

Binocular rivalry and visual awareness

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Physiological studies of binocular rivalry have provided important clues to the relationship between neural activity in the brain and visual awareness. However, uncertainty about these insights has been raised by a recent study showing that the events underlying binocular rivalry occur earlier in the visual pathway than was previously thought.

In his *Treatise on Physiological Optics*¹, Helmholtz described perceptions as 'unbewusster Schluss' (unconscious conclusions). He argued that our perception of the visual world is based on inferences about inherently ambiguous sensory information. Because we are not ordinarily aware of this process of deduction, he surmised that what we see is the conclusion of the process, but not the process itself. Ambiguous figures offer a potentially fruitful tool for understanding which signals in the brain represent the conscious 'conclusion' and which are involved in the preconscious 'process' (see Fig. 1). This is because the physical nature of the retinal stimulation does not change, therefore any shifts in perception are presumably mirrored only by brain areas directly involved in awareness. A number of recent reports using one ambiguous stimulus (binocular rivalry) have provoked a lively debate over which signals in the visual system promote awareness.

Binocular rivalry occurs when a stimulus that is clearly visible when presented to one eye, is periodically rendered invisible when a different stimulus is presented to the other eye^{1,2}. Physiological studies show that, during binocular rivalry, some areas of visual cortex modulate their activity with the changes in perception, but others do not. For example, in primary visual cortex, although neurons exhibit significant suppression during contour rivalry³, only a small proportion of such neurons display fluctuations in activity that co-vary with the shifts in perceptual dominance⁴. In fact, many neurons at the early stages of processing in visual cortex continue to respond to their preferred stimulus

regardless of whether it is perceptually dominant⁴. It is only in 'higher' visual areas, particularly within the temporal lobe, that a greater proportion of neurons show activity that mirrors the ongoing alternations in perceptual dominance observed during binocular rivalry^{5,6}. It has even been reported that the shifts in perception are directed by non-visual areas in the frontal lobe⁷ or result from competition between the cerebral hemispheres⁸. Based on this and other evidence, it has been argued that neurons in early visual areas (such as primary visual cortex) do not contribute directly to conscious perception. Although this conclusion has been challenged recently⁹, there exists a more general dilemma about the interpretation of these studies that relates to the mechanism by which a visual stimulus is suppressed during binocular rivalry.

There are two general theories for how two incompatible monocular images compete for perceptual dominance (see Fig. 2). One possibility is that binocular rivalry reflects a competition between different stimulus representations. This would be comparable to the viewing of other ambiguous figures, such as the Necker cube or Rubin's vase-face stimulus (Fig. 1), and as such would be relevant to visual awareness in other situations. The alternative hypothesis is that visual information is suppressed by inhibitory interactions before the stage of binocular convergence. In this theory, changes in perception would be mediated by shifts in the balance of suppression between neurons selective for one or other monocular image. As these interactions must occur early in the visual pathway (e.g. the lateral geniculate nucleus, or layer IV of primary visual cortex), any changes in the activity of neurons in higher visual areas would be explained by a loss of input, equivalent perhaps to closing one eye. Previous reports have failed to provide a definitive answer as to which of the two mechanisms is dominant¹⁰.

In a recent study, Frank Tong and Stephen Engel appear to provide the first

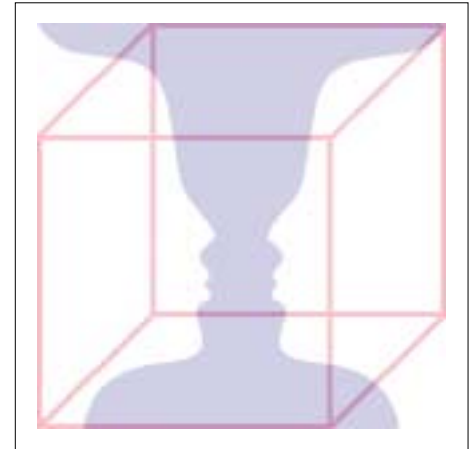


Fig. 1. Although fascinating in their own right, ambiguous figures, such as the depth-reversing Necker cube (red outline) or Rubin's vase-face stimulus, also provide an excellent opportunity for cognitive scientists to discover which areas in the brain instantiate our conscious perception of the visual world.

