REVIEWS

VISUAL COMPETITION

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Binocular rivalry — the alternations in perception that occur when different images are presented to the two eyes — has been the subject of intensive investigation for more than 160 years. The psychophysical properties of binocular rivalry have been well described, but newer imaging and electrophysiological techniques have not resolved the issue of where in the brain rivalry occurs. The most recent evidence supports a view of rivalry as a series of processes, each of which is implemented by neural mechanisms at different levels of the visual hierarchy. Although unanswered questions remain, this view of rivalry might allow us to resolve some of the controversies and apparent contradictions that have emerged from its study.

AMBIGUOUS FIGURES
Images that can be interpreted as representing more than one object or scene.

MIRROR STEREOSCOPE
A device that uses mirrors to allow different images to be presented simultaneously to the two eyes of an observer.

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The human brain, although renowned for its awesome computational powers, lapses into profound confusion when it receives conflicting views of the visual world. Consider, for example, the so-called AMBIGUOUS FIGURES presented in FIG. 1. The optical input to vision remains unchanged, and yet the resulting perceptual interpretation vacillates over time between alternative views — the behaviour called 'bistability'. These fluctuations presumably occur because the brain is receiving ambiguous information about the nature of an object at a given location in visual space. Faced with ambiguity, the brain fluctuates between different neural states over time[1–6].

In recent years, neuroscientists have become fascinated with one particularly striking form of bistability — binocular rivalry — produced by presenting dissimilar images to corresponding regions of the two eyes (FIG. 2). Rather than cooperatively melding into a single, coherent view, the two images compete for perceptual dominance: one image can dominate conscious awareness for several seconds at a time, only to be supplanted in consciousness by the previously suppressed rival image. Rivalry was first mentioned by Porta in the sixteenth century, and was more carefully described in the eighteenth century by DuTour, who commented on both colour and form rivalry[7]. However, credit for the first systematic study of rivalry goes to Sir Charles Wheatstone[8], who documented the conditions that elicit rivalry using his newly invented MIRROR STEREOSCOPE. In the years shortly after Wheatstone's seminal publication, binocular

rivalry captured the attention of some of the leading scientific minds of the nineteenth and twentieth centuries (BOX 1), and questions concerning the nature of rivalry have generated lively debate ever since.

Several intriguing features of binocular rivalry make it an especially effective tool for studying the neural correlates of visual perception. Dominance fluctuates irregularly over time[9] and spreads in a wave-like manner over space[10], indicating the operation of nonlinear dynamical processes not unlike those that govern other biological phenomena, including cortical spreading depression and slow-wave sleep. In addition, the rivalrous perception that dominates at a given moment can comprise local visual features that are distributed widely throughout the visual field, and, for that matter, contained in both the left and right eyes' views. Dominance, in other words, reveals important grouping properties[11,12]. Finally, and perhaps most significantly, rivalry provides a powerful tool for studying the neural concomitants of conscious visual awareness. After all, during rivalry, a normally visible, potentially interesting visual object can be suppressed from consciousness for several seconds at a time, only to emerge into awareness at the expense of its competitor. So, neural activity during rivalry must fluctuate at some stages within the visual pathways, thereby promoting this fascinating dissociation between unchanging physical stimulation and fluctuating conscious awareness[13–16]. What is the nature of these fluctuating neural events, and where do they transpire within the brain?
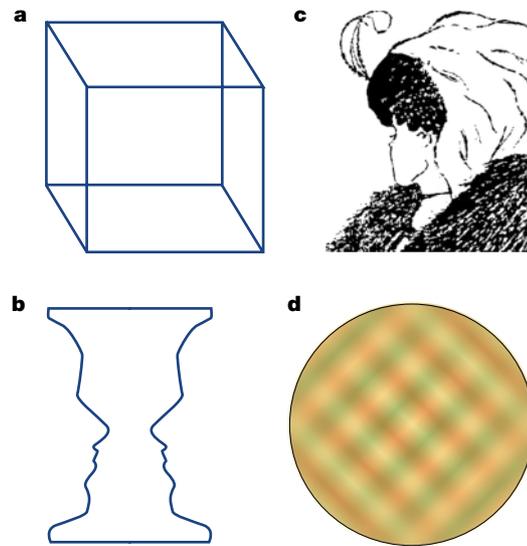
Figure 1 | **Examples of some well-known ambiguous figures, the perceptual appearance of which fluctuates over time despite unchanging physical stimulation.** **a** | The Necker cube. **b** | Rubin's vase/face figure. **c** | E. G. Boring's old lady/young woman figure. **d** | Monocular rivalry, in which two physically superimposed patterns that are dissimilar in colour and orientation compete for perceptual dominance[113]. Readers are encouraged to view each figure for durations sufficient to experience alternations in perception, which, for naive viewers, can take some time. Evidently, when one views figures such as these, the brain vacillates between alternative neural states; for this reason, such multistable figures offer a promising means to study the neural bases of visual perception.

Definitive answers to these questions are not yet available, but this review summarizes what we know at present. We start with an overview of the hallmark perceptual properties of binocular rivalry, for these will illuminate the search for its neural concomitants. From the outset, it is important to keep in mind that rivalry probably does not stem from a single, omnibus process; in our view, it is near-sighted to speak of 'the' neural mechanism of binocular rivalry. Instead, multiple neural operations are implicated in rivalry, including: registration of incompatible visual messages arising from the two eyes; promotion of dominance of one coherent percept; suppression of incoherent image elements; and alternations in dominance over time. These distinct operations might be implemented by neural events distributed throughout the visual pathways, an overarching theme that we shall develop in this review.

