

R482 Dispatch

Visual perception: An alternative view of perceptual rivalry

Frank Sengpiel

The mechanism by which one or the other view of an ambiguous figure – such as the Necker cube – gains dominance has been unclear. Recent evidence suggests that the right frontoparietal cortex is responsible for the selection process, and that each cortical hemisphere represents one of the two rivaling percepts.

Address: Cardiff School of Biosciences, Museum Avenue, P.O. Box 911, Cardiff CF1 3US, UK.
E-mail: SengpielF@cf.ac.uk

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Vision is in large part interpretation — the brain's guess as to the most likely real-world situation to account for the pattern of retinal stimulation that it experiences. But sometimes the pattern of stimulation does not permit unambiguous interpretation. So-called 'ambiguous figures' allow two different perceptual interpretations without any change in the physical appearance of the visual stimulus. Classical examples include the Necker cube, Rubin's vase and reversing pictures like Boring's 'My wife and my mother-in-law' (Figure 1). Most psychophysical and physiological investigations of bistable visual perception, however, have concerned the phenomenon of binocular rivalry, where images are shown separately to the two eyes that are too different to be fused into a single stable percept, for example, a horizontal and a vertical grating.

Common to all ambiguous figures, including cases of binocular rivalry, is the fact that the two possible interpretations, though equally plausible, are mutually exclusive; perception alternates between the two views every few seconds, and voluntary control over this switching is limited, suggesting the operation of an autonomous mechanism. During the past decade a number of physiological and imaging studies have addressed the question of *which* neurons in the visual pathway resolve the conflict between the two eyes' views during binocular rivalry [1–4]. Although considerable progress has been made in this enterprise, it has not done much to improve our understanding of *how* neurons come to respond to just one of the two views. Two recent papers [5,6] have now offered such an explanation; one, just published in *Current Biology* [6], has come up with the astounding result that each view is adopted by a separate cortical hemisphere.

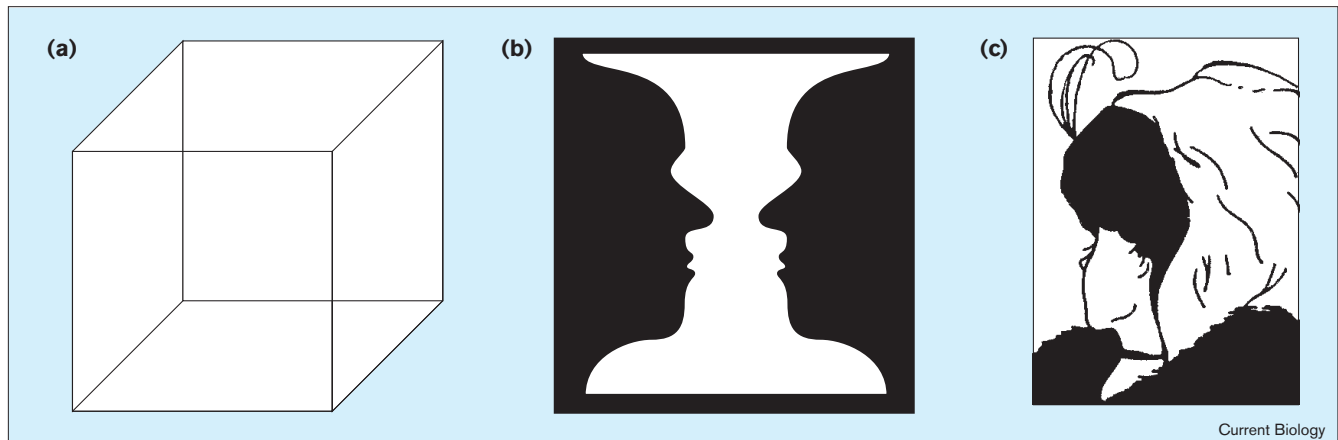
The first models of binocular rivalry interpreted the phenomenon as being the result of competition between inputs from the two eyes, which would be resolved by

mutual inhibition between groups of monocular neurons [7]. But single-cell recordings showed that suppression of neuronal firing by presentation of rivalrous stimuli first occurs among binocular neurons in V1, the primary visual cortex [1,2]. Moreover, it is only in higher visual areas, such as monkey V4 (important for colour and form perception) and inferotemporal cortical area IT (where neurons respond selectively to faces and objects), that a high percentage, or even a majority, of neurons have been found to modulate their firing between an active and a suppressed state in a way that is positively correlated with perception [2,3]. At these stages, however, information on the eye of origin of the dominant stimulus is lost. It therefore seems that competition may take place between stimulus representations rather than between eyes.