physiological evidence for interocular competition being the primary mechanism in binocular rivalry¹¹. Using fMRI, they monitored activity in primary visual cortex while gratings of different orientation were presented independently to the two eyes. The novel feature of this study was that the competing stimuli overlapped a region of visual space that stimulates only one eye; the lack of activation in the corresponding region of the other eye arises from an absence of photoreceptors in the retina (the blind spot). Despite the lack of direct stimulation, the blind spot was perceptually filled in by the surrounding region of visual space and the subjects reported that the two gratings competed for perceptual dominance in a manner similar to that reported for foveal vision. Tong and Engel's results clearly show that activity in the blind-spot representation of primary visual cortex decreased when perception shifted to the grating in the 'blind-spot' eye, but increased when dominance changed to the grating in the other eye. Because the blind-spot region of cortex receives direct stimulation from only one eye, it seems reasonable to conclude that the fluctuations in activity in this area of cortex during rivalry result from competitive interactions that occur



Fig. 2. *St Lucy* by Francesco del Cossa (reproduced with permission from National Gallery of Art, Washington). A plant form with eyes held by the saint in one hand and a palm branch in the other refers to the medieval legend that St Lucy, patron saint of vision, sacrificed her sight for her Christian faith. The story goes that she rebuked a nobleman, who wished to marry her for the beauty of her eyes, by tearing them out saying, 'now let me live to God'.

The image of St Lucy is also useful in illustrating the two opposing theories that explain the phenomenon of binocular rivalry: one explanation is that visual information coming from one eye is suppressed early in the visual pathway ('eye-rivalry'; see St Lucy's left hand), whereas the alternative hypothesis regards the competition to be between neurons representing different stimulus representations ('pattern-rivalry'; see St Lucy's right hand).

prior to binocular convergence. This is supported by the fact that the changes in signal strength were comparable to those obtained when the input was physically changed.

Nevertheless, it is difficult to reconcile this conclusion with previous single-unit studies showing that signals from both eyes are preserved in binocular neurons over several processing stages³⁻⁵. So, could there be an alternative interpretation of Tong and Engel's study? One possibility relates to the fact that, although the neurons in the blind-spot representation are by definition monocular, they are also selective for other aspects of the visual scene, not least form. It is conceivable, therefore, that input from binocular neurons representing neighbouring areas of visual space could selectively inhibit orientation-selective cells within the blind-spot representation, resulting in the same periodic fluctuations in fMRI signal. Outside the blind spot this orientation-based suppression would not

necessarily target monocular neurons, only rival orientations that just happen to be monocular in the blind spot. The interaction between neurons representing neighbouring regions of visual space is consistent with the observation that complementary portions of images presented separately to the two eyes during binocular rivalry are often grouped^{12,13}. This interpretation of the results would lead to a fundamentally different explanation of binocular rivalry. Rather than competition between monocular channels, shifts in perceptual dominance would be a direct function of interactions between binocular neurons that code for different orientations. In this event, it would be interesting to discover whether a similar pattern of activation and suppression occurs in this region of visual cortex, if the two competing stimuli do not specifically activate different groups of orientation-selective neurons.

If competition between different pattern representations could explain the shifts in perception during binocular rivalry, a similar alternation in perception might be expected to occur when orthogonal gratings are superimposed and presented simultaneously to the two eyes. Remarkably, this does happen and although less frequent and less complete, these perceptual fluctuations in normal viewing are otherwise similar to those that occur when incompatible scenes are presented dichoptically^{1,14}. The idea that different stimulus representations compete for dominance is further supported by psychophysical studies that show that different attributes of a visual stimulus can compete independently for perceptual dominance during binocular rivalry¹⁵⁻¹⁷. For example, when stimuli of different orientation are presented to the two eyes, contour rivalry can occur independently of binocular interaction for movement¹⁷. Additional evidence for pattern rivalry is apparent in situations when discrepant images in the two eyes are rapidly swapped. Despite fast changes in input to the two monocular channels, in some circumstances subjects continue to perceive slow alternations in perceptual dominance¹⁸. These examples notwithstanding, there is plenty, arguably more, psychophysical evidence that supports interocular competition as the mechanism underlying binocular rivalry^{2,19,20}. An interesting line for further investigation would be to understand why

different stimulus configurations favour different types of competition during binocular rivalry.

