Visual consciousness: the binocular rivalry explosion

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A new behavioural technique solves a long-standing puzzle of binocular suppression, demonstrating that adapting reciprocal inhibition governs visual sensitivity, and raising key questions about visual awareness.

Usually our two eyes receive similar views of the world, and the brain is able to combine, or 'fuse', these into a single, stable percept. But when the eyes report very different images, the brain is faced with a paradox: which image is correct? Like a canny investor, the brain chooses to hedge its bets. Instead of choosing just one image, or combining the two, we experience alternations between them, typically every few seconds. This phenomenon (illustrated in Figure 1A) is known as binocular rivalry, because it is as though the neural representations of the two images are competing against each other in a continuous 'tug of war'. At a given point in time, one image is dominant (perceived) and the other is suppressed entirely from awareness, yet both remain present at the retina.

Aside from some early investigations, rivalry alternations were largely treated as a curiosity until, in 1965, W.J.M. Levelt's doctoral research [1] brought a quantitative rigour to study of the phenomenon. This prompted several investigations into the basic mechanisms of rivalry over subsequent decades. However, interest in rivalry really exploded (see the graph of publications by year in Figure 1B) after 1998, when Francis Crick and Cristof Koch [2] popularized the idea that rivalry was a promising opportunity to study visual consciousness, owing to the dissociation between stimulus and percept.

Over the past decade, studies on rivalry have proliferated, taking advantage of varied techniques including psychophysics, neuroimaging, psychopharmacology and single-cell recording (see [3]). Some of this work has been concerned with isolating the anatomical location at which rivalry alternations begin; the implication being that this is the earliest possible site of visual consciousness (a neural correlate of consciousness, or NCC). However, binocular rivalry also has the potential to address questions about other aspects of conscious experience, such as what fate befalls information suppressed from awareness, and whether we can respond to something of which we are unaware.

A new behavioural technique, developed by Alais, Cass, Blake and O'Shea [4] may prove a useful tool in answering such questions. In their study, these authors asked whether sensitivity to a change in stimulus contrast (termed a probe) depended on whether the change occurred in the dominant or suppressed rivalry epoch. Furthermore, they wanted to know whether sensitivity varies during a period of suppression or dominance, or remains constant.

This is important because the principal model architecture used to understand rivalry (e.g. [5,6]) requires that the neural response to the dominant image decreases (adapts) over time, but increases (recovers) for the image which is suppressed. When coupled with mutual inhibition between the neural representations of the two images, this process of adapting reciprocal inhibition drives rivalry alternations. It also predicts that sensitivity to a probe will depend not only on whether it is in the dominant or suppressed image, but also how far into a period of dominance it is presented. Previous studies have not conclusively demonstrated that this is the case, casting doubt on the validity of the adapting reciprocal inhibition model.