But how do the perceptual fluctuations that are characteristic of binocular rivalry and of viewing ambiguous figures come about? Of course mutual inhibition between groups of cells responding to one or the other stimulus is conceivable, but the distributed nature of the representation of complex objects in the visual cortex makes this explanation quite unlikely. Lumer *et al.* [5] directly investigated the source of the trigger mechanism for the perceptual switches by imaging cortical activity during the perceptual transitions, rather than activity associated with each one of the two perceptual states. Data were obtained by functional magnetic resonance imaging (fMRI) in humans who reported their percepts under two different viewing conditions. In the first condition, subjects viewed two rivalrous stimuli binocularly and indicated their perception by pressing one of two keys. In the second condition, the same two stimuli were presented monocularly in a 'replay' sequence of the percepts reported by key presses in the first condition.

Visual perception therefore was very similar under the two conditions used by Lumer *et al.* [5], as was their subjects' motor response. Comparing the fMRI signals under both conditions, activity related specifically to the rivalrous perceptual transitions was found in extrastriate visual area 19 and in the inferior parietal, superior parietal and inferior frontal cortex of the right hemisphere — in these regions, activity was greater during perceptual alternations in the rivalrous condition than in the replay condition. These frontoparietal areas have been implicated before in visual tasks requiring spatial shifts of attention [8]. Although binocular rivalry differs significantly from visuo-spatial attention, in that there is no spatial component to changes of perception in the former and that rivalrous transitions occur in the absence of voluntary control, the phenomena have in common that the observer becomes unaware of the

Figure 1



Classical ambiguous figures. **(a)** The Necker cube can be perceived as viewed from the right and above or from the left and below. **(b)** Rubin's vase is a typical example of figure-ground reversal – it can be

perceived as either a vase or two faces. **(c)** Boring's 'My wife and my mother-in-law' is one of a number of reversing pictures where two interpretations are equally plausible.

presence of certain visual stimuli. The right frontoparietal cortex may therefore play a role in the selection of neuronal responses leading to conscious perception [5].

The paper published recently in *Current Biology* by Miller *et al.* [6] challenges all current notions of what actually rivals during binocular rivalry. Starting from the evidence of binocular rivalry as a high-level process, these authors propose that it is neither stimuli nor eyes that compete with each other for perceptual dominance, but rather cortical hemispheres. In other words, they suggest that each hemisphere 'adopts' one of the two rivaling percepts. They support their hypothesis with evidence obtained from normal human observers who had one cortical hemisphere artificially activated or inactivated while viewing either a rivalrous stimulus pair or a Necker cube. In both cases, a consistent change in the relative perceptual dominance of the rivalrous stimulus and the two perspectives, respectively, was observed.