Perceptual characteristics of rivalry

Temporal dynamics. Fluctuations in dominance and suppression during rivalry are not regular, like the oscillations of a pendulum. Instead, successive periods of dominance of the left-eye stimulus and the right-eye stimulus are unpredictable in duration, as if being generated by a STOCHASTIC PROCESS driven by an unstable time constant[9,17,18]. It is possible, however, to bias this dynamic process by boosting the strength of one rival figure over another. In this case, the 'stronger' competitor enjoys an

STOCHASTIC PROCESS
A process of change governed by probabilities at each step.

advantage in overall predominance, as indexed by the percentage of total viewing time for which it is dominant. So, for example, a high-contrast rival figure will be visible for a greater percentage of time than a low-contrast one[19], a brighter stimulus patch will predominate over a dimmer one[20], moving contours will enjoy an advantage over stationary ones[21], and a densely contoured figure will dominate a sparsely contoured one[17,22]. Does a 'strong' rival figure enjoy enhanced predominance because its periods of dominance last longer, on average, than those of a weaker figure, or because its periods of suppression are abbreviated, on average? The evidence favours the latter explanation: variations in the stimulus strength of a rival target primarily alter the durations of suppression of that target, with little effect on its durations of dominance[17,23].

Can these unpredictable fluctuations in dominance and suppression be arrested by mental will power? Hermann von Helmholtz, among others, believed that they could[24]. Observing rivalry between sets of orthogonally oriented contours presented separately to the two eyes, Helmholtz claimed to be able to hold one set of contours dominant for an extended period of time by attending vigorously to some aspect of those contours, such as their spacing. Ewald Hering, Helmholtz's long-standing scientific adversary, characteristically disagreed with this claim, arguing that any ability to deliberately maintain dominance of one eye's view could be chalked up to eye movements and differential retinal adaptation[25]. Which view does the weight of evidence favour? It does appear that, with prolonged practice, attention can be used to alter the temporal dynamics of rivalry[26] without resorting to oculomotor tricks. However, this evidence also indicates that observers cannot maintain dominance of one rival figure to the exclusion of another[26], even when that temporarily dominant figure comprises interesting, potentially personal visual material[27] — an attended rival figure eventually succumbs to suppression despite concentrated efforts to maintain its dominance. In this respect, binocular rivalry differs from dichotic listening, in which a listener can maintain focused attention indefinitely on one of two competing messages broadcast to the two ears.

There is reason to believe that 'top–down' attentional modulation of rivalry operates by boosting the effective strength of a stimulus during dominance. Ooi and He[28] found that a dominant stimulus was less susceptible to a perturbing event presented to the other eye when observers voluntarily focused attention on that dominant stimulus. However, we know that voluntary attention cannot be guided by visual cues presented during suppression phases of rivalry[29]; evidently, then, voluntary attention does not have access to information portrayed in a suppressed figure. However, involuntary attention can be captured during suppression: stimulus events known to capture involuntary attention — such as the sudden onset of motion in a previously stationary figure — are sufficient to rescue a stimulus from suppression, thrusting it into conscious awareness at the expense of its competitor[30–32]. So, voluntary, 'endogenous' attention seems to operate

effectively only during dominance, whereas involuntary, 'exogenous' attention continues to work during suppression.

Besides stimulus strength and attention, visual context can also influence the predominance of a figure during rivalry. Look at the two pairs of rival targets in FIG. 2a,b. Within the circular regions of both pairs, horizontal
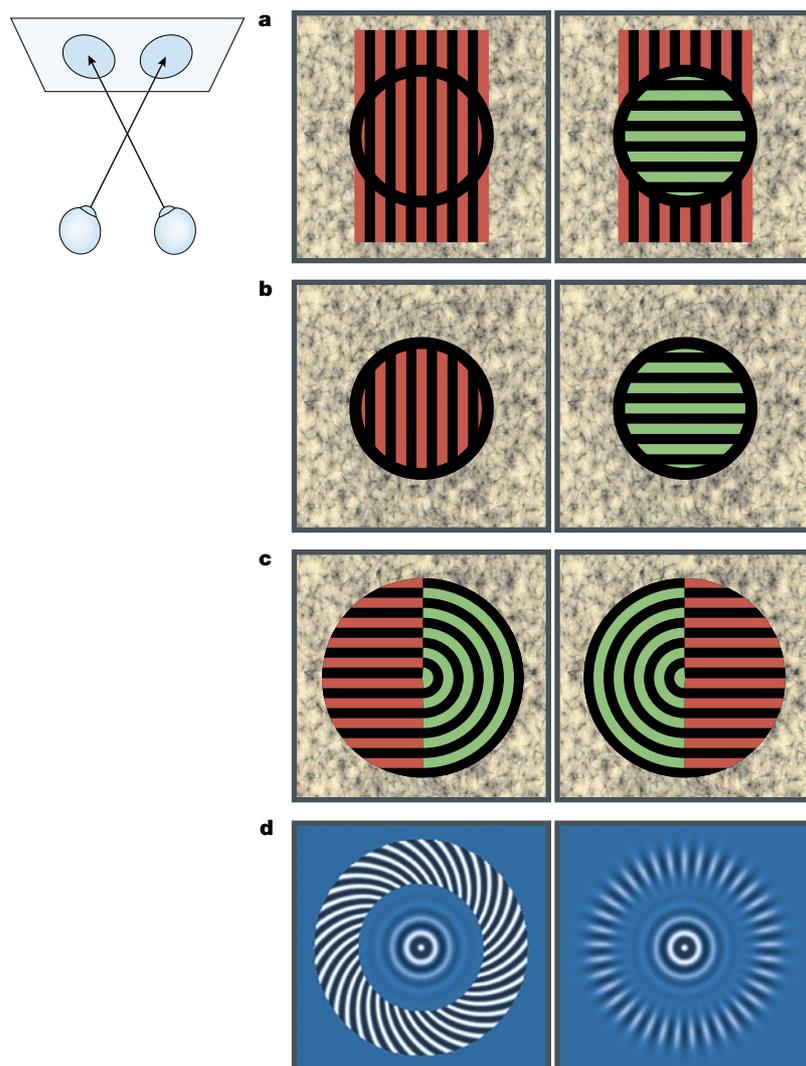

