



Opinion piece

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Can binocular rivalry reveal neural correlates of consciousness?

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This essay critically examines the extent to which binocular rivalry can provide important clues about the neural correlates of conscious visual perception. Our ideas are presented within the framework of four questions about the use of rivalry for this purpose: (i) what constitutes an adequate comparison condition for gauging rivalry's impact on awareness, (ii) how can one distinguish abolished awareness from inattention, (iii) when one obtains unequivocal evidence for a causal link between a fluctuating measure of neural activity and fluctuating perceptual states during rivalry, will it generalize to other stimulus conditions and perceptual phenomena and (iv) does such evidence necessarily indicate that this neural activity constitutes a neural correlate of consciousness? While arriving at sceptical answers to these four questions, the essay nonetheless offers some ideas about how a more nuanced utilization of binocular rivalry may still provide fundamental insights about neural dynamics, and glimpses of at least some of the ingredients comprising neural correlates of consciousness, including those involved in perceptual decision-making.

1. Introduction

The topic of this special issue—perceptual awareness and its neural basis—has intrigued philosophers for centuries, and in recent years it has become a core focus within cognitive neuroscience. Central to this topic is the notion 'neural correlates of consciousness' (NCsC) [1–6]. These are the brain events that underlie the conscious states experienced by sentient observers, the 'minimal neuronal mechanisms jointly sufficient for one specific conscious percept' [4]. In pursuit of clues for identifying NCsC, psychologists and neuroscientists have focused especially on a variety of compelling visual phenomena for which one's conscious percept changes over time even though the objects or events one is viewing remain unchanged [7,8]. These fluctuations in visual awareness occur because these objects or events are ambiguous with respect to their identity and, therefore, plausibly support conflicting interpretations. This combination of unchanging physical stimulation and varying awareness is valuable because it allows a comparison of neural events between moments that differ specifically with regard to conscious state, and not with regard to physical input.

Within the stable of visual phenomena that have been deployed to implement this strategy, binocular rivalry stands out as a real workhorse. In binocular rivalry, one eye views a given image while a different image is presented to the corresponding region of the other eye. This incongruence causes the observer to perceive only one of the images at a time, with perception alternating between images every few seconds. We can think of several possible reasons why scientists have been attracted to this particular form of perceptual bistability.

- (i) Rivalry is compelling: a normally visible, potentially interesting and complex image (e.g. your own face) can appear and disappear from awareness for several seconds at a time.

- (ii) Rivalry is very robust with regard to the content of the images: whether one is interested in perception of faces or perception of, say, colours or lines, rivalry is elicited by a broad range of images presented in interocular conflict.
- (iii) Perceptual dominance fluctuates unpredictably over time during rivalry, implying the underlying involvement of dynamic neural processes.
- (iv) Fluctuations in perception during rivalry can be influenced by manipulating simple stimulus variables such as contrast or contour density, and some evidence suggests that object-related properties of images (e.g. figural coherence) also can impact rivalry dynamics.

For these reasons, rivalry has become a paradigm phenomenon for pursuing the NCsC, at least as that term applies to visual awareness (e.g. [9]). Without a doubt, the fluctuations in visual awareness one experiences during rivalry are of particular interest to the neuroscience of consciousness, as they are endogenously mediated, being produced by variations in neural activity within visually activated regions of the brain. As such, these fluctuations are distinct from those experienced, say, when viewing two different stimuli that are physically turned on and off reciprocally over time, a sequence of events that will cause changes at many neural stages, including peripheral ones more closely associated with sensation than with perception (e.g. the photoreceptors in the retina).

While acknowledging this special position of rivalry in the search for NCsC, we here ask a more specific question: if one can identify the neural events driving perception during binocular rivalry, will one have identified NCsC? This is certainly what is explicitly or implicitly assumed by many studies on the topic, but our aim in this essay is to outline reasons that prompt scepticism. From the outset, we want to acknowledge that others have written cogent, critical essays on the potential pitfalls of drawing conclusions about consciousness from percept-related fluctuations in activity [10–12]. While our essay will touch on some of these same pitfalls, our focus is uniquely on binocular rivalry and what it can tell us about conscious visual perception. Our ideas are presented within the framework of four broad concerns about the use of rivalry for this purpose, one being methodological and the other three being conceptual. As the essay unfolds, we will offer some ideas about how a more nuanced utilization of binocular rivalry may still provide fundamental insights about neural dynamics and glimpses of at least some of the ingredients comprising NCsC. We start with our practical concern.

2. Concern 1: what constitutes an adequate comparison condition to rivalry?

Our first concern focuses on an experimental design issue when using binocular rivalry as an inferential tool for disrupting visual awareness. The concern, in a nutshell, centres on the selection of the appropriate comparison condition(s) with which to contrast observations made during binocular rivalry. Historically, this concern pertains to studies seeking to learn the extent to which a visual stimulus remains effective despite being suppressed from awareness [13], but it also arises when using rivalry as a tool for identifying NCsC.

The most straightforward way to introduce this concern is by way of an example.

Decades ago, one of us (R.B.) co-authored a paper describing the influence of rivalry on the build-up of two well-known visual after-effects produced by prolonged adaptation to a grating pattern [14]. One after-effect is the temporary elevation in contrast threshold for subsequently viewed gratings identical to the adapting grating, and the other one is the brief misperception of the spatial frequency of gratings similar, but not identical, to the spatial frequency of the adapting grating. Knowing that these after-effects increased in strength with the duration of pattern adaptation, we asked what would happen if a monocularly viewed, high contrast adaptation grating was suppressed for a portion of the adaptation duration owing to its being engaged in rivalry with a dissimilar image presented to the other eye. To quote from that 1974 paper,

If the inducing stimulus remains effective while suppressed, the magnitude of the aftereffect will correspond to the duration of physical stimulation. But if the stimulus is rendered ineffective by suppression the aftereffect will be weakened, and its magnitude will correspond to the duration of phenomenal viewing [14, p. 488].