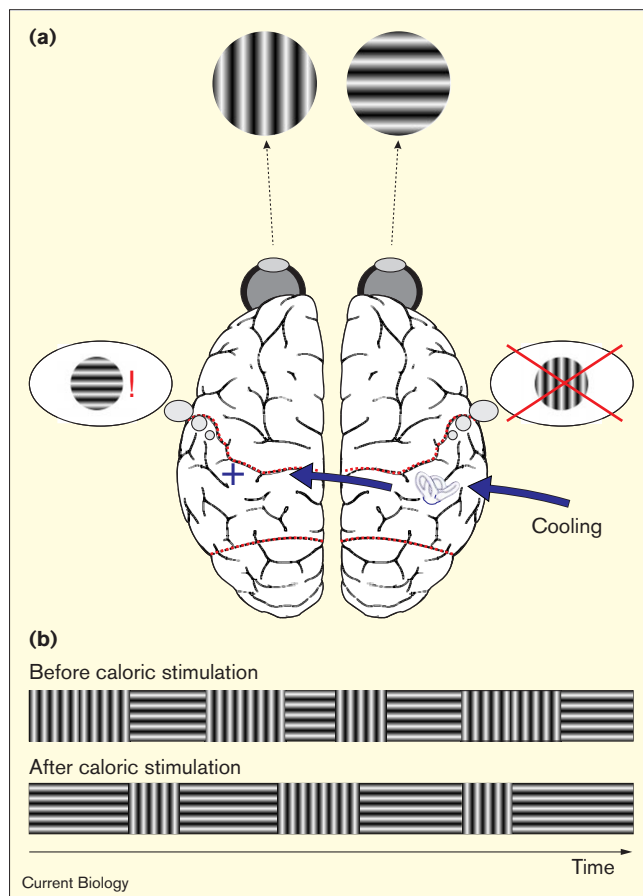
Miller *et al.* [6] first examined the effects of caloric vestibular stimulation on the perception of a rivalrous stimulus pair consisting of a vertical and a horizontal grating (Figure 2). For each subject, the relative amount of time that the vertical and horizontal grating, respectively, dominated perception — as indicated by key presses — was determined as the V/H ratio. Subjects then had one ear irrigated with ice-cold water until they reported vertigo and a kind of involuntary eye movement known as nystagmus was observed, and the V/H ratio was re-determined. Cold vestibular stimulation is known to activate, among others, cortical areas of the contralateral hemisphere that are involved in shifts of attention and perceptual transitions during binocular rivalry [5]. If, as

the authors predicted, rivalrous alternations are mediated by interhemispheric switching of dominance rather than by within-hemisphere stimulus competition, a change in the predominance of one stimulus relative to the other should occur after ear irrigation.

Indeed, a group of 20 subjects, who had their left cortical hemispheres activated by right-ear caloric stimulation, were found to exhibit a significantly greater change in V/H ratio following stimulation than was observed during successive epochs of unstimulated viewing. In a group of 12 control subjects — irrigated with water at body temperature — no such change was observed. Interestingly, right-hemisphere activation was also ineffective. Similarly, when right-oblique (45°) or left-oblique (135°) gratings were used, left-hemisphere-activated (right-ear stimulated) subjects exhibited a significant change in the relative dominance of the two gratings, observed on comparing ratios before and after caloric stimulation, but right-hemisphere-activated and control groups did not. In summary, left-hemisphere caloric activation changed perception of rivalrous stimuli in a way that was consistent with the idea that each stimulus of a pair is represented in one cortical hemisphere. The ineffectiveness of right-hemisphere activation might be a result of the lateralization of the trigger mechanism for perceptual switches: parietal activity on the right side signals alternations, while activation of corresponding areas on the left may lead to a choice being made in favour of the stimulus represented on that side.

Surprisingly, left-hemisphere activation produced a directional bias in the change of perception of vertical and horizontal rivalrous gratings: of the twelve subjects with the clearest effects, nine showed a shift towards increased

Figure 2



The use of caloric stimulation to shift relative perceptual dominance during binocular rivalry, as in the recent work of Miller *et al.* [6].

(a) Sketch of the experimental design. The two eyes separately view two gratings of different orientations (vertical and horizontal, as indicated here, or left-oblique and right-oblique). When the semicircular canals of the right inner ear are cooled by irrigation of the outer ear canal with iced water, left temporoparietal cortical areas are activated. Dashed red lines delimit the parietal lobe against frontal and occipital lobes.

(b) Rivalrous fluctuations in stimulus dominance before and after caloric stimulation. The observer's percept was monitored during six blocks of 7 minutes each of viewing the rivalrous stimulus pair, three of them before caloric stimulation and three afterwards. The fill types of the bars represent the orientation of the grating dominant at the time (total time shown approximately 10 seconds). During normal viewing, vertical and horizontal gratings are dominant for roughly equal lengths of time (the V/H ratio is approximately 1). After caloric stimulation of the left cortical hemisphere, the horizontal grating is dominant for up to twice as long as the vertical grating in some observers (V/H ratio approximately 0.5).

predominance of the horizontal grating, but only three exhibited an increase in predominance of the vertical grating. A similar directional bias was seen when rightward and leftward tilted gratings were used. More specifically, in most observers, the horizontal and the rightward-tilted gratings, respectively, appeared to have been adopted by the left hemisphere, and the vertical and leftward tilted gratings by the right hemisphere. Caloric activation of the

left, but not the right, hemisphere also changed perception of the Necker cube, in some cases even more dramatically. In this case, however, the direction of the perceptual shift was not consistent across subjects — there was no tendency for one particular perspective to become associated with one hemisphere in a majority of observers.