Figure 2 | Binocular rivalry. These rival targets — designed to be viewed by crossing the eyes to superimpose the two half-images binocularly (inset) — illustrate several hallmark characteristics of binocular rivalry. **a,b** | Using the two pairs of rival targets in **a** and **b**, compare the incidence of dominance of the central red/green grating when it appears in a consistent global context (**a**) and when it does not (**b**). **c** | This rival target closely resembles a figure devised by Diaz-Caneja[11] (for a translation of his paper, which was written in French, see REF. 118). Notice how frequently you experience a complete 'bullseye' or a complete set of horizontal contours, perceptual outcomes that indicate interocular grouping. **d** | A rivalry target illustrating the tendency of dominance to emerge locally and then spread globally. Once these two half-images have been fused, fixate the central 'bullseye', but observe the alternations in dominance between this pair of rival gratings (one a spiral grating and the other a radial grating). In particular, note how the radial grating emerges from suppression at a single point, with dominance radiating in both directions from this location. Wilson *et al.*[10] used rival figures such as this to estimate the rate at which dominance spreads. Rather than wait for dominance spontaneously to emerge at unpredictable locations, they introduced abrupt contrast increments to disrupt suppression locally, and measured the speed at which the resulting dominance wave travelled around this essentially one-dimensional figure. Readers can view further demonstrations of rivalry by navigating to R.B.'s Binocular Rivalry web page. Part **d** modified with permission from REF. 10 © 2001 Macmillan Magazines Ltd.

contours are pitted against vertical, but in FIG. 2a, the vertical competitors appear in a larger, globally congruent context that is not present in the bottom pair of targets. When observers 'track' periods of dominance and suppression while viewing displays like these, the target embedded in the meaningful, congruent context tends to predominate relative to the same target in the incongruent context[33]. Moreover, observers need not be consciously aware of the meaningful structure of a rival target that promotes its predominance — the boosting effect of context operates even when observers do not realize that a target can be globally organized into a meaningful pattern (for example, a Dalmatian dog)[34]. With displays such as those shown in FIG. 2, enhanced predominance comes about through a lengthening of the durations of dominance of that target, not through reductions in the durations of its suppression phases. It is interesting to note that a similar pattern of results is observed for variations in predominance of the vase/face bistable figure (FIG. 1b) — making the figure more face-like increases the durations of 'face' dominance but does not affect their suppression durations (the periods for which the figure is seen as a vase; D. A. Leopold, unpublished observations).

The inability of context to counteract suppression indicates that neural processes that amplify the salience of a dominant target are not engaged during suppression. The differential effect of stimulus strength and context on the perceptual predominance of a pattern is strong evidence that dominance and suppression rely on distinct neural processes, a conclusion that is supported by electrophysiological studies in monkeys reporting binocular rivalry (see below).

Spatial attributes of rivalry. Perceptual dominance during rivalry can take on a 'patchy' appearance when the inducing figures are relatively large, as if rivalry were occurring simultaneously within zones distributed over the visual field[35]; this tendency is particularly strong for foveally viewed rival targets[36]. However, the dominance phases of locally distributed rival targets can nonetheless become entrained, thereby creating an overall pattern of coherent perceptual dominance[11,12,37]. Remarkably, the consolidation of local rivalry into global dominance occurs readily even when the component features are distributed between the two eyes, as can be experienced using the pair of rival figures reproduced in FIG. 2c. It is tempting to conclude that perceptual grouping during rivalry results from the same cooperative/competitive interactions that promote figural grouping during normal vision[38,39].

A second striking spatial feature of rivalry concerns the transition periods when one figure overthrows another to achieve perceptual dominance. Typically, these transitions are not instantaneous, like successively exposed snapshots of one image and then the other. Instead, dominance emerges in a wave-like fashion, originating at one region of a figure and spreading from there throughout the rest of the figure. Wilson *et al.*[10] were able to estimate the speed with which dominance spreads by using rival targets in which dominance was forced to spread along a given path; an example of their rival

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Box 1 | **Historical views of rivalry**

During the nearly two centuries for which rivalry has been studied, ideas about rivalry have themselves fluctuated between two broad accounts. One view attributes rivalry to relatively 'high-level' mental operations, in which conflicting perceptual interpretations compete for dominance. Advocates of this position include Hermann von Helmholtz[24] and William James[99], both of whom equated rivalry with voluntary attention. Also favouring the high-level interpretation was Sir Charles Sherrington[100], who, in his famous monograph *Integrative Action of the Nervous System,* wrote: "Only after the sensations initiated from right and left corresponding points have been elaborated, and have reached a dignity and definiteness well amenable to introspection, does interference between the reactions of the two eye-systems occur … In retinal rivalry we have an involuntarily performed analysis of this sensual bicompound. The binocular perception in that case breaks down, leaving phasic periods of one or other of the component sensations bare to inspection."

The high-level view dominated well into the late twentieth century[101]. It was W. J. M. Levelt's influential monograph[17] that laid out a convincing, alternative view: rivalry is a relatively 'low-level' process involving competition between unrefined image primitives, with predominance governed by energic variables, such as luminance, contrast and contour density. At about the same time, neurophysiologists were providing the first real glimpses of the neural events transpiring in the mammalian visual cortex[102], including potent excitatory and inhibitory events thought to underlie binocular vision. These discoveries, coupled with Levelt's ideas, encouraged vision scientists to construe rivalry as the product of reciprocal inhibition between feature-detecting neurons in early vision[103–107]. However, during the past decade, compelling perceptual experiments showing global, contextual effects in rivalry[12] have created renewed support for the high-level view. Evidence presented in this review leads us to favour an amalgam of both views, with neural events underlying rivalry operating at distributed sites throughout the visual hierarchy.

ACCOMMODATION REFLEX
A reflex oculomotor response, involving contraction of the ciliary muscle to thicken the lens, that occurs when the focus of vision moves from a distant object to a near one.

OPTOKINETIC NYSTAGMUS
Involuntary, horizontal eye movements that allow the eyes to track a moving visual stimulus.

TILT AFTEREFFECT
If you stare at a set of lines that are tilted in one direction from upright, upright lines will subsequently look as though they are tilted in the opposite direction.

MOTION AFTEREFFECT
Also known as the waterfall illusion. Prolonged observation of a moving stimulus will lead to an aftereffect in which stationary objects appear to move in the opposite direction.

figures is shown in FIG. 2d. They found that the speed of dominance waves depended on the eccentricity of the annular gratings (it was faster for targets imaged in the periphery) as well as on the spatial configuration of the contours comprising a rival grating (waves travel faster around concentric gratings than they do around radial gratings). These results indicate that global perceptual dominance during rivalry is promoted by cooperative interactions between neighbouring neural mechanisms that are laid out in a retinotopically organized map.

