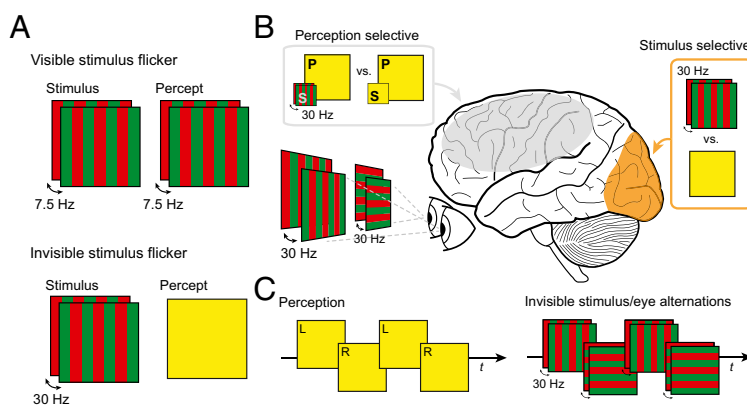


# Binocular rivalry outside the scope of awareness

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The human visual system usually receives input from two eyes that each capture a slightly different perspective of the world. Conscious visual perception, on the other hand, is unitary, and the brain uses the minor disparity between the two retinal projections as an important cue to reconstruct and perceive depth. This mechanism of binocular fusion falls apart when the input to the two eyes becomes too different (1). Under these conditions, binocular rivalry takes over and visual awareness stochastically alternates between the conflicting images presented to the two eyes. Binocular rivalry has fascinated scientists for centuries because its characteristic dissociation of fluctuating perception and constant visual input offers an experimental window on the neural

mechanisms of consciousness (2–5). Although much of the experimental work on binocular rivalry has focused on stimulus parameters (3) and contextual influences (6) that modulate its phenomenology, or on the computational principles that could underlie perceptual alternations (7), the actual cause of binocular rivalry has received far less investigation. The cortical processing level at which the “fusibility” of the two eyes’ images is evaluated, for instance, has strong implications for the neural mechanisms involved in binocular rivalry and the conceptual interpretation of a vast amount of experimental results (8, 9). The two most likely scenarios are that rivalry is either instigated in higher level brain areas involved in cognitive functions like decision-making, attention, and awareness or in early visual cortex, where basic stimulus features are processed. A study in PNAS by Zou et al. (10) now provides evidence in favor of the latter by revealing that awareness of conflicting interocular information is not necessary for binocular rivalry to occur. Conflicting orientation information that is registered in early visual cortex, but not in higher level parietal of frontal regions, is sufficient to drive interocular dominance fluctuations that remain invisible to the observer.



**Fig. 1. Invisible orientation conflict evokes binocular rivalry.** (A) Human visual system fuses images that are flickered at a temporal frequency above ~15–20 Hz (the flicker fusion threshold). If counterphase grating stimuli are flickered at 7.5 Hz, the stimulus flicker perceived (Top), but if the stimulus flickers at 30 Hz, observers will perceive a stable, uniform yellow stimulus (Bottom). (B) Zou et al. (10) used a classic binocular rivalry paradigm to present individual eyes with orthogonal gratings, each flickering in counterphase at 30 Hz. Separate experiments demonstrated that although activity in early visual cortex dissociates fast-flickering counterphase gratings from perceptually identical, actual uniform yellow stimuli (marked in orange), this dissociation is not found in frontal and parietal brain areas (marked in gray) (Inset) S denotes stimuli, and P indicates percept. (C) Binocular rivalry between fast-flickering orthogonal gratings evokes (invisible) alternations between perceptually identical eye-based stimulus representations (L and R denote percepts based on left eye and right eye input, respectively).

## Stimulus Flicker Abolishes Perceptual Conflict

Zou et al. (10) employed a clever trick to arrive at this important insight: they had observers view orthogonal isoluminant grating stimuli that flickered in counterphase at a rate above the human critical flicker fusion (CFF) threshold, which is ~15–20 Hz. At these high flicker rates, observers no longer perceive such stimuli as flickering, because the counterphase gratings perceptually blend into a uniformly colored disc (Fig. 1A). Under these circumstances, observers were incapable of reporting the orientation of the flickering gratings above chance level. The nice thing about this stimulus manipulation is that although perception, as a whole, is incapable of tracking stimulus flicker above the CFF, individual components of the visual system can have very different CFF thresholds. Retinal cones, for instance, can easily track flicker up to ~60 Hz, whereas