For the purposes of comparison that study included two monocular control conditions. The first involved presenting the high contrast adapting grating to one eye without pairing it with a rival grating in the other eye, thus providing an estimate of the after-effect strength expected if suppression had no effect on adaptation. The second condition, dubbed the rivalry mimic condition, entailed presenting and removing the monocular adaptation grating in a temporal pattern that followed the alternations of rivalry reported on a previous, genuine rivalry trial (figure 1). This latter condition, therefore, aimed to estimate the amount of reduction that would be expected if suppression did indeed render the adapting grating ‘ineffective’.

Versions of this experimental design, based on the same logic laid out in the 1974 paper, have been employed in many subsequent studies of rivalry suppression and visual adaptation [15–25], often with the aim of gauging the involvement of the adapting neural processes in conscious perception. Moreover, there are examples in the rivalry literature where measures of visual processing other than adaptation have been assessed under rivalry suppression and compared to values measured under non-rivalry, monocular conditions [26,27].

We can envision several potential problems associated with this strategy. First, the logic of the approach entails comparing measures obtained under monocular viewing without rivalry to measures obtained during rivalry. This comparison, however, introduces the possibility of confusing effects of invisibility with effects of the presence of a rivalling counterpart but not specific to periods of invisibility. After all, monocular stimulation is demonstrably different from binocular stimulation in other respects [28,29], and in several contemporary models of binocular vision those differences are embodied in contrast gain control mechanisms sensitive to the relative strengths of inputs to the two eyes [30,31]. In keeping with this notion, activity in visual cortex (as measured with functional magnetic resonance imaging, fMRI) evoked by a monocular image is reduced when a conflicting pattern is presented to the other eye, regardless of whether this conflicting pattern is strong enough to cause the original image to perceptually disappear [32].

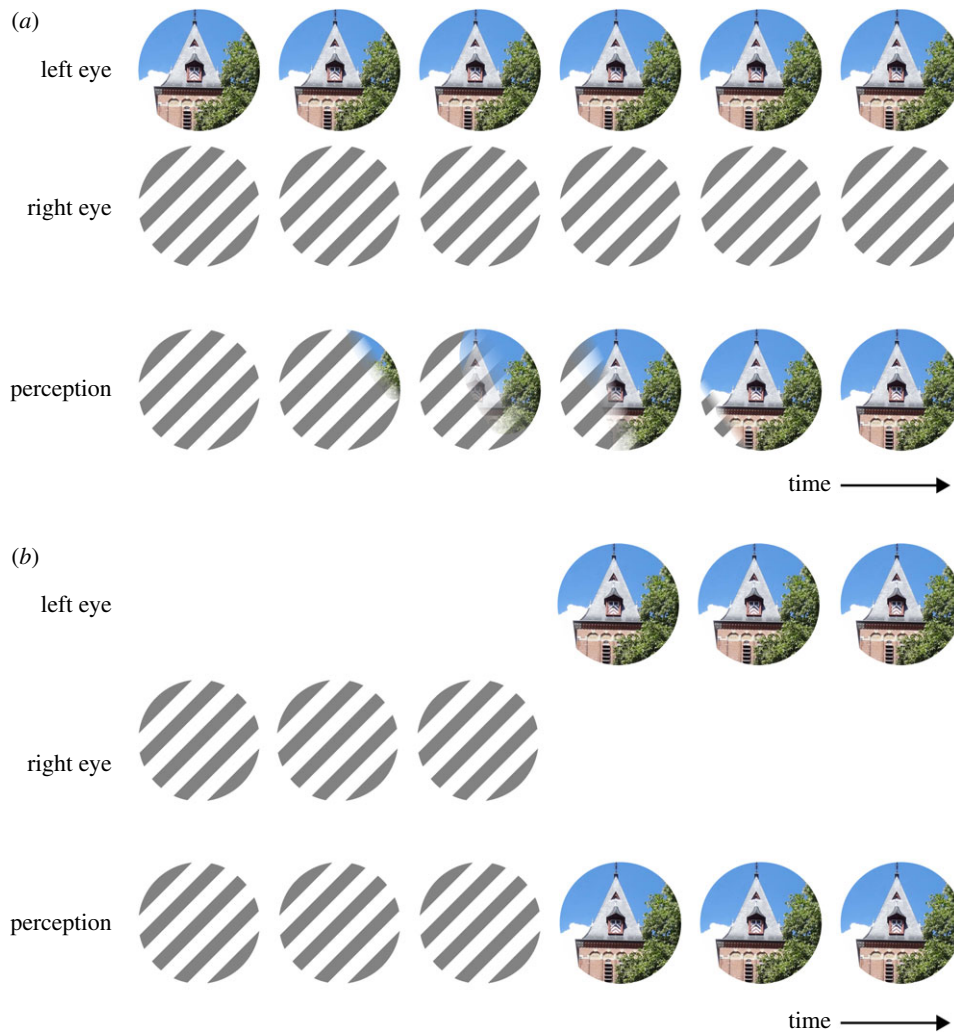


Figure 1. Binocular rivalry and a rivalry mimic condition. (a) During binocular rivalry, each eye views a different image, and transitions in dominance from one image to the other often take the form of a wave whereby one image is swept from awareness by the other. (b) Many experimental designs also include a rivalry mimic condition, where the perceptual experience reported during rivalry is approximated using on-screen replay. In the implementation devised by Blake & Fox [14] illustrated here, two monocular images are alternately removed following a time series matching that actually reported on a previous trial of genuine rivalry alternations. Mimic conditions provide a baseline that approximates what would happen during rivalry if perceptual suppression completely eradicated neural processing of the suppressed image. A limitation of mimic conditions is that the perceptual match with real rivalry is only approximate. Notably, the dynamically changing perceptual experiences accompanying wave-like dominance transitions are not captured by standard mimic conditions. (Online version in colour.)