Alais et al. [4] identify two problems with earlier work. Firstly, the probe stimuli used to measure sensitivity were typically very different from the images undergoing rivalry (e.g. small letters and large 'bullseye' targets [7]). This was likely because rivalry suppression was not thought to depend on the spatial properties of the stimuli (a view that has since been challenged [8,9]). But it probably also means that the neurons representing the probe were not subject to the same adaptation processes as those representing the rivalling stimuli. The second problem is that because alternations are stochastic, one cannot predict how long a given period of dominance will last. This makes presenting probe stimuli towards the end of an epoch problematic, as a switch will often occur before or during probe presentation.
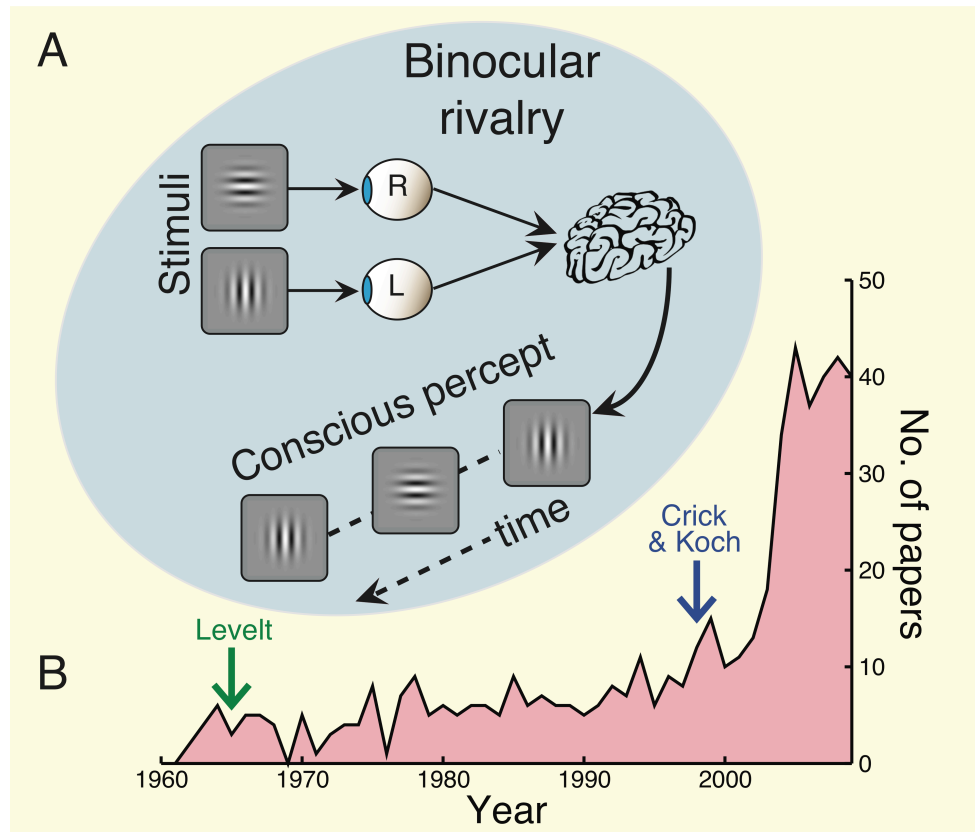
Figure 1. Binocular rivalry phenomenon and publications.
(A) Cartoon illustrating the binocular rivalry phenomenon. Conflicting images (stripes of different orientations) are shown to the two eyes. The observer perceives each image in turn, with the conscious percept switching stochastically over time. (B) Graph shows number of papers indexed by PubMed with 'binocular rivalry' appearing in the title or abstract, by year (note that additional publications discussing rivalry doubtless exist but were not identified by these criteria). Arrows indicate the publication of Levelt's [1] thesis (1965) and Crick & Koch's [2] article on consciousness and neuroscience (1998).

The elegant solution to this second problem is to present the probe stimuli at random times, on average every three seconds. Observers respond to the probe (a contrast increment to either the top or bottom of the image) whilst simultaneously indicating which of the rivalling images they perceive as dominant. After the experiment, the probe presentation times can be referenced to the percept reports to calculate precisely when during a dominance period the probe was shown. Using this technique, Alais et al. [4] demonstrate clearly that at the start of a dominance period, probe sensitivity is higher for the dominant image, and lower for the suppressed image, but that this difference reduces towards equal sensitivity by the end of the epoch. This result is precisely what is predicted by the adapting reciprocal inhibition model, removing the only major empirical obstacle to this explanation of rivalry alternations.

As well as providing crucial evidence to validate the adaptation model architecture, this study raises important questions about visual consciousness. When the suppressed eye is probed, observers are apparently able to respond to a stimulus they are not consciously aware of, with accuracy levels above chance. Of course, it is conceivable that the probe presentation itself causes a reversal of dominance, enabling it to be detected, though features of the experimental design make this explanation unlikely. Taken at face value, this effect is very similar to the clinical phenomenon of blindsight [10], but occurring in normal observers (see also [11]). Participants literally communicated information they did not know they had! Such paradoxical behaviour might indicate that visual awareness manifests either after, or in parallel with, the stage at which motor responses are programmed.

The task in the Alais et al. [4] study required information about both contrast and spatial location in the suppressed image in order for a correct response. Might other visual attributes, such as colour, orientation, spatiotemporal frequency, motion, or higher level properties also be preserved during suppression? Recent evidence suggests that information about the emotional expression of faces can survive suppression sufficiently to influence subsequent percepts [12]. This suggests that complex processing of visual information can still occur despite complete suppression from conscious awareness. The probe detection technique refined by Alais et al. [4] promises to be a powerful tool in unravelling many such aspects of visual consciousness. Perhaps it will encourage a further explosion of research addressing this most elusive aspect of cognitive function.

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