Armed with this overview of the perceptual characteristics of rivalry, we are now prepared to consider its neurophysiological underpinnings.

Neural concomitants of rivalry

What transpires within the visual nervous system as one experiences fluctuations in dominance and suppression of a figure engaged in rivalry? At first glance, we might expect these neural events to be as marked as those associated with physically turning that stimulus on and off irregularly over time. Of course, intermittent presentation of a visual stimulus produces pronounced fluctuations in neural activity throughout the visual pathways, from the retina onwards. Rivalry, on the other hand, need not arise from such remarkable neural events. Indeed, modest shifts in the balance of activity between competing neural representations could be sufficient to trigger alternations in perception. For that matter, suppression phases could be accompanied by temporary disruptions in the temporal patterning of activity in populations of neurons, not by large-scale reductions in response level[40,41].

With these caveats in mind, we next consider indirect evidence, followed by more direct evidence, bearing on the neural concomitants of binocular rivalry.

Indirect evidence

Visual sensitivity during suppression. During the dominance phases of rivalry, observers show normal visual sensitivity for the detection of probe targets briefly superimposed on the dominant stimulus. But during suppression phases, those same probe targets are more difficult to detect, regardless of whether the probe resembles the suppressed rival figure[42–48]. By the same token, reaction times in response to probes are significantly slowed when the probes are presented during suppression[49,50]. In general, suppression phases are accompanied by a general loss of visual sensitivity in the order of 0.3–0.5 log units; suppression, in other words, behaves like a neutral density filter, effectively subtracting luminance energy from the triggering probe. It is interesting to note that reductions in sensitivity of the magnitude measured during suppression phases of rivalry are also found in other perceptual contexts. For instance, contour discontinuity is harder to detect in an area perceived as background than in an area perceived as figure[51], and orientation judgements are less accurate when lines are flashed in the ground rather than the figural region of Rubin's reversible goblet–faces picture[52]. Such findings indicate that the performance of perceptual tasks can be facilitated by perceived 'figureness' or, conversely, inhibited by perceived 'nonfigureness.' However, what is remarkable about binocular rivalry is that people fail to notice even large-scale changes in a suppressed rival figure itself, if those changes are not accompanied by abrupt transients[53]. Moreover, losses in sensitivity extend beyond perceptual judgements to adversely affect oculomotor reflexes: blurring a pattern that is suppressed in rivalry fails to stimulate the normal ACCOMMODATION REFLEX[54], pupillary constrictions to light flashes presented during suppression are significantly reduced in amplitude[55,56], and the gain of OPTOKINETIC NYSTAGMUS is reduced and the latency is longer in response to motion viewed during rivalry[57]. Exactly why visual inputs are weakened during suppression remains a mystery, but the generality of the attenuating effect of suppression indicates that the neural events that mediate suppression of a rival target are not exclusively tailored to the configuration of that target. Suppression, in other words, operates non-selectively to weaken all inputs to the suppressed eye by an amount sufficient to compromise, but not abolish, visual performance.

Visual adaptation during suppression. In contrast to its large-scale weakening of target visibility, suppression, ironically, has no effect on the build-up of several well-known visual adaptation aftereffects. So, for example, a full-blown TILT AFTEREFFECT — a form of adaptation thought to arise in orientation-selective neurons in visual area V1 (REF. 58) — is observed immediately after a period of adaptation during which the inducing pattern was phenomenally suppressed from vision for a substantial portion of the adaptation period[59]. The same is true for the translational MOTION AFTEREFFECT[60,61] and the aftereffects of grating adaptation[62]. Several other visual aftereffects, however, are

reduced in magnitude by rivalry suppression — these are aftereffects attributable to global, rather than local, motion adaptation[63,64]. All of these results fully support the idea that the mechanisms responsible for suppression are cortical. The extent to which these adaptation results indicate the involvement of different visual areas in suppression clearly requires further psychophysical investigation, in concert with imaging experiments in humans and electrophysiological experiments in animals.

Visual priming during suppression. Exposure to a visual stimulus can make other, related stimuli easier to identify, as indexed by faster performance and improved accuracy — the initial stimulus, in other words, 'primes' visual processing of the subsequent stimulus. Does priming occur if the priming stimulus is rendered invisible by binocular suppression? For visual tasks involving higher-level cognitive processes, including picture priming[65] and semantic priming[66], the answer clearly is 'no' — suppression renders normally effective priming stimuli impotent. These results are not too surprising, for both of these priming paradigms call for relatively refined analyses of visual information, of the sort conventionally attributed to high-level visual processing outside the domain of early visual areas. Evidently, during suppression phases of rivalry, input to those processing stages is effectively blocked.

Direct evidence
Visual evoked responses. A handful of studies has used scalp electrodes placed over the occipital lobe to record visually evoked responses (VERs) while observers experience binocular rivalry; with one exception[67], these studies have found reductions in the amplitude of the VER signal associated with the suppressed target[68–72]. These findings, however, were based on time-averaged recordings pooled over the left and right eyes, making it impossible to link fluctuations in VER amplitude with shifts in dominance and suppression measured in real time.

To achieve this kind of tight linkage, Brown and Norcia[73] repeatedly modulated the contrast of two dichoptically viewed, orthogonally oriented gratings at slightly different rates, thereby 'tagging' the VER waveforms associated with the two rival gratings. VERs were recorded while observers pressed buttons to track fluctuations in dominance and suppression between the gratings. The resulting tagged waveforms associated with the two gratings showed conspicuous, inversely related modulations in amplitude: when the amplitude of one grating was large, that of the other grating was invariably small. Moreover, these modulations were tightly phase-locked to the observers' perceptual reports of dominance and suppression (FIG. 3).

These VER measurements, although establishing a firm coupling between brain signals and perception during rivalry, do not tell us where within the visual pathways these signals are arising — electrodes placed over the occipital pole could be registering neural signals arising from any of the multiple visual areas contained within the folds of the occipital cortex. To get at the question of neural locus requires the deployment of brain-activity measurements with considerably greater spatial resolution. With that end in mind, we turn next to studies using functional brain-imaging techniques.

