PRIMARY VISUAL CORTEX AND VISUAL AWARENESS

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The primary visual cortex (V1) is probably the best characterized area of primate cortex, but whether this region contributes directly to conscious visual experience is controversial. Early neurophysiological and neuroimaging studies found that visual awareness was best correlated with neural activity in extrastriate visual areas, but recent studies have found similarly powerful effects in V1. Lesion and inactivation studies have provided further evidence that V1 might be necessary for conscious perception. Whereas hierarchical models propose that damage to V1 simply disrupts the flow of information to extrastriate areas that are crucial for awareness, interactive models propose that recurrent connections between V1 and higher areas form functional circuits that support awareness. Further investigation into V1 and its interactions with higher areas might uncover fundamental aspects of the neural basis of visual awareness.

COGNITIVE NEUROSCIENCE

PRIMARY VISUAL CORTEX
The first cortical area to receive inputs from the eye via the geniculostriate pathway; also referred to as V1, area 17 and striate cortex.

EXTRASTRIATE CORTEX
A belt of visually responsive areas of cortex surrounding the primary visual cortex.

MT AND MST
Motion sensitive areas of extrastriate cortex.

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Human vision seems so fast, effortless and reliable that most people mistake their perceptual experience for a direct reflection of reality — after all, 'seeing is believing'. In reality, visual perception is an interpretative act that consists of two key components: information analysis and subjective awareness. Unlike a camera, which simply collects and stores raw visual information projected from the environment, we experience the world as a detailed analysis of vivid visual features, forms and objects. Our visual system analyses low-level feature information, such as colour, orientation, texture, motion, depth and form, as well as the high-level structure and meaning of visual objects. In principle, information analysis alone could support visually guided behaviour — we could wander through the world as mindless robots. But recent studies indicate that many of the analyses performed by our brains are closely tied to the visual features and objects that reach our awareness.

Information processing in the visual system has been investigated for decades, but only in recent years has a keen interest developed in visual awareness. Although we know more about the information-processing properties of PRIMARY VISUAL CORTEX than of any other cortical area, the role of this region in conscious perception remains widely debated. This review focuses on the relationship between activity in V1 and visual awareness, and discusses theories and evidence pertaining to whether V1 might have a direct and necessary role in conscious vision.

Overview of the primate visual system
Connectivity. Studies in the macaque monkey indicate that about half of the cortex is involved in visual processing[1]. In this vast network, V1 is uniquely positioned as the primary distributor of almost all visual information that reaches other cortical areas. About 90% of projections from the eye are channelled through the lateral geniculate nucleus (LGN) to V1. (The remaining 10% of retinal fibres project to various subcortical structures, and include a pathway from the retina through the superior colliculus to the pulvinar, which has reciprocal connections with several EXTRASTRIATE areas[2].) From V1, information is disseminated to various extrastriate visual areas for further analysis, including areas V2, V3, V3A, V4, MT, PO and PIP (REFS 1,3) (FIG. 1). These extrastriate areas receive almost all of their inputs, either directly or indirectly, from V1. Areas such as V4 and MT project directly to visual areas in the parietal

Figure 1 | **Connections between a subset of cortical visual areas (schematic diagram).** Primary visual cortex (V1) has direct reciprocal connections with posterior extrastriate areas V2, V3, V3A, V4 and MT (**REFS 1,3**; red). (Not all back-projections to V1 are shown; extensive reciprocal connections between extrastriate areas are omitted.) Some of these posterior extrastriate areas have reciprocal connections with area LIP (lateral intraparietal),the frontal eye fields (FEF) and area 46 (blue), which are involved in visual attention and motor planning. According to some hierarchical models, only extrastriate areas such as MT, V4 and inferotemporal cortex, which project directly to frontal-parietal areas that are involved in attention or motor planning, can contribute directly to visual awareness. By contrast, interactive models propose that recurrent loops between V1 and posterior extrastriate areas (such as MT and V4) are essential for maintaining a visual representation in awareness.

and frontal lobes that are implicated in attention, working memory and motor planning. Most connections between visual areas consist of both feedforward and feedback connections, indicating that there is a high degree of interactive processing. However, V1 receives feedback projections from many areas to which it does not directly project, including areas MST, FST, STP, TEO, TE, TH, LIP, FRONTAL EYE FIELDS (FEF) and auditory cortex[3–5].