In a related vein, the alternating monocular stimulation regime, illustrated schematically in figure 1*b*, was meant to mimic what an observer experiences during genuine binocular rivalry. For several reasons, we doubt whether this condition is sufficient for that purpose. First, neural events associated with suppression of a stimulus are certainly not equivalent to those associated with complete, intermittent removal of that stimulus—during suppression phases, evidence for traces of residual neural activity associated with the suppressed stimulus can be found within early stages of visual processing as well as in higher tier visual areas [33–37]. At best, therefore, a rivalry mimic condition can reveal the upper limit on the extent to which rivalry suppression might squelch visual responses. This nuance becomes particularly important if the dependent variable being used to assess suppression's effect scales in a saturating fashion with stimulus strength (e.g. visual contrast), which is true for many variables used in this context, such as after-effect strength or fMRI response amplitude. In such cases, the mimic condition can be misleading. An illustration of this problem is the 1974 study we mentioned at the start of this section [14], which mistakenly inferred that suppression had no effect on

the build-up of pattern adaptation produced by rival gratings. Subsequent work has since taught us that suppression can, in fact, weaken pattern adaptation but that this weakening only shows up for adapter gratings of moderate to low contrast, as a consequence of the saturating contrast dependence of pattern adaptation [38]. A more appropriate mimic condition for this form of adaptation, in other words, would be a monocular grating whose actual contrast was modulated over time between one value and another, with the lower value matched to the effective contrast reduction associated with suppression. Visual adaptation after-effects arising at higher visual stages [25] are more likely to require greater attenuation in stimulus strength to mimic an effect of suppression [39].

The second potential problem with the rivalry mimic condition pertains to studies that focus, not so much on the neural events that distinguish dominance from suppression states, but on neural events that co-occur with the alternations between states. This concern, too, can be illustrated by an example from the literature. In a highly influential paper, Lumer *et al.* [40] found that fronto-parietal areas of the human brain become temporarily active around the

time an observer experiences a perceptual alternation during binocular rivalry, yet those same areas remained relatively inactive during conditions in which rivalry is mimicked by turning the left- and right-eye patterns on and off alternately over time (figure 1*b*). These differences in cortical activity during genuine and mimicked rivalry were taken as evidence that endogenous alternations in perception during rivalry were controlled by those fronto-parietal networks.

However, a different slant on this result was offered by Knapen *et al.* [41], who opined that the rivalry mimic condition, in fact, does not adequately recreate the potentially confusing perceptual judgement confronting observers during transitions in dominance from one rival stimulus to the other. Rather than dominance switching abruptly from one stimulus to the other, transitions in dominance are often dynamic and unpredictable: during a transition, one can experience mixed dominance where bits and pieces of both stimuli are simultaneously visible either superimposed or within different portions of the visual field, and the transition itself can resemble a wave whereby one image appears to be swept from awareness by the other (figure 1*a*). Consequently, an observer instructed to track switches in dominance (e.g. by pressing buttons) faces uncertainty about when or if to make a perceptual report (i.e. button press). The confusion and heightened attention prompted by these dynamic mixed perceptual states are not instigated by the conventional mimic condition (figure 1*b*). Indeed, when Knapen *et al.* [41] repeated Lumer *et al.*'s [40] procedure using more realistic mimic conditions that included mixture periods, they found that genuine rivalry and the mimic condition produced comparable activity in fronto-parietal networks. It remains to be learned just what role this activity has in rivalry, and that is going to hinge in part on when in time the activity arises relative to alternations [42]. But the methodological point remains indisputable: the oft-used mimic procedure is not perceptually equivalent to genuine rivalry alternations. In principle, this problem can be reduced by devising more realistic simulations of rivalry that include periods of mixed dominance using cross-faded blends as well as waves that originate at unpredictable locations and spread smoothly to produce a complete alternation [43–45]. However, nobody has yet devised a mimic condition so realistic that an informed observer might mistake it for rivalry.

How can these potential problems with monocular control conditions be avoided? With regard to work that aims to identify the neural and behavioural markers that distinguish two perceptual states, the most direct way is to compare measures obtained during dominance phases of a stimulus to those obtained during suppression phases of that same stimulus, so that the observer is viewing the same stimulus all along. This maximizes the likelihood that the stimulus conditions during periods of awareness of a given stimulus match the stimulus conditions during periods of unawareness of that stimulus. Comparing measures obtained during suppression to those obtained during dominance is the strategy very often employed in psychophysical studies using the so-called test probe technique [46], and the strategy can also be employed in concert with the adaptation procedure described above, by capitalizing on the fact that rivalry state durations vary considerably during the course of extended viewing (e.g. fig. 5 in [23]; fig. 3 in [38]). Moreover, it is the comparison often used in neurophysiological investigations of binocular rivalry [33,34], as well as in fMRI studies, in which the time course of fMRI response modulation is compared with the time course of perceptual dominance [35,47].

Next, we turn to the conceptual concerns that arise when using binocular rivalry to infer NCsC.

3. Concern 2: distinguishing abolished awareness from inattention

It is intuitively clear that there is a tight link between directing attention to an item and being aware of that item, prompting the question whether attention and awareness can, in fact, be studied as separate entities. The answer to this question remains a point of contention within the cognitive neuroscience literature (for reviews, see [48,49]). Side-stepping that debate, we want to discuss a more specific question: is it possible to distinguish a concomitant of stimulus invisibility during rivalry from inattention to that stimulus? When, for example, rivalry suppression reduces the effectiveness of an adaptation stimulus, is that reduction attributable to intermittent awareness of the stimulus or to intermittent withdrawal of attention from the stimulus? Or when the fMRI responses vary in strength over time in synchrony with alternations in perceptual dominance of a rival stimulus, is that variation in cortical activity attributable to neural suppression or to intermittent removal of attention?