Functional magnetic resonance imaging. In the past 4 years, several groups have used functional magnetic resonance imaging (fMRI) to identify brain regions in which blood oxygen level dependent (BOLD) signals fluctuate in synchrony with binocular rivalry alternations. One study[74] documented the existence of multiple cortical areas in which levels of brain activity (inferred from modulations in the BOLD signal) were reliably associated with spontaneous changes in rivalry state while viewing dichoptically presented face and grating stimuli. Bilateral transient activation was observed in a region of the fusiform gyrus that is implicated in the processing of facial information, and in the frontoparietal areas of the right hemisphere, which are implicated in spatial attention. This study focused on transitions in
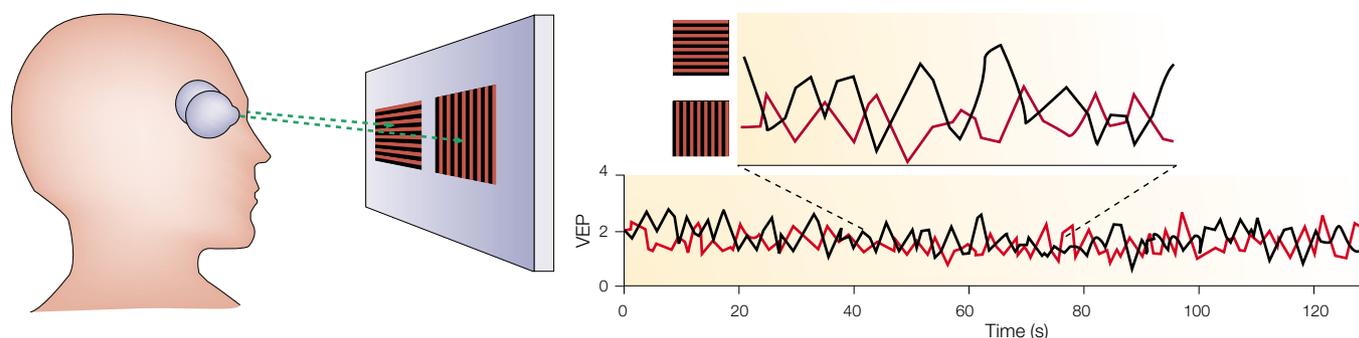

Figure 3 | **Visually evoked potentials recorded during rivalry.** Observers view a pair of orthogonally oriented gratings, one imaged to each eye. The bars of the grating flicker repeatedly in counterphase, producing reliable, time-locked modulations in the amplitude of the visually evoked potential (VEP) recorded from scalp electrodes placed over the occipital pole. The flicker rate of the left eye's grating differs from that of the right eye, such that each grating produces its own distinct waveform that can be teased apart from the other, followed over time, and correlated with the observer's record of rivalry alternations. This reveals robust, reliable modulations in the VEP amplitudes of the two waveforms, both highly correlated with the perceptual state of the evoking grating[73]. This pattern of results clearly reveals a neural signature of binocular rivalry arising within the occipital cortex, but it is not possible to pinpoint definitively from which visual area(s) these signals arise. Modified with permission from REF. 73 © 1997 Elsevier Science.
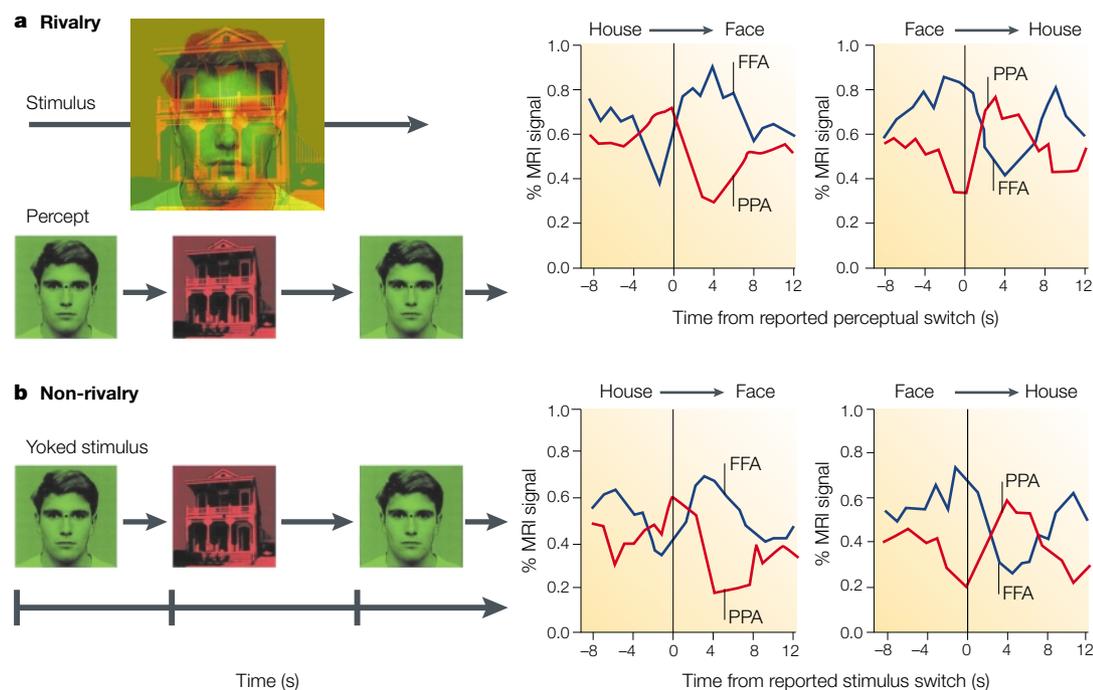
a | Rivalry

b | Non-rivalry

Figure 4 | **Functional magnetic resonance images of rivalry.** While lying in a magnetic resonance imaging (MRI) scanner, a person dichoptically views two rival targets, one the picture of a face and the other the picture of a house; during viewing periods lasting several minutes, the person presses buttons to indicate which of the two rival images is currently dominant. At the same time, functional MRI (fMRI) signals are measured simultaneously from two brain regions: a region along the fusiform gyrus known to be selectively responsive to faces (FFA), and a region in the parahippocampus known to be selectively responsive to spatial locations and buildings (PPA). **a** | The magnitude of the fMRI signals from these two brain areas fluctuates over time in phase with the observer's perceptual experience (taking into account the temporal lag of the haemodynamic response, the basis of the fMRI signal). In fact, signal changes during rivalry are as pronounced as those measured when the two pictures are physically presented and removed in a manner mimicking the alternations of rivalry (**b**). These results indicate that the competition between these conflicting perceptual images has been resolved by the time neural signals arise within these higher visual areas[75]. Modified with permission from REF. 75 © 1998 Elsevier Science.

rivalry state — that is, brain activations correlated with points in time when observers experienced changes in rivalry state, rather than the particular perceptual state being experienced — and concluded that such transitions might be instigated by the frontoparietal areas. It should be stressed, however, that this study, because of the nature of the stimuli used, was unable to distinguish between the BOLD signals associated with the two rival stimuli in any of the early visual areas.