A final thought from Tong and Engel is that primary visual cortex plays an important role in the selection and expression of signals for visual awareness. Certainly, if rivalry were based on interocular competition, lateral inhibition between monocular neurons in layer IV of primary visual cortex² or feedback inhibitory connections to the lateral geniculate²¹ would be fundamental in *selecting* which signals are suppressed. However, it is not clear whether their data support a role for primary visual cortex in the *expression* of conscious visual information. This is because suppression at an early stage of processing would prevent signals from reaching subsequent levels of analysis in visual cortex. Showing that neuronal activity represents the physical characteristics of the stimulus, such as the orientation of a grating, does not necessarily imply that those signals provide consciousness. On the other hand, if competition between different stimulus representations were the mechanism by which the images in the two eyes vied for perceptual dominance, this would be compelling evidence for primary visual cortex being directly involved in the expression of visual awareness. Nonetheless, the continued controversy over the mechanism that underlies binocular rivalry suggests that the time may be right to use less controversial ambiguous stimuli in our quest to unravel the blueprint that links activity in the brain to our conscious experience of the world.

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Meeting Report

Predicting in Prague

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The Fifth International Conference on Artificial Neural Networks and Genetic Algorithms (ICANNGA) was held in Prague, Czech Republic, April 22–25, 2001.

ICANNGA 2001 was the fifth in a series of conferences focusing on artificial neural networks, genetic algorithms and related topics. This year's meeting was held at the beautiful Lichtenstein Palace in Prague. The splendid setting and relaxed atmosphere promoted a pleasant and lively conference, which included a social trip to a country chateau and a gala party at the Michna Palace.

A glance through the conference programme revealed 30 papers dealing with topics in neural-network theory, such as activation functions, rates of approximation, associative computation, learning, prediction and neuroscience. There were 20 papers on neural-net applications, including feature extraction, character recognition, robot navigation, power-plant optimization, random-number generation and time perception. Genetic-algorithm theory attracted 13 papers, on topics including predicate inversion, convergence of algorithms, information dimension of an attractor, measures for non-stationary optimization and sensitivity analysis. There were 13 more papers on applications of genetic algorithms and eight on soft computing. These included classifiers, scheduling, parameter identification, routing, and

connections with neuroscience and artificial life. In addition to the main sessions of this information-rich congress, there were 37 papers in special sessions.

The first of the seven invited speakers at the conference (and recent winner of the first Rumelhart Prize), Geoff Hinton (London, UK) described a learning algorithm for multilayer feedforward networks: an image is input, which gives rise to pairwise correlations between pixel values and the activations of feature detectors. The feature detectors reconstruct the image, and the difference in the pairwise statistics on real data and on reconstructions is used to reduce the error. This type of learning is excellent at discovering good feature detectors that provide a generative model for each class and hence perform classification. This provides a way to train products of experts, and is therefore connected with several previous studies by Hinton and colleagues.

The presentation by Thomas Saaty (Pittsburgh, PA, USA) was in a new direction for neural network theory. He suggested that ratio scales are critical for modeling neural synthesis in the brain. Thus, his work is related to measurement theory and to a tradition in mathematics going back to Aristotle and Poincaré. Saaty writes, 'We experience the world according to the capacity of our nervous system to register the stimuli we receive.' He showed that response to stimuli should satisfy the functional equation

$F(ax) = bF(x)$. This is related to the mode of operation of the neuronal firings.

Yoshifa Ito (Aichi-Ken, Japan) addressed the question of what a neural network can do without a scaling activation function. He generalized the properties of interpolation and approximation for feedforward neural networks to allow activation functions that include both radial-basis functions and sigmoids as special cases. He considered functions defined on compact subsets of Euclidean space as well as those defined on the corresponding spheres obtained by adding a 'point at infinity'.

Paul Kainen's (Washington, DC, USA) talk described integral formulas, using Heavisides, which are the continuum extension of feedforward neural nets. Some connections with classical applied mathematics (e.g. of Courant and Hilbert) were sketched, as were the possibilities of implementation via physical fields, and output representations based on lattices.

Ivan Havel (Prague, Czech Republic) proposed the concept of a causal domain. Certain complex phenomena, such as the seeming directedness of evolution or the intentionality of mental events, can be tentatively viewed as being supported by mutual interaction of a multitude of different causal domains.

Petr Hajek (Prague, Czech Republic) surveyed mathematical fuzzy logic, including continuous t-norms, syntax and semantics of fuzzy predicate calculus, as