It is plausible that part of the modulations that occur concomitantly with rivalry suppression arise from changes in attention. Some studies investigated the effectiveness of an adaptation stimulus that was suppressed during rivalry, while the observer was asked to direct his or her attention to either a feature (orientation; [50]) or the location [51] that was shared by this invisible stimulus. These studies found that the reduction in effectiveness of a suppressed stimulus can be partly recovered by this kind of attention instruction. Apparently, inattention contributes to the reduction in effectiveness that accompanies suppression in the absence of such an attention instruction. In a similar vein, Bahrami *et al.* [52] measured the fMRI responses in primary visual cortex (V1) to a stimulus suppressed in rivalry and reported that the smaller responses commonly found under suppression can be either compounded or partially counteracted, depending on the difficulty of a concurrent target detection task that presumably impacts the availability of residual attention that can be allocated to the suppressed stimulus.

In sum, several studies have now demonstrated that inattention is a likely contributor to modulations that occur during perceptual suppression. What has proved more difficult, however, is separating the effects of inattention from those of perceptual suppression *per se*. In this context, we would like to discuss two instances where such a separation has been claimed, but prematurely in our view. In one instance, observed changes in V1 fMRI response during perceptual suppression were reported to be entirely due to inattention, with no influence of perceptual suppression itself [6,53]. The second instance involves the opposite claim, namely that a particular suppression-related effect, in this case the modulation of negative afterimages, cannot be due to inattention, and must be due to perceptual suppression instead [23,54]. Interestingly, both these instances are associated with a very similar experimental approach, which we will discuss in more detail next.

The approach requires that an observer view a monocular stimulus that is either visible or suppressed in binocular rivalry, and at the same time the observer must attend either

to the location of that stimulus or to another location elsewhere. The approach, in other words, entails a two-by-two design where attention and suppression are both varied, with the intention of separately assessing the effects of each factor. The approach was first developed by van Boxtel *et al.* [23] in a study that measured negative afterimages, a psychophysical marker of neuronal adaptation. This study demonstrated that afterimages were less persistent after viewing an adapter suppressed in binocular rivalry than after viewing a visible adapter (confirming [19,20]), yet more persistent after attending away from the adapter than after attending toward it (consistent with [54,55]). Thus, perceptual suppression reduced afterimage durations, whereas inattention enhanced them. These opposite effects would seemingly imply that reduced afterimage duration represents one effect of rivalry suppression that cannot be ascribed to inattention.

This implication would be premature, however, as revealed by a closer look at inattention's counterintuitive tendency to increase afterimage duration. This tendency is counterintuitive because inattention weakens neural responses and, presumably, the neural adaptation that underlies the formation of afterimages. A plausible resolution to this paradox is imaginable: there exists a second form of adaptation, pattern adaptation, that does not lead to afterimage formation but does impair sensitivity on visual detection tasks. This form of adaptation, too, is diminished when attention is diverted away from the adapter [55,56]. Asking an observer to report the duration of an afterimage after attending elsewhere than the location of the adapter, therefore, boils down to asking a more sensitive observer to report on a weaker stimulus, leaving room for a range of outcomes. Indeed, subsequent work has shown that inattention can either shorten or lengthen afterimage duration, depending on the exact stimulus conditions [24]. More importantly, this work demonstrated that inattention and suppression have qualitatively similar effects when the two contributing types of adaptation are assessed independently, thus leaving open the possibility that the effects of suppression on afterimages are, in part, due to inattention after all.

Using a design very similar to that of van Boxtel *et al.* [23], Watanabe *et al.* [53] also independently manipulated attention and stimulus awareness, now using fMRI to measure cortical activity in human V1. In this case, the design led to the conclusion that modulations of V1 activity that co-occur with absence of awareness are entirely due to inattention, not unawareness. This study found that directing attention toward the spatial location of a grating enhanced fMRI responses relative to attending elsewhere, and that this was true regardless of whether the grating was perceptually suppressed (replicating e.g. [52,57,58]). More surprisingly, the study also reported that perceptual suppression left V1 responses altogether unaffected, which contradicts earlier findings (see review by Tong *et al.* [59]). Watanabe *et al.* [53] concluded that those earlier findings must have reflected an artefact caused by a reduction of attention concurrent with rivalry suppression, and that rivalry suppression, in itself, does not modulate V1 activity. What is unsatisfying about this conclusion, however, is that Watanabe *et al.* failed to observe suppression-related modulation of V1 activity even in their condition requiring observers to attend to the grating's location, an instruction that exactly matches that of earlier studies that did find such modulation. Attributing the positive outcome of earlier studies to a temporary reduction of attention during suppression, as Watanabe *et al.* did, raises

the question of why the matching condition in their experiment did not show the same result. A different study, co-authored by one of us (D.H.), reached the opposite conclusion as Watanabe *et al.* did, using substantially the same stimulus configuration and test procedure [60]. We did find reliable differences in V1 activity between conditions with and without suppression, with attention diverted away from the grating location. We suggested statistical power as one possible reason for the negative finding in the Watanabe *et al.* study.

Where do the above considerations leave us with regard to making a distinction between effects of suppression of awareness and effects of inattention? We have argued that inattention likely does contribute to modulations that co-occur with rivalry suppression, and that existing studies have not yet been entirely successful in teasing apart these two contributions. Also, we have pointed to designs that manipulate the amount of attention paid to a rival stimulus. With regard to this latter strategy, we would like to make the following additional note. Manipulations of attention are actually known to influence the dynamics of rivalry (for reviews, see [61,62]). In particular, rivalry alternations slow when attention is diverted to a concurrent task, with the degree of slowing directly related to the difficulty of the distracting task [63]. Even more remarkable, when attention is completely and unequivocally diverted for a few seconds away from the continued presence of rival stimuli, rivalry appears to cease altogether as evidenced by the state of rivalry when attention subsequently returns to the rival stimuli [64]. This latter finding dovetails with the finding that withdrawing attention from rival stimuli (i) abolishes the neural signature of changing states of rivalry, as measured with visually evoked responses recorded from human occipital cortex [65], and (ii) erases rivalry-related fMRI responses measured in human V2 and V3, but not V1, in response to exogenously triggered transitions in rivalry state [66]. These findings underscore the potential for confusion when trying to untangle the effects of inattention and stimulus invisibility by withdrawing attention from a rival stimulus.