Response properties. The response properties of neurons indicate how they analyse the visual scene. As one ascends the visual hierarchy, neurons have progressively larger receptive fields and prefer more complex stimuli.

Neurons in the retina and LGN are monocular and have small centre–surround concentric receptive fields. In V1, neurons show many new tuning properties, including selectivity for orientation, motion direction and binocular disparity, and retain small receptive fields to provide detailed feature information at a high spatial resolution[6–9]. V1 neurons are also sensitive to colour, contrast, spatial frequency and ocular dominance[8,10]. V1 therefore provides many feature analyses of the visual scene at a fine scale before selective aspects of this information are channelled to more specialized areas that comprise the DORSAL- and VENTRAL-STREAM pathways[11]. Whereas dorsal regions such as MT and LIP are implicated in motion and spatial perception, ventral regions such as V4 and inferotemporal cortex are implicated in colour and form perception.

Effects of lesions. Lesion studies indicate that V1 is necessary for normal visual function and awareness. After considerable research and debate, early scientists identified V1 as the primary cortical site of vision (BOX 1). Cortical bullet wounds in soldiers revealed a precise retinotopic map in V1, as these small lesions in V1 led to scotomas or phenomenal blindness restricted to corresponding regions of the visual field[12,13]. Do these findings indicate that V1 itself is important for visual awareness or that damage to V1 robs higher visual areas of their necessary input?

Theories of visual awareness
This review focuses on neural localizationist theories that pertain to the role of V1 and extrastriate areas in visual awareness. Localizationist theories assume that specific neural regions or circuits are important for awareness because of their functional properties, connectivity or functional role in the network.

Although the subjective nature of awareness eludes formal definition, visual awareness will be considered here as the specific contents of consciousness for items in immediate sight. Scientists rely on operational definitions of awareness to investigate these issues empirically (BOX 2). Visual awareness can be distinguished from attention; directed attention is necessary for most forms of awareness but does not ensure that an item will be consciously perceived (BOX 3).

Hierarchical models. These models propose that only higher-level extrastriate areas are directly involved in visual awareness — damage to V1 simply disrupts the flow of information to these high-level areas[14,15] (FIG. 1). According to hierarchical models, raw visual input is analysed at increasing levels of complexity and specificity and thereby becomes increasingly accessible to awareness at higher levels of visual cortex. It is assumed that extrastriate areas, such as V4, MT and inferotemporal cortex, directly represent conscious information about colour, motion and object identity, respectively[16–19]. By contrast, V1 provides necessary visual input, just as the eyes do, but is assumed to have no function in representing conscious visual information. Crick and Koch have further argued that only extrastriate visual areas that project

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Box 1 | **The search for primary visual cortex**

Panizza (1855) seems to have been the first to identify the visual cerebrum. He discovered that damage to an eye, in various animals, led to degeneration in posterior cortex on the contralateral side. His work, published in Italian, remained largely unknown to neuroscientists outside Italy[128].

Ferrier (1876) erroneously identified the angular gyrus in the monkey parietal lobe as the seat of vision because electrical stimulation of this region evoked eye movements, and lesions here led to temporary blindness[129]. By contrast, lesions of the occipital lobe led to mild deficits, perhaps because Ferrier's lesions failed to encompass the anterior portion of the primary visual cortex (V1) that corresponded to the fovea.

Munk (1881), an opponent of Ferrier, correctly identified the occipital lobe as the seat of vision in dogs and monkeys. Lesions of the occipital lobe led to severe visual impairment for stimuli presented to the contralateral hemifield[130].