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individual neurons in monkey primary visual cortex (V1) respond to flicker between 30 and 60 Hz (11), and human visual cortex is also sensitive for perceptually invisible chromatic flicker at 30 Hz (12). In their study, Zou et al. (10) first confirm that although chromatic gratings that flicker in counterphase at 30 Hz are perceived as uniformly colored discs, they nonetheless still evoke orientation-specific adaptation, tilt after-effects, and they produce responses in early visual cortex, but not in parietal or frontal regions (Fig. 1B). Turning then to binocular rivalry, they show that these invisible gratings more effectively suppress visible orthogonal gratings presented to the other eye than perceptually identical uniformly colored discs. In one experiment, a monocularly viewed figure, rendered invisible by flicker, nonetheless biased subsequent dominance of a dissimilar stimulus presented to the other eye later, a phenomenon known as flash suppression (13). In another experiment, two invisible orthogonal gratings still produced sustained binocular rivalry (Fig. 1C), as confirmed by a probe detection task.

### The What, Where, and How of Binocular Rivalry

Over the years, the question of what is rivaling during binocular rivalry (14) has pitted eye-based rivalry against stimulus rivalry and low-level sensory cortex against higher levels of processing (2). Currently, however, binocular rivalry is mostly considered a hierarchical process (7, 15) that comprises both low-level eye-based components and higher level pattern-based elements, with the precise locus of rivalry resolution depending on detailed stimulus characteristics. Phenomenological similarities between binocular rivalry and other forms of bistable perception (3, 14) have promoted the implicit idea that the perceptual conflict resulting from dissimilar visual input is the driving force behind the perceptual alternations in binocular rivalry. Contrary to this view, Zou et al.'s results (10) show that the eye-based component of binocular rivalry can also be triggered in the absence of perceptual conflict. Their approach essentially isolates the one element in which binocular rivalry undeniably differs from other bistable phenomena like the Necker cube or ambiguously rotating structure-from-motion and reveals that this element alone is sufficient to evoke visual competition and interocular dominance switches.

The current observation of binocular rivalry in the absence of awareness provides an interesting notion for the debate on whether attention and awareness are distinct processes or two sides of the same coin (16, 17). Because previous work has shown that binocular rivalry does not occur when attention is directed away from the rivaling stimuli (18, 19), Zou et al. (10) suggest that their finding of rivalry without awareness supports the proposed dichotomy between attention and awareness. Things are a little bit more complicated than that, however. Although observers were not aware of the grating orientations, they were aware of the uniform discs that arose from the fused percept. Furthermore, although observers could not direct their attention to the invisible conflicting stimulus

orientations, they nonetheless had to attend the stimuli to detect the monocular probes. Thus, whether binocular rivalry from invisible flickering gratings should then be interpreted as attended or unattended, and aware or unaware, strongly depends on the unknown neural organization of supra- and subperceptual stimulus feature representations, as well as on their interaction with the brain's attention mechanisms.

A more readily accessible implication of Zou et al.'s results (10) is that frontal and parietal cortices are probably not necessary for

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binocular rivalry. This conclusion is in line with recent findings that show negligible blood oxygen level-dependent activity in these areas under stimulus conditions where observers do not perceive perceptual switches (20). Together, the present and previous studies strongly argue against a causal role of the frontoparietal network in generating perceptual switches. Instead, the reported involvement of these areas (8) in binocular rivalry more likely reflects the recruitment of executive systems in response to transient visual events like the visual events associated with perceptual switches (9, 20, 21). This notion does not, of course, rule out that frontoparietal regions might very well be capable of influencing the binocular rivalry process, perhaps through feedback down to earlier cortical areas where the competition is initiated. However, binocular rivalry can occur without such frontoparietal involvement.

The fact that binocular rivalry can occur between stimuli whose conflicting features are processed outside of awareness illustrates the intricate parallel nature of the primate visual system. Much like the dissociation of visual processing in ventral and dorsal streams allows the possibility that visual information not accessible to perception can nevertheless be used for visuomotor planning (22), stimulus features that do not reach awareness due to their fast flicker can nevertheless have profound neural consequences that bias the competition between the two eyes. Zou et al.'s work (10) not only confirms the idea that visual information not processed beyond early visual cortex is unlikely to reach awareness (23), it also shows that this information is nonetheless sufficiently potent to cause perceptual after-effects and instigate rivalry between the eyes.

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