4. Concern 3: do neural correlates of rivalry suppression generalize?

Studies of NCsC during rivalry typically assume that the results will generalize to other stimulus conditions and perceptual phenomena. The NCsC paradigm depends on such an assumption. If the NCsC differ for each and every stimulus condition, then there would be no way to get traction. But there is cause for concern.

Computational models posit a hierarchy of processing stages in binocular rivalry [67,68]. According to those models, component areas in the hierarchy may be differentially involved, depending on the nature of the stimuli used to instigate bistability and the manner in which those stimuli are presented. Some stimuli (for example, patterns comprising oriented contours) are optimally configured to evoke cooperative and competitive interactions among neurons in V1, because those neurons are functionally organized in a retinotopic map and within orientation and ocular dominance columns. Other stimuli, because of their more complex spatial configuration [39,69] or their dynamic properties [70,71], may evoke stronger neural competition in high-tier visual areas where neurons are selective for object categories [47,72] or for

motion [73]. In other words, such models suggest that perceptual suppression may have different neural correlates, depending on the visual images and bistable phenomenon involved. Indeed, we will next discuss empirical observations that confirm this prediction.

As summarized above, binocular rivalry is accompanied by neural modulations within human primary visual cortex, which to the line of thinking about NCsC, could be suggestive evidence that V1 contains correlates of consciousness. Yet, other fMRI work that has measured V1 activity in observers experiencing motion-induced blindness, another compelling form of bistable perception in which conscious awareness fluctuates over time [74], found no hints of percept-dependent activity in V1 [75]. Instead, percept-related fluctuations in cortical activity were found only in higher tier areas of both dorsal and ventral streams. This disparity in results within V1 implies that the correlation between perception and V1 activity during rivalry may be a by-product of using rivalry as a tool.

Similar disparities have been observed, even within the binocular rivalry paradigm itself. Maier *et al.* [76] found that the firing rate of neurons in cortical area MT of macaque monkeys signalled perceptual dominance of these neurons' preferred grating stimulus when this stimulus was engaged in rivalry with a particular conflicting image, but ceased to signify perception when the same preferred grating rivalled with a different image. Strikingly, the monkey's subjective experience during perception of the preferred grating is unlikely to depend much on what is perceptually suppressed at that moment, yet these findings indicate that the neural correlates of this experience do.

This brings us to our fourth and final concern, which is really a culmination of thoughts raised in the earlier parts of this essay together with broad concerns about the logic involved in identifying NCsC using any single phenomenon, for example rivalry.

5. Concern 4: are neural correlates of rivalry perception NCsC?

In developing their idea of NCsC, Crick & Koch [1,2] endorsed the use of binocular rivalry and other forms of bistable perception to separate neural populations into distinct categories, one consisting of neurons whose activity changes with perception and the other consisting of neurons whose activity remains invariant despite changes in perception, a division that builds on earlier notions in the psychology literature [77,78]. A widely cited example of this strategy in action is provided by the study by Leopold & Logothetis [34]. Recording single-unit activity from neurons in early visual cortex of alert, behaving monkeys, they categorized neurons in terms of whether or not the neurons' activity was modulated in synchrony with the perceptual reports made by the monkey (figure 2*a*). As indicated by the title of that paper—'Activity changes in early visual cortex reflect monkeys' percepts during binocular rivalry'—some (but not all) neurons did indeed exhibit percept-related activity, with the proportion of percept-related neurons increasing in higher tier areas compared with V1. Brain imaging studies in humans using fMRI point to the same general findings, namely modulations in neural responses time-locked to fluctuations in perceptual dominance during rivalry (figure 2*b*).

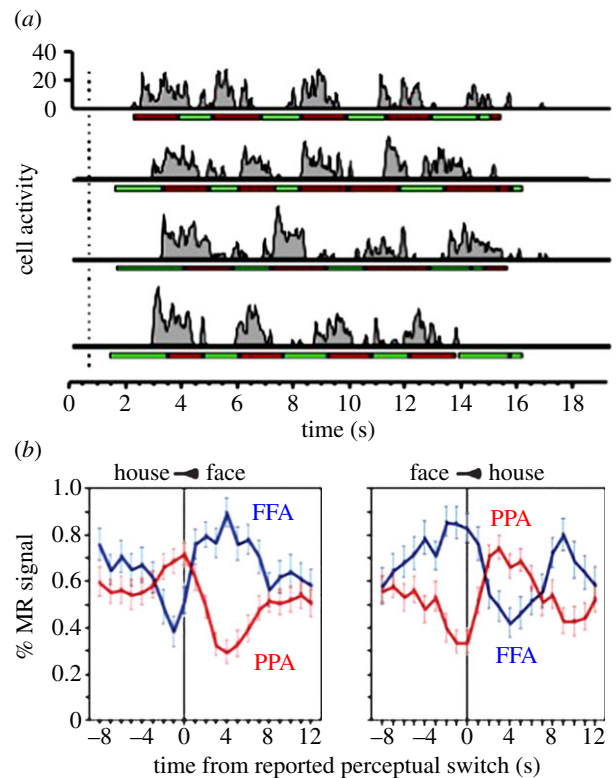


Figure 2. Two examples of modulations in neural responses coincident with fluctuations in perceptual state during binocular rivalry. (*a*) Neural spiking activity in a single cortical neuron recorded from an alert, behaving monkey trained to report fluctuations in perceptual dominance, which are denoted by the light and dark (red and green, respectively, online) horizontal lines below the spike train time series. Adapted from [7]. (*b*) Modulations in fMRI responses, timelocked to transitions in perceptual state during rivalry produced by dichoptic presentation of the image of a house and of a face. These modulations were measured in two ventral stream areas within the human brain, the fusiform face area (FFA) and the parahippocampal place area (PPA). Adapted from [47]. (Online version in colour.)