Henschen (1893) reviewed more than 160 human clinical cases of visual loss and identified the calcarine sulcus as the site of vision[131].

Inouye (1909) and Holmes (1918) studied soldiers with cortical gunshot wounds to develop the first detailed maps showing the retinotopic organization of V1 (REFS 12,13).

Box 2 | Operational definitions of awareness

Although a researcher can never have first-hand knowledge of another person's experiences, most of us will accept that other people are conscious and that they can report their visual experiences reliably. In human studies, visual awareness can be operationally defined and objectively measured by instructing the subject to make one of two responses to indicate whether stimulus A or B was perceived. Language provides some assurance that the subject is responding consciously rather than automatically; subjects can be asked to describe what they are conscious of seeing and doing.

Defining awareness is more problematic in animal studies. Animals can be trained to perform comparable visual discrimination tasks through reinforcement learning, but it is difficult to evaluate whether the task is being performed consciously or automatically. However, scientists have become more willing to assume that some animals, such as monkeys, can be trained to report their perceptions reliably. If a monkey's perceptual report seems to be reliable, resembles human perceptual performance and is effective at identifying correlated neural activity, it therefore seems reasonable to assume that the monkey is providing a reliable report of its conscious perception.

directly to prefrontal cortex can directly contribute to consciousness, on the assumption that all conscious experiences must be reportable and capable of directly generating a motor act[15]. Because V1 lacks direct projections to prefrontal cortex, this theory assumes that V1 cannot directly contribute to visual awareness. More recent proposals assume that both frontal and parietal attention-related areas are important for conscious perception[14], and that top–down signals from these areas to the extrastriate cortex might be important for selecting specific visual representations for awareness[20]. Hierarchical models predict that awareness should be more tightly correlated with activity in extrastriate areas than in V1, and that disruption of activity in V1 should not impair awareness if extrastriate activity remains intact.

Interactive models. Interactive models propose that V1 participates directly in visual awareness by forming dynamic recurrent circuits with extrastriate areas[21–23]. V1 has reciprocal connections with many extrastriate areas, including areas V2, V3, V3A, V4 and MT[1] (FIG. 1).

According to interactive models, sustained activity between a given extrastriate area and V1 is necessary to maintain a visual representation in awareness. So, despite its lack of direct feedforward connections with the prefrontal cortex, V1 can determine what extrastriate information reaches prefrontal areas by supporting or failing to support the information represented in intermediate extrastriate areas. This proposed organization allows V1 to exert 'veto' power over higher areas, raising the question of which areas should be considered to form the 'top' or 'bottom' of an interactive network.

Recurrent connections with V1 are assumed to have other important functions. Higher areas might send feedback signals to confirm the reliability of the information they receive from V1 or to modulate V1 activity on the basis of top–down knowledge, perceptual grouping or attentional selection. Recurrent connections with V1 could also function as an indexing system for perceptual binding of disparate types of information that are analysed in separate visual areas or pathways. Perceptual binding refers to the problem of how the brain integrates diverse information about colour, orientation, motion, form and so on into a single coherent perceptual representation[24]. Because V1 contains a high-resolution map of almost all relevant feature information, and forms well-organized connections with retinotopic extrastriate areas, it could function as a 'master map' or spatial–featural index to bind perceptual information across multiple areas. Interactive models predict that disruption of V1 activity should always impair awareness even if extrastriate activity remains intact. Some versions of this theory might also predict some correlation between V1 activity and awareness.

Alternative models. Other intermediate accounts illustrate the range of possible relationships between V1 activity and awareness. For example, a distributed model of awareness might predict similar effects of V1 disruption as the interactive model without assuming an essential

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DORSAL STREAM
Visual brain areas that are involved in the localization of objects and are mostly found in the posterior/superior part of the brain.