A clearer demonstration of perception-related activation changes was provided soon after, by a second study[75] that capitalized on the stimulus selectivity of two brain regions: the parahippocampal area, which responds preferentially to images of indoor and outdoor scenes, such as houses, and the fusiform area, which responds preferentially to human faces. Brain-activation maps were obtained using fMRI while observers tracked fluctuations in rivalry between the image of a house viewed by one eye and the image of a face viewed by the other eye. Reciprocal modulations in BOLD signal levels were found in the parahippocampal area and the fusiform area, and these signals were highly correlated with observers' perceptual reports (FIG. 4). When the face image was dominant in rivalry, activity levels were relatively high in the fusiform area and low in the parahippocampal area; the converse pattern of signal levels was

observed when the house was dominant. In fact, the fluctuations in BOLD signal within the two areas during rivalry were just as pronounced as those measured when the images of the house and face were presented intermittently, mimicking the alternations of rivalry. These results strongly imply that the neural events underlying the dominance and suppression phases of rivalry have been fully elaborated by the time signals arise within these stages of processing.

Important as these observations are, they do not definitively pinpoint the site at which the neural signatures of dominance and suppression are first impressed upon the brain. In fact, several more recent fMRI studies indicate that a reliable neural signature of rivalry is measurable within the primary visual cortex, where information from the two eyes first converges anatomically. In the study by Polonsky *et al.*[76], orthogonally oriented gratings were presented separately to the two eyes. To tag the BOLD signal associated with each grating, the contrast of one was higher than that of the other, by an amount sufficient to produce significant differences in the magnitude of the BOLD signal measured under non-rivalry conditions. Observers tracked fluctuations in rivalry between these two rival gratings while BOLD signals were recorded from the retinotopically identified region of visual area V1 that was activated by the gratings. Signal

levels in this region were modulated in phase with observers' reports of rivalry, with larger BOLD signals coincident with dominance phases of the higher-contrast grating, and vice versa. Unlike those in the parahippocampal and fusiform areas, however, these fluctuations in BOLD signal were less pronounced than those measured when the gratings were actually turned on and off over time in a pattern mimicking rivalry. Using a different, block design procedure, Lee and Blake[77] have replicated this pattern of results (reduced V1 BOLD signal associated with a suppressed stimulus) using both gratings and meaningful images, including a house and a face.

Recently, Tong and Engel[78] devised a novel strategy to verify the involvement of V1 in binocular rivalry. They first isolated the region of V1 that corresponds to the blindspot of one eye; BOLD signals originating solely from this region of interest (ROI) can be isolated[79], and they can arise only from neural responses associated with stimulation of the ipsilateral eye. Once this ROI was delineated in each observer, Tong and Engel measured BOLD signals originating from this ROI while these observers tracked fluctuations in binocular rivalry between dichoptically presented, orthogonally oriented gratings, one of which was centred on the blindspot. fMRI activity within this monocularly innervated patch of cortex fluctuated in synchrony with the observers' reports of dominance and suppression, indicating that signals from the ipsilateral eye to the V1 blindspot representation were suppressed when the competing grating viewed by the other eye achieved perceptual dominance. In fact, the changes in BOLD level were equivalent to those measured during conditions in which the gratings were turned on and off to mimic rivalry, leading Tong and Engel to conclude that rivalry is completely resolved within area V1. It remains for future work to reconcile this pattern of results with those found by Polonsky *et al.*[76], in which the 'mimicry' condition produced larger fluctuations in BOLD response than did the rivalry condition.

So, to date, five fMRI studies — each using a different technique — have reported neural correlates of binocular rivalry alternations in the human brain. Interpretation of these findings, however, must be qualified by our lack of complete understanding of the origins of the BOLD signal measured using fMRI. It is generally agreed that synaptic events are responsible for the lion's share of cellular metabolic activity that generates the BOLD signal. But are these synaptic events always tightly correlated with neural spike activity of the cortical projection neurons?

Very recent concurrent measurements of BOLD signal, single-unit activity and local field potentials (LFPs)[80] indicate that fluctuations in BOLD signal can be correlated both with multi-unit spiking activity and with LFPs associated with neuromodulatory events that do not necessarily result in spiking activity. Viewed in this light, at least some of the modulation in BOLD signal within V1 during rivalry could arise from feedback connections from higher visual areas. Of course, this interpretation of the origin of the BOLD signal does not negate the role of V1 in rivalry, but it does underscore limitations in our ability to use fMRI to pinpoint sites at which the neural concomitants of rivalry are first triggered.

Neuromagnetic responses. Besides fMRI, there are other potentially powerful imaging techniques available for correlating brain activity with perception. Among these is magnetoencephalography (MEG), a brain-imaging technique that yields signals with high temporal resolution that are thought to reflect the synchronous spiking activity of large ensembles of cortical neurons. Two studies[41,81] have measured MEG signals while observers experience binocular rivalry, the aim being to identify synchronization in neural activity between spatially distributed cortical areas associated with dominance phases. Like the VER study mentioned above[73], these MEG studies used rival gratings flickering at slightly different rates to tag the MEG signals associated with the two gratings. Over a wide array of sensor locations encompassing the occipital, parietal, temporal and frontal lobes, the amplitudes of the MEG responses were significantly correlated with observers' reports of dominance and suppression. Dominance phases of rivalry were also associated with marked increases in synchronization of MEG signals recorded from widely distributed sensors, with the most prominent examples of coherence arising in frontal areas of the brain. In agreement with fMRI and electrophysiology studies (see below), the anatomical distribution of these rivalry-modulated MEG signals studies shows extensive involvement of almost the entire visual cortex in the differential processing of stimuli during rivalry.