Those rivalry-related modulations in neural responses, like the single-unit responses, tend to be more pronounced within higher tier visual areas, particularly in the ventral stream pathway [47,72,79], but reliable rivalry modulations are also measurable in very early stages of the visual pathways including the thalamus [80,81] and primary visual cortex [35,36,81,82].

What conclusions can one draw from results like these? In particular, assuming that appropriate conditions are in place to rule out alternative accounts for such modulations, for example those raised by us in the earlier sections, and assuming that one thus obtained unequivocal evidence for a causal link between a fluctuating measure of neural activity and fluctuating perceptual states during rivalry, would this unequivocally show that this neural activity is part of the NCsC? We think not, as we will explain below.

Papers touting binocular rivalry as a powerful inferential tool for pursuing NCsC often include a statement to the effect that physical stimulation remains invariant while perception fluctuates during rivalry, the implication being that binocular rivalry dissects input-related neural events from percept-related neural events and, therefore, potentially reveals NCsC. But this characterization of rivalry and its associated implication we find questionable for two reasons.

First, the proximal stimulus, rather than remaining invariant, probably does change in subtle ways during rivalry, owing to

tiny eye movements that arise consequent to rival stimulation [83] and to pupillary dilations preceding [84,85] and during [86] state changes in rivalry. Moreover, the neural representations of rivaling left- and right-eye inputs are impacted very early in visual processing, both in strength and in fidelity [87]. These consequences of rival stimulation, while percolating on to subsequent stages of visual processing, may have no bearing at all upon NCsC under non-rivalry conditions.

Second, the dichotomy drawn between input-related events and NCsC is probably oversimplified in the first place. This verdict of oversimplification has been voiced by others as well [10,11], and it follows from several of the issues discussed earlier in our essay. For instance, we now know that some neural events transpiring during rivalry turn out to correlate neither with the input nor with conscious perception *per se*, but instead with attention. Moreover, other neural events may correlate with perception when binocular rivalry is involved, but not when using a different phenomenon, for example motion-induced blindness to produce fluctuations in awareness. In other words, correlates of rivalry perception are not necessarily NCsC. What one ideally would want in the experimental search for NCsC is a procedure that not only leaves physical stimulation intact while perception fluctuates, but that also leaves all neural processing intact apart from that which is part of the NCsC for the particular perceptual states experienced by the observer. But the evidence indicates that binocular rivalry does not quite allow this idealized experimental approach.

6. Conclusion

The idea to use binocular rivalry to search for NCsC was never naive. As Crick and Koch developed the idea, spurred on by experimental results in monkeys undergoing rivalry [33,34], they noted that ‘just because a particular neuron follows a percept, it does not automatically imply that its firing is part of the NCC’ [1]. Since then the focus in the experimental literature has been on exploring the new territory in terms of its empirical characteristics (‘what correlates with rivalry dominance?’), but this exploration has unearthed new experimental hurdles, described in our first concern (§2), as well as problems of interpretation, described in the remaining concerns (§§2–5). Consequently, we have grown more sceptical about the utility of binocular rivalry as a tool for discovering the NCsC.

But in the process, we believe that there has been considerable progress toward a different goal of characterizing neural processing and neural dynamics. Binocular rivalry provides

a unique window into neural dynamics. Indeed, a number of dynamic systems models have been proposed to explain the alternating periods of perceptual dominance for rival stimulation, including the periods of mixed percepts and travelling waves of changing dominance [31,88–92]. There is increasing evidence that the brain relies on a set of canonical neural computations, repeating them across brain regions and modalities to apply similar operations to different problems [93]. Consequently, the computational principle revealed by binocular rivalry may very well generalize and have widespread application, including shedding light on clinical conditions. Specifically, there is evidence that rivalry dynamics depend on the balance of excitation and inhibition in neural circuits [94], and an imbalance of excitation and inhibition has been hypothesized to underlie neural dysfunction in developmental disabilities, psychiatric illnesses and neurological diseases [95]. Such hypotheses can, therefore, be tested non-invasively through simple behavioural experiments with binocular rivalry [96].

Where, then, does this leave us with respect to the goal of characterizing the neural basis of perceptual awareness? Our guess is that fluctuations in perceptual awareness during rivalry and, for that matter, during other forms of multistable perception may depend critically on processes involved in perceptual decision-making. After all, when participating in a rivalry experiment, observers are instructed to press one of several buttons to indicate their changing perceptual state. Following that, instruction involves making an ongoing series of perceptual decisions (‘Do I see this image or that image?’), not unlike the perceptual detection and discrimination decisions that have been studied for decades using conventional psychophysical procedures with sequences of discrete trials. There is a large, growing literature on the neural circuits and computations underlying such perceptual decisions [97]. We are intrigued by the possibility that judgments about perceptual awareness (‘Do I see something, and if so, was it this image or that image?’) may, in fact, be embodied in the same neural machinery responsive for other forms of perceptual decisions.

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which enables researchers to examine the contents of hundreds of bamboo crates packed with dinosaur bones that have remained unopened since they were brought by ship almost a century ago.

Specimens such as a finely written 16th century log book and museum director Reinhold Lienfelder's personal favourite, a sea-foam-coloured cabinet full of rare corals, have been restored. And items with a darker history, such as the panda that Herman Goering ordered to be prepared for the Berlin 1935 'hunting exhibition' are also on display. Even the remains of a parrot called Jacob, the favourite pet of Alexander von Humboldt, are there.

"Animals that are now under the strictest of protections were at one time trophies," says Ferdinand Damaschun, head of exhibitions.