VENTRAL STREAM
Visual brain areas that are involved in the identification of objects and are mostly found in the posterior/inferior part of the brain.

Box 3 | Visual attention and primary visual cortex

Visual attention can be directed to a particular region of space, visual feature or object, and can enhance the neural processing of attended stimuli and suppress the processing of irrelevant stimuli. Behavioural studies indicate that attention is necessary but not sufficient for visual awareness — even during sustained attention, awareness can fluctuate (as during binocular rivalry[61]) or fail to isolate the target stimulus (as during perceptual crowding[132]).

Early single-unit studies in the monkey yielded few reports of attentional modulation in the primary visual cortex (V1; REF. 133), whereas effects in extrastriate visual areas such as V4 were observed more often[134]. However, in recent years there have been several reports of attentional modulation in V1 (REFS 135,136), consistent with the proposal that V1 activity reflects the perceptual saliency of visual items[75,76]. Monkeys performing a mental line-tracing task show enhanced responses in V1 if the neuron's receptive field lies on the target curve rather than on the distractor curve, and the latency of these attentional effects is closely linked to the time required to mentally trace through the curves[137]. Multiple recordings of intracortical event-related potentials indicate that attentional modulation effects occur well after the initial transient response in V1 and that attentional effects in V4 and inferotemporal cortex precede those in V1 (REF. 138). Several fMRI studies have also revealed strong attentional modulation effects in V1 as a function of visual task[139], spatial locus of attention[140–142] and the visual feature to be attended[143]. Shifts in spatial attention modulated V1 fMRI responses by about 25–50% of the magnitude of those evoked by physical stimulus alternation, and in some studies effects in V1 were comparable to those observed in higher visual areas. Attentional modulation in V1 can also occur in the absence of visual stimulation when subjects anticipate a visual stimulus[78]. These findings help to support the more controversial claim that V1 can be activated by visual imagery in the absence of physical stimulation[112]. Recent fMRI and metabolic labelling studies indicate that lateral geniculate nucleus activity can also be modulated by visual attention[144,145].

role for recurrent V1–extrastriate activity. As the primary input layer, V1 might exert a powerful organizing influence on patterns of activity across multiple extrastriate areas such that in its absence, only degenerate activity patterns can occur in the remainder of the network. In this context, V1 would have an integral and necessary role in the distributed representation of awareness.

Alternatively, the relationship between V1 activity and awareness might be flexible and situation-dependent rather than hard-wired. Perhaps the information represented in V1 is necessary only for certain types of awareness (such as figure–ground segmentation, perception during focal attention, perception of low-level features and so on). Some theories consider consciousness in terms of a dynamic, global neuronal workspace in which any given brain region, such as V1, can participate in awareness if its information is widely broadcast across many brain areas[25]. Oscillation models propose that complex distributed patterns of synchronized high-frequency neural activity are important for awareness[26,27]. These models emphasize temporal structure rather than localization of function, and do not address the role of V1 in awareness. In the current context, oscillations might be involved in the representation of visual information in extrastriate areas (hierarchical models) or the formation of dynamic circuits between V1 and higher areas (interactive models).

Lesion studies

Blindsight. Patients with V1 lesions typically report a complete loss of awareness in the corresponding region of the visual field, but some patients still retain residual visual function or 'blindsight'[28]. In forced-choice tasks, patients with blindsight can discriminate the presence, location, orientation, wavelength and direction of movement of a target stimulus at levels significantly above chance despite reporting no awareness of the stimulus[28–31]. Monkeys with unilateral V1 lesions show similar evidence of blindsight — they fail to report stimuli presented to the impaired hemifield in detection tasks but can accurately discriminate the properties of such stimuli under forced-choice conditions, in a similar way to human patients tested under non-verbal conditions[32,33].