Single-unit recording. The neural bases of binocular vision have been studied extensively using single-neuron recording techniques, but most of that work has made use of matching left- and right-eye images that do not trigger binocular rivalry. Moreover, most of these recordings were obtained from anaesthetized, paralysed cats or monkeys, making it impossible to relate neural activity to concurrent perceptual experience. Without going into details, suffice it to say that these studies have generated conflicting results concerning the extent of response modulation associated with dichoptic presentation of dissimilar stimuli (for a review, see REF. 3). Here, we focus on that handful of experiments in which single-unit responses were recorded from alert, behaving monkeys trained either to gaze passively at rival patterns, or to report fluctuations in dominance and suppression while viewing them (FIG. 5). Neural responses have been studied in the lateral geniculate nuclei (LGN) and the visual cortex.

In species with well-developed binocular vision, the retinal terminals from each eye project to different laminae in the LGN, so that they remain segregated. Each lamina receives excitatory input from one eye and contains a detailed retinotopic map of the contralateral visual field. The maps are in perfect register and receive feedback from primary visual cortex[82–84], which can detect mismatches in visual attributes such as orientation, spatial frequency or direction. Adjacent laminae thus form an ideal substrate for inhibitory interactions between the two eyes. But electrophysiological experiments in
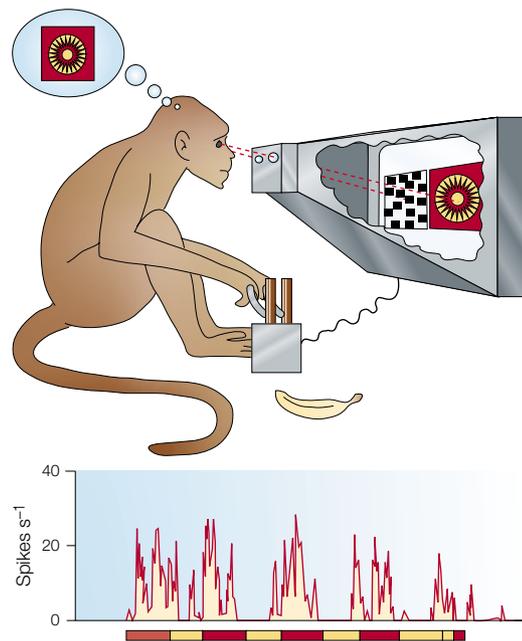
Figure 5 | **Single-cell recordings during rivalry.** Using operant conditioning techniques, monkeys are trained to operate a lever to indicate which one of two competing monocular images is dominant over time (see REF. 13 for details of training). Activity recorded from single cells in the awake, behaving monkey can be correlated with the animal's perceptual reports, thereby identifying brain regions in which cellular activity mirrors perceptual experience. The bar along the *x* axis indicates alternating awareness of the two images.

the LGN of the alert, fixating monkey provided no evidence for rivalry inhibition at the subcortical level in the geniculostriate system[85].

Neurons in the cortex behave differently. Experiments with monkeys reporting rivalry showed that inhibition of responses during binocular suppression is evident as early as the primary visual cortex[86]. In these experiments, the animals reported the perceived orientation of rivalling gratings by pulling levers, while maintaining fixation on a central light spot for several seconds. Notably, the psychophysical performance of these trained monkeys was similar to that obtained from human observers, indicating that similar neural mechanisms might underlie rivalry in the two species.

The extent to which neural activity was modulated in phase with the animal's perceptual report increased in successive stages of early visual cortical areas. Curiously, however, some extrastriate neurons were excited only when their preferred stimulus was visible, whereas others were excited when it was suppressed[87,88]. The latter neurons, the activity of which is in reverse correlation with the animals' perception of their preferred stimulus, might be part of an inhibitory mechanism that is separate from and, to some extent, independent of the mechanisms of perception. Such an independent mechanism was predicted by psychophysical measurements of the effects of the strength of a stimulus on its predominance[17,22,23]. It also offers a possible explanation for the differential effects of stimulus strength and context on

suppression described earlier. Overall, both striate and early extrastriate areas (such as areas V4 and MT) showed activity changes during rivalry, but for most cells the activity modulations, although highly significant in a statistical sense, were modest compared with the perceptual changes experienced during rivalry. Moreover, almost none of the neurons ceased to fire completely during suppression.

Responses were markedly different in the temporal lobe. The inferotemporal cortex, a region starting just in front of area V4 and continuing almost up to the temporal pole, has an essential role in higher visual functions, including pattern perception and object recognition[89]. Inferotemporal neurons respond with high selectivity to complex, two-dimensional visual patterns, or even to entire views of natural and artificial objects. Damage to the inferotemporal cortex typically produces severe deficits in perceptual learning and object recognition, even in the absence of significant changes in basic visual capacities. It was natural to query the types of response change observed during rivalry in this high-level area. The monkeys participating in these experiments reported whether they perceived a sunburst-like pattern, or images of animate or man-made objects[89]. Recordings showed that most of the inferotemporal neurons were active only when their preferred stimulus was perceived. In other words, in contrast to neurons in areas V4 and MT, inferotemporal neurons showed essentially no activity during the perceptual suppression of the stimulus, indicating that the studied areas represent a stage of processing beyond the resolution of perceptual conflict.

The intriguing complexity and diversity of responses in early extrastriate cortex during rivalry hints at its role in perceptual organization. The areas surrounding the primary visual cortex, including V4 and MT, are in an anatomical position to integrate information from ascending and descending visual streams, and to interact with structures that are crucial for object vision. Responses in these areas can be considerably enhanced or inhibited when the monkey attends to the cell's preferred or non-preferred stimulus, respectively[90,91], even when there is no concomitant change in the stimulus itself, and the mechanisms underlying such changes are also competitive in nature[92]. Damage to area V4 and posterior inferotemporal cortex disrupts the top–down input to early areas, strongly interfering with the animal's ability to ignore distracters in the lesioned areas[93] and to detect less salient stimuli[94,95]. In short, the diverse activity observed in early extrastriate cortex might reflect the competitive interactions that characterize all those selection processes involved in image segmentation and grouping, interactions that are greatly accentuated during binocular rivalry.