Many items and oddities like the stuffed parrot, collected by researchers around the world, are exhibited for the first time in the show and among them are blown-glass models of jellyfish.

The museum's half million visitors per year, along with the many researchers who come from around the globe, can now view and investigate some 270,000 specimens of fish, snakes, snails, frogs and other animals collected over the years.

The massive newly restored room, full from floor to ceiling with the illuminated jars of preserved specimens, is undoubtedly the highlight of the museum's anniversary celebration.

"These are valuable, irreplaceable cultural assets that have been collected over two centuries and remain indispensable for biological research to this day, and are extensively used internationally," says Damaschun.

"It is a milestone for the preservation of our collections," he says. For the exhibition — called Klasse, Ordnung, Art — the museum turns the magnifying glass back on itself, exploring the evolution of natural history itself, the changing ideas of collection strategies, and how the country's political history has coloured this past.

"We have a lot of curiosities here," says Damaschun.

The exhibition Klasse, Ordnung, Art is open until February 28, 2011.

Q & A

Randolph Blake

Randolph Blake is Centennial Professor of Psychology and Professor of Ophthalmology at Vanderbilt University and Professor of Brain and Cognitive Sciences at Seoul National University. Using psychophysics, neural modeling and brain imaging, he studies human perception and its neural concomitants. He is a member of the American Academy of Arts and Sciences, and his awards and honors include the 2006 IgNobel Prize for his anguishing study of the chilling sound of fingernails on a chalkboard.

What got you interested in psychology in the first place?

Entering college I had no career goals and just took courses willy-nilly. One was introductory psychology, and it really struck a chord in me. Experimental psychology, in particular, brought together my interests in math and science with my nascent enthrallment with human behavior. In my senior year I completed a reaction-time study of the psychological refractory period — the inability to do two things at once — and that culminated in my first publication. (My parents kept a reprint of the paper on their living room coffee table.) I was hooked and decided to tackle graduate school at Vanderbilt University.

Who cultivated your interest in visual perception? Robert Fox, my graduate adviser, infected me with curiosity about vision. He shaped my naïve ideas into tractable research questions; he also encouraged me to refine my twangy Texas accent. I spent time at Groningen University with W.J.M. Levelt, who at that time was the recognized expert on binocular rivalry, my dissertation topic. The opportunity to see what he was doing and how he was doing it was inspiring. I also took a memorable graduate seminar at University of Minnesota, led by the legendary perception psychologist J.J. Gibson. What an impressive scholar! The first day Gibson grilled each of us about our research interests, and he characterized mine — binocular rivalry — as a laboratory curiosity. I was unprepared for his bluntness and

learned a valuable lesson: science can be a rough and tumble activity.

What about your career trajectory after graduate school? I spent two years at Baylor College of Medicine receiving postdoctoral training in physiology and anatomy. That experience taught me that I have neither the patience nor the temperament to be neurophysiologist. On a positive note, I did develop and refine behavioral techniques for studying vision in the cat, and I carried that research program to Northwestern University, where I began my career as a professor.

What have cats taught us about vision that we couldn't have learnt from humans? For decades the cat had been the species of choice among neuroscientists studying vision. Consequently, there existed a wealth of information about the feline visual system, and behavioral studies could tell us what the world looks like to an animal whose visual nervous system was reasonably well understood. And we learned that cats and humans do not live in the same visual world. For example, we see fine spatial detail invisible to cats, whereas cats can see large, low contrast objects invisible to us. Ironically, this realization that cats and humans see things differently may have undermined the validity of cats as an animal model for human vision. In any event, I was lucky to be at Northwestern, for it was a very special place to be doing that kind of work.

And why was that? In those days, Northwestern was a major outpost for the study of spatial vision. Among its faculty was Robert Sekuler, a superb scientist, an effective teacher and a marvelous role model for a beginning assistant professor. Bob and I produced a perception textbook that has survived through five editions and three different publishers. We also spent enjoyable afternoons at Wrigley Field watching the Chicago Cubs lose baseball games. While at Northwestern, I had the good fortune to be taken under the wing of Christina Enroth-Cugell, at that time a world expert on the mammalian retina. Her lab attracted a steady stream of current and future stars in visual neuroscience, and I was a beneficiary of her magnetism. My research interests expanded to include human

stereopsis. Luckily for me that spring-boarded into an enduring research collaboration with Hugh Wilson, who at the time was at University of Chicago.

Why did you leave Northwestern and return to Vanderbilt? The opportunity to chair the Department of Psychology and help implement its radical reorganization emphasizing cognitive neuroscience. We also launched the Vanderbilt Vision Research Center, an interdisciplinary program whose impact has grown steadily over the years. With the move to Vanderbilt, my research interests broadened to include motion perception, perceptual organization, multi-sensory integration and synesthesia. I also had a hand in the embryonic brain imaging initiative launched at Vanderbilt University. Today that initiative has evolved into the Vanderbilt Institute of Imaging Sciences, one of the top imaging centers in the world.

And now you've joined the faculty at Seoul National University — how did that career decision come about? Two years ago, the Korean Ministry of Education, Science and Technology launched what is called the World Class University initiative. As part of that program, Seoul National University received a major grant to launch a new Department of Brain and Cognitive Sciences. Included were funds to recruit foreign scholars, including me, to help get the program off the ground. I already had in place collaborations with several Korean scientists, so spending one semester a year there was a natural extension of what I was already doing. Vanderbilt University liked the idea of my participating because they are committed to establishing ties with major universities outside the US. And my life-partner Elaine, who loves a good adventure, was excited by the challenges of living part-time in Seoul. My experiences so far have redoubled my enthusiasm for the program.