These findings indicate that there might be a dissociation between information processing and awareness — sufficient information is reaching the visual system to allow subjects to make forced-choice discriminations, but this information cannot support awareness. However, one concern is whether visual awareness is completely absent in blindsight. Patients might be reluctant to report weak, degraded visual impressions that are nonetheless sufficient for making forced-choice discriminations. Similar effects can occur in normal subjects under near-threshold conditions. There is some evidence that blindsight differs from near-threshold vision in normal subjects, especially for static stimuli[34]. However, blindsight patients do seem to have residual impressions of salient moving stimuli, which they describe as "black moving on black"[30,35,36]. One blindsight patient, DB, has also reported awareness of visual afterimages despite his inability to perceive the original

adapting stimulus[37]. Phenomenal vision in blindsight is severely degraded but not always completely absent.

Intact extrastriate cortex might be crucial for blindsight, as patients who have had an entire hemisphere removed show little evidence of residual visual discrimination abilities[38]. Although the geniculostriate pathway (from the retina to LGN to V1) provides most of the visual input to the cortex, alternative subcortical pathways project to extrastriate areas[2]. Single-unit recordings in monkeys indicate that visual information can still reach extrastriate areas after V1 has been lesioned or inactivated. Although their firing rates are reduced, a substantial proportion of neurons in areas MT and V3A remain responsive to visual stimuli and retain their direction selectivity to moving bars[39,40]. Nonetheless, monkeys with V1 lesions perform poorly on motion-detection tasks except under forced-choice conditions[41]. Recent neuroimaging studies of patients with unilateral V1 damage indicate that a network of extrastriate areas can still be activated during stimulation of the blind hemifield[42] (FIG. 2). Unperceived stimuli presented to the blind hemifield still evoke robust functional magnetic resonance imaging (fMRI) responses from the motion-sensitive areas MT and V3A, the colour-sensitive area V4/V8 and lateral occipital regions involved in object perception. So, considerable stimulus selectivity is maintained in extrastriate cortex, but this activity seems to be insufficient to support awareness in the absence of V1, consistent with the predictions of interactive models. However, it is possible that extrastriate signals are too weak or degraded to support conscious perception but are sufficient to support forced-choice discrimination. Further comparisons of extrastriate responses to weak but perceptible stimuli presented to the intact hemifield, and strong stimuli presented to the blind hemifield might help to address these issues.

Extrastriate lesions. By contrast to the devastating effects of V1 lesions, damage to any other cortical visual area leads to more restricted deficits in visual perception. Lesions of area V2 can lead to impairments in perceptual grouping but do not impair visual acuity or contrast sensitivity[43]. Large bilateral lesions encompassing area MT and extensive surrounding areas have led to the loss of motion perception in at least one patient[44,45], but more restricted MT/MST lesions in humans or monkeys lead to moderate deficits in direction discrimination that can partially recover over time[46,47]. Damage to the lingual gyrus region encompassing ventral area V4 and/or putative area V8 can lead to the loss of conscious colour perception[48–52], whereas lesions of inferotemporal cortex can impair face or object recognition[53,54].