Miller *et al.* [6] further tested their interhemispheric rivalry hypothesis by examining whether transcranial magnetic stimulation (TMS) could trigger switches of stimulus dominance. Pulses of TMS are known to disrupt cortical processing and can, for instance, largely wipe out visual awareness when applied to the primary visual cortex. The temporal precision allows one, in contrast to caloric stimulation, to apply TMS repeatedly exactly at the time when one or the other of a rivalrous pair of stimuli becomes dominant. The authors found that, for five out of seven subjects, TMS of the left hemisphere selectively switched perceptual dominance when applied at the onset of a phase of dominance of one, but not the other, grating. This finding provided additional support for the notion that each percept has a distinct hemispheric representation, and for the interhemispheric switching model of binocular rivalry.

These findings are provocative and likely to raise at least as many questions as they answer. For instance, one would like to know how reproducible the hemispheric association of stimuli is for each person. If left-hemisphere activation prolongs relative dominance of a horizontal grating in one session, does it have the same result when repeated the following day or even immediately after the effect has worn off? Moreover, as the horizontal and rightward-tilted stimuli were always presented to the right eye, contralateral to the stimulated hemisphere, one wonders whether in fact it was that eye rather than particular stimuli which had a tendency to be represented in the left hemisphere. In that case, the relative dominance of vertical and leftward tilted gratings should be increased if stimuli were swapped between the eyes. Miller *et al.* [6] report preliminary evidence that this is at least partly true, although there also seems to be a genuine bias for representation of some stimuli in a particular hemisphere (S.M. Miller and J.D. Pettigrew, personal communication). Furthermore, this interpretation is consistent with the absence of a 'preferred' direction of the predominance shift when the Necker cube was used, as this was viewed binocularly and there could have been no association between an eye and a particular percept. If confirmed, this is good news for eye-dominance, rather than stimulus-dominance, based models of binocular rivalry, which can still explain a majority of psychophysical observations [9]. It should be emphasized, however, that this rivalry between eyes does not result from competition between monocular channels, but rather reflects the different probabilities with which each hemisphere represents the two images. In this sense, eye-of-origin information is preserved as a representational bias.

As for the site of the interhemispheric switching mechanism, Miller *et al.* [6] mention the corpus callosum connecting the cortical hemispheres as an obvious candidate, but consider a bistable oscillator in the brainstem more likely. So-called periodic alternating nystagmus — side-to-side alternation of eye movements every 90 seconds or so — occurs in humans with midline cerebellar or brainstem lesions, and the perception of one such patient during binocular rivalry was consistent with interhemispheric switching (S.M. Miller and J.D. Pettigrew, personal communication).

Evidence for or against the corpus callosum as mediator might be obtained from split-brain patients: do they experience binocular rivalry? An experimental approach to determining at which level the two hemispheres might interact is that of a transection of only the posterior callosum, a method recently used to study the retrieval of visual long-term memory in monkeys [10]. Direct interactions between visual cortical areas of both hemispheres could thus be distinguished from a ‘top-down’ control. On the other hand, the role of a brainstem oscillator in perceptual rivalry could be to increase synchronization of firing of visual cortical neurons in the hemisphere that will then dominate perception [11]. This hypothesis could be tested by simultaneous bilateral recordings of multi-unit activity in alert monkeys.

The crucial question, however, is this: how does one hemisphere come to adopt one of a rivalrous pair of stimuli or one perspective of an ambiguous figure? While the interhemispheric switching model offers an explanation of the perceptual alternations, it seems that the mechanism underlying perceptual disambiguation has not been found but has just been moved to yet another level. A natural propensity for domination of each cortical hemisphere by the contralateral eye might at least partly explain the findings on binocular rivalry, but it cannot explain the association of views with cortical hemispheres in cases, like that of the Necker cube, where retinal stimulation is identical for both eyes. Ambiguous figures certainly continue to be an intriguing paradigm for studying mechanisms of perception and the neuronal basis of visual awareness.

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