You mentioned synesthesia: that's a research field that seems to have blossomed into a cottage industry — what drew you into the mix? A casual conversation with one of my Vanderbilt colleagues who matter-of-factly described how black-and-white letters and numbers appeared colored to him, each

character having its own distinct, enduring hue. Intrigued but skeptical, I tried devising visual tasks where, unbeknownst to my synesthetic colleague, his illusory colors should either help him or hurt him if his colors were indeed “real.” Bottom line: he — and, subsequently, other color/orthographic synesthetes recruited into our project — performed on most tasks as if their colors were real, not simply metaphorical. Those devious studies were challenging to design and great fun to carry out. But they failed to answer the real perplexing question: how and why does the brain fabricate those illusory sensory experiences?

What led you to get involved in human brain imaging? My desire to resolve a controversy concerning the neural concomitants of binocular rivalry. I was introduced to brain imaging — baptized so to speak — by David Heeger, who at the time was at Stanford University. David, his student Alex Polonsky and I used functional magnetic resonance imaging (fMRI) to identify modulations in neural responses within primary visual cortex synchronized with fluctuations in visual perception during rivalry. That finding, since replicated in other studies, ran counter to the idea that rivalry was solely a high-level visual process. Upon returning to Vanderbilt, I cajoled Emily Grossman into using fMRI to pinpoint brain areas involved in another intriguing visual phenomenon, perception of biological motion. Her work blossomed into an excellent dissertation.

What stands out as a highlight accomplishment for you? I'd say my *Psychological Review* paper laying out a neural theory of binocular rivalry. The theory attributes rivalry to modulations in activity within neurons sensitive to eye of origin, with inhibitory interconnections creating suppression and adaptation causing alternations. Because it made explicit, testable predictions, the theory stimulated lots of experiments, including some of the influential studies by Nikos Logothetis and colleagues. Today, we know the theory was wrong in some respects, but aspects of it have survived testing. It is gratifying to have conceptualized an account of rivalry that helped accelerate interest in this beguiling phenomenon. It reinforces a lesson learned as a graduate student:

good theories, in principle, are easily disproved.

And has there been a particularly disappointing experience in your research career? Yes, the inability to get across the ideas developed by Sang-Hun Lee and me concerning temporal structure and visual grouping. To us, temporal structure was a refined, quantitative index of the Gestalt notion of ‘common fate’ — the tendency for stimulus features to cohere into a unified visual form when those features undergo correlated changes over time. Unfortunately, we didn't do a good job separating our ideas from the controversial notion of temporal synchrony as a neural coding strategy. We also never resolved a debate over the role of contrast summation in our novel grouping displays. Still, the notion of temporal structure as a form of ‘glue’ that binds features into objects remains compelling to me. It's a very Gibsonian idea, focusing as it does on information contained in the optic array of an active observer immersed in dynamic visual environment.

Well since you mention Gibson, let's return to his challenge to you concerning the relevance of studying rivalry — what maintains your interest in this so-called laboratory curiosity? The answer is easy: rivalry remains as fascinating to me today as it did four decades ago when Robert Fox first introduced me to it. Think about it: an ordinarily visible, interesting visual image — a familiar face, for example — disappears from awareness for seconds at a time, only to perceptually reemerge as another, equally meaningful stimulus viewed by the other eye drops out of awareness. You could believe that the experimenter operating the equipment was alternately switching the two pictures on and off, but in fact it's your brain that's responsible for the switching.

But is it just a laboratory curiosity? It's more than that. Rivalry and other forms of perceptual bistability allow us to investigate dynamical neural interactions within brain circuits promoting perception. Rivalry also provides an effective tool for probing aspects of visual information processing transpiring outside of awareness. Some think that rivalry

could shed light on the neural bases of the clinical condition called strabismic suppression, the brain's natural response to incompatible monocular stimulation arising when the eyes are misaligned. And work by Jack Pettigrew, Steven Miller and others suggests that rivalry may represent an endophenotype for certain psychopathologies.

Are there any striking differences between science today and when you started your career?

Technological advances, of course, but that goes without saying. One of the most impactful developments affecting my work is the explosion in the number of journals I must keep track of. Reading the relevant literature was easy when I got started — only handful of journals published what you needed to know. That's no longer true. Incidentally, the growth in the number of journals has been accompanied by enormously increased emphasis on citation data and indices of impact. This trend risks distorting the perceived quality of a journal and papers appearing in it. It also encourages investigators first to submit to a high profile journal and then work their way down the pecking order.

And what's wrong with that? The increased workload for editors and reviewers and the discouragement experienced by investigators when their papers are rejected. In addition, those papers targeting high profile journals tend to be brief, with important details omitted or relegated to web supplements. That brevity sometimes follows the paper as it finds its appropriate home.

Last question: as a scientist and a professor, can you offer others any advice that has served you well?

Yes, three gems of wisdom embodied in quotes that I have pasted on my wall: "Everything should be made as simple as possible, but not simpler" (Albert Einstein); "Anything worth doing is worth doing slowly" (Gypsy Rose Lee); "The more the teacher teaches, the less the student learns" (John Amos Comenius).

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Audubon set to hit the record books

Sotheby's, the international auction firm, have announced that they will sell next month a copy of one of America's most famous, and valuable, books: John James Audubon's *Birds of America*.

The volume comes for sale as part of the estate of Frederick Fermor-Hesketh, second baron Hesketh, a member of the British aristocracy whose family had collected books from the nineteenth century onwards and was obsessed by art.

Hesketh was an example of 'high spot collecting' — he did not

specialise but wanted a bit of the best of everything and had a major bout of purchasing in the 1950s.

Now, 55 years after his death, trustees of his estate are selling a number of books, manuscripts and letters, expected to raise £8–10 million.

Within this collection, the copy of *Birds of America* is expected to attract bids of around £4–6 million.

The book is bound at huge size — a 'double elephant folio' — because Audubon wanted to paint birds at life-size. He travelled across America, shooting his specimens before carefully arranging them on wires to paint them.

Audubon was not only a skilled artist but also a talented salesman.



Famous: Some of Audubon's illustrations of American birds are the most highly prized in the country. (Photo: © INTERFOTO/Alamy.)