Finally, it should be noted that, in any area of the brain, the absence of changes in firing rate should not be interpreted as an absence of perceptual state changes, as populations of neurons can increase and decrease the coherence of their firing as a function of time. Such increases in coherence have significant effects on the next stage of processing, as synchronized inputs produce higher and more steeply depolarized membrane excursions for

Box 2 | Unresolved issues

Eye versus stimulus suppression

During suppression phases of rivalry, what, exactly, is suppressed? Perceptually speaking, it is a visual figure that disappears from conscious awareness, but several pieces of evidence indicate that suppression operates more generally than this. As pointed out in the main body of the review, a wide range of probe targets is also adversely affected by suppression. In addition, it is possible to swap the two rival targets between the eyes, placing the dominant target in the eye viewing the suppressed one, and vice versa. When this happens, observers reliably experience an immediate switch in dominance, indicating that a given region of the eye was dominant, not a particular stimulus[108]. On the other hand, the striking interocular grouping seen in FIG. 2c, an effect documented more systematically by others[3,12,33,109], clearly shows that dominance can be distributed between the eyes. So it cannot be an entire eye that is dominant at any given moment. Moreover, a given rival stimulus can remain suppressed for several seconds at a time when that stimulus is repeatedly exchanged between the eyes several times per second[110], an observation that has stimulated further work to establish the boundary conditions for its occurrence[111,112].

Single-unit results versus fMRI

Several functional magnetic resonance imaging (fMRI) studies have found robust modulations in blood oxygen level dependent (BOLD) signals measured from human V1 during rivalry. However, single-unit studies in alert monkeys experiencing rivalry indicate relatively weak modulations in neural responses coincident with the monkey's perceptual reports. Why the apparent discrepancy? Polonsky *et al.*[76] discuss several possible reasons, including species differences, eye movements, and uncertainties involving the relationship between BOLD signals and neuronal activity. Clearly, further work is needed to dissect effects attributable to local processing from the effects of the neuroanatomically well known, massive feedback from higher visual areas to striate cortex. In passing, it is interesting to note that the same discrepancy arises when comparing the effects of attention on single-unit activity versus BOLD responses measured from V1.

Perceptual bistability

Binocular rivalry is just one of several phenomena that are characterized by fluctuating perceptual experience in the face of unvarying visual input. Other examples of bistable perception include ambiguous figures and monocular rivalry[113] (FIG. 1), as well as motion-induced blindness[114] and the kinetic depth effect[115]. What all these phenomena, including binocular rivalry, have in common is the presence of contradictory information about the identity of an object located at a given region of visual space. Faced with this contradiction, the visual nervous system evidently vacillates between alternative brain states associated with different perceptual interpretations. It remains to be learned whether common neural mechanisms underlie these various forms of perceptual instability, as some have proposed[3,116]. In this regard, it is noteworthy that the successive durations of perceptual dominance evoked by bistable figures of different sorts all conform closely to the GAMMA DISTRIBUTION[4].

Hemispheric switching

On the basis of converging lines of evidence, Pettigrew[117] has arrived at the intriguing idea that rivalry alternations result from switches in activation between left and right hemispheres, the switching being driven by an oscillator located in the subcortical neuraxis. The theory leaves important questions unanswered, such as how a given hemisphere inherits a particular monocular image during rivalry. Still, this novel theory deserves careful consideration, in part because it attempts to place binocular rivalry in the larger context of individual differences, circadian rhythms and mood disorders.

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equal numbers of spikes[96]. For example, synchrony between neurons sometimes signals the presence of a stimulus more reliably than does the spiking of any one of those neurons[97,98]. However, preliminary results indicate that synchronization of responses during rivalry is not directly related to a particular perceptual state. Specifically, multi-unit recordings in monkeys show that increases or decreases in coherence are closely correlated with the presentation of congruent and rivalling stimuli, respectively, rather than with the perceptual dominance of any pattern (D. Leopold, personal communication).

Final thoughts

We have gleaned an important lesson from the studies reviewed here: it is an oversimplification to speak of 'the' neural mechanism or 'the' neural site of binocular rivalry. As we have learned, the stimulus determinants of suppression phases (for example, pattern contrast) are different from the determinants of dominance phases (for example, global context). In a similar vein, a dominant rival stimulus readily benefits from the spatial context in which it appears, whereas a suppressed stimulus does not. Dominance and suppression, in other words, are not two sides of the same coin. It seems clear that a dominant stimulus in rivalry engages the same neural machinery as that activated during normal, non-rivalrous viewing. To put it another way, visual information associated with a dominant stimulus flows uninterrupted throughout the visual pathways, triggering the normal complex of feedback connections, and making neural contact with all those processes that signal the semantic and affective connotations of a visual object or event. And however attention influences perception of a visual scene, it can likewise influence the perception of a dominant stimulus. The same cannot be said for a suppressed stimulus, however. VER, fMRI, MEG and single-unit studies all point to potent disruptions in neural processing during suppression phases of rivalry. Although controversial issues remain to be resolved (BOX 2), the emerging idea that rivalry involves multiple, distributed processes offers a very promising means to reconcile conflict in the rivalry literature.

GAMMA DISTRIBUTION
A probability density function that plays an important role in statistics; the exponential distribution and chi-square distribution are special cases of the gamma distribution.

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Online links

FURTHER INFORMATION
Binocular Rivalry:
http://www.psy.vanderbilt.edu/faculty/blake/Rivalry/BR.html
Encyclopedia of Life Sciences: http://www.els.net/
Sherrington, Charles Scott
MIT Encyclopedia of Cognitive Sciences:
http://cognet.mit.edu/MITECS/
electrophysiology, electric and magnetic evoked fields | Helmholtz, Hermann Ludwig Ferdinand von | James, William | magnetic resonance imaging | single-neuron recording | top–down processing in vision | visual anatomy and physiology
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