Salzman, C., Murasugi, C., Britten, K. H., & Newsome, W. T. (1992). Microstimulation in visual area MT: Effects on direction discrimination performance. *Journal of Neuroscience*, 12(6), 2331–2355.
- Seely, J., & Chow, C. C. (2011). The role of mutual inhibition in binocular rivalry. *Journal of Neurophysiology*, 106(5), 2136–2150.
- Sengpiel, F., Freeman, T. C. B., Bonhoeffer, T., & Blakemore, C. (2001). On the relationship between interocular suppression in the primary visual cortex and binocular rivalry. *Brain and Mind*, 2, 39–54.
- Shannon, R. W., Patrick, C. J., Jiang, Y., Bernat, E., & He, S. (2011). Genes contribute to the switching dynamics of bistable perception. *Journal of Vision*, 11(3), 8. doi: 10.1167/11.3.8

- Sobel, K. V., & Blake, R. (2002). How context influences predominance during binocular rivalry. *Perception, 31*(7), 813–824.
- Stollenwerk, L., & Bode, M. (2003). Lateral neural model of binocular rivalry. *Neural Computation, 15*(12), 2863–2882.
- Stosiek, C., Garaschuk, O., Holthoff, K., & Konnerth, A. (2003). In vivo two-photon calcium imaging of neuronal networks. *Proceedings of the National Academy of Sciences USA, 100*(12), 7319–7324.
- Stuit, S. M., Verstraten, F. A. J., & Paffen, C. L. E. (2010). Saliency in a suppressed image affects the spatial origin of perceptual alternations during binocular rivalry. *Vision Research, 50*(19), 1913–1921.
- Suzuki, S., & Grabowecy, M. (2007). Long-term speeding in perceptual switches mediated by attention-dependent plasticity in cortical visual processing. *Neuron, 56*(4), 741–753.
- Svoboda, K., & Yasuda, R. (2006). Principles of two-photon excitation microscopy and its applications to neuroscience. *Neuron, 50*(6), 823–839.
- 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., & Kanwisher, N. (1998). Binocular rivalry and visual awareness in human extrastriate cortex. *Neuron, 21*(4), 753–759.
- Treisman, A. (1962). Binocular rivalry and stereoscopic depth perception. *Quarterly Journal of Experimental Psychology, 14*(1), 23–37.
- Tsuchiya, N., & Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nature Neuroscience, 8*(8), 1096–1101.
- van Boxtel, J. J. A., Alais, D., Erkelens, C. J., & van Ee, R. (2008). The role of temporally coarse form processing during binocular rivalry. *PLoS ONE, 3*(1), e1429. doi:10.1371/journal.pone.0001429
- van Boxtel, J. J. A., Knapen, T., Erkelens, C. J., & van Ee, R. (2008). Removal of monocular interactions equates rivalry behavior for monocular, binocular, and stimulus rivalries. *Journal of Vision, 8*(15), 13. doi:10.1167/8.15.13
- van Boxtel, J. J. A., & Koch, C. (2012). Visual rivalry without spatial conflict. *Psychological Science, 23*(4), 410–418.
- van Boxtel, J. J. A., Tsuchiya, N., & Koch, C. (2010). Opposing effects of attention and consciousness on afterimages. *Proceedings of the National Academy of Sciences USA, 107*(19), 8883–8888.
- van Ee, R. (2005). Dynamics of perceptual bi-stability for stereoscopic slant rivalry and a comparison with grating, house-face, and Necker cube rivalry. *Vision Research, 45*(1), 29–40.
- van Ee, R. (2009). Stochastic variations in sensory awareness are driven by noisy neuronal adaptation: Evidence from serial correlations in perceptual bistability. *Journal of the Optical Society of America A: Optics, Image Science, and Vision, 26*(12), 2612–2622.
- van Ee, R. (2011). Percept-switch nucleation in binocular rivalry reveals local adaptation characteristics of early visual processing. *Journal of Vision, 11*(2), 13. doi:10.1167/11.2.13
- van Ee, R., van Boxtel, J. J. A., Parker, A. L., & Alais, D. (2009). Multisensory congruency as a mechanism for attentional control over perceptual selection. *Journal of Neuroscience, 29*(37), 11641–11649.
- Watanabe, M., Cheng, K., Murayama, Y., Ueno, K., Asamizuya, T., Tanaka, K. et al. (2011). Attention but not awareness modulates the bold signal in the human V1 during binocular suppression. *Science, 334*(6057), 829–831.

- Wen, Y., & Zhang, Q. (2009). Ensemble cortical responses to rival visual stimuli: Effect of monocular transient. *Biochemical and Biophysical Research Communications*, 380(1), 105–110.
- Wheatstone, C. (1838). Contributions to the physiology of vision. – Part the first. On some remarkable, and hitherto unobserved, phenomena of binocular vision. *Philosophical Transactions of the Royal Society of London*, 128, 371–395.
- Whittle, P. (1963). *Binocular rivalry*. (Doctoral dissertation, Cambridge University, 1963).
- 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 USA*, 103(46), 17507–17512.
- Wilson, H. R. (2003). Computational evidence for a rivalry hierarchy in vision. *Proceedings of the National Academy of Sciences USA*, 100(24), 14499–14503.
- Wilson, H. R. (2007). Minimal physiological conditions for binocular rivalry and rivalry memory. *Vision Research*, 47(21), 2741–2750.
- Wilson, H. R., Blake, R., & Lee, S.-H. (2001). Dynamics of travelling waves in visual perception. *Nature*, 412(6850), 907–910.
- Wolfe, J. M. (1986). Stereopsis and binocular rivalry. *Psychological Review*, 93(3), 269–282.
- Wunderlich, K., Schneider, K., & Kastner, S. (2005). Neural correlates of binocular rivalry in the human lateral geniculate nucleus. *Nature Neuroscience*, 8(11), 1595–1602.
- Yacoub, E., Shmuel, A., Logothetis, N., & Uğurbil, K. (2007). Robust detection of ocular dominance columns in humans using Hahn Spin Echo BOLD functional MRI at 7 Tesla. *Neuroimage*, 37(4), 1161–1177.
- Yang, Y., Rose, D., & Blake, R. (1992). On the variety of percepts associated with dichoptic viewing of dissimilar monocular stimuli. *Perception*, 21(1), 47–62.
- Zhou, W., Jiang, Y., He, S., & Chen, D. (2010). Olfaction modulates visual perception in binocular rivalry. *Current Biology*, 20(15), 1356–1358.