Lesions of the posterior parietal lobe and/or superior temporal gyrus can lead to global deficits in visual attention and awareness[55,56]. Patients with unilateral lesions often show spatial neglect — the inability to attend to or report awareness of stimuli presented to the contralesional hemifield. Bilateral lesions can lead to a more profound deficit, Balint's syndrome, which is
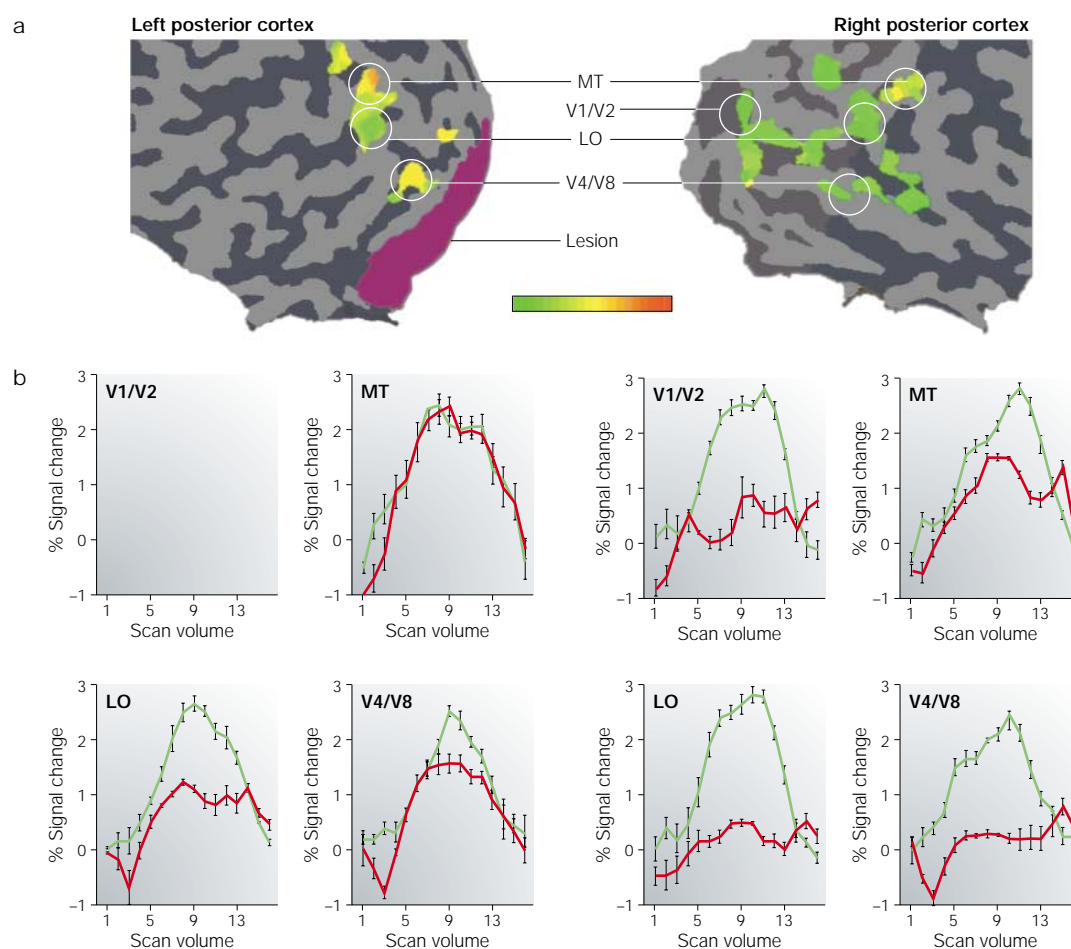
Figure 2 | **Extrastriate activations to objects in the absence of primary visual cortex (V1) and reported awareness.** **a** | Flattened cortical representation of left and right posterior cortex for blindsight patient GY with the site of the V1 lesion shown in purple. Regions activated by objects presented to either the intact left visual field or impaired right visual field are indicated by a colour scale (green represents left visual field only; red represents right visual field only; yellow represents both fields). Areas MT, V4/V8 and the lateral occipital area (LO) were all activated by stimuli presented to the blind hemifield. **b** | Time course of functional magnetic resonance imaging activity from visual areas V1/V2, MT, LO and V4/V8 for perceived left hemifield objects (green line) and unperceived right hemifield objects (red line). Reproduced, with permission, from REF. 42 © (2001) Elsevier Science.

characterized by the inability to perceive or attend to more than one object at a time (simultanagnosia), deficits in shifting attention, and impairments in visually guided actions and eye movements[57]. In monkeys, lesions of any single parietal visual area lead to mild deficits in visually guided eye movements or actions[58], whereas lesions of the superior temporal gyrus can lead to more neglect-like deficits[59]. Because the lesions that lead to neglect in humans are typically large and variable, controversy surrounds the question of which visual areas are implicated in this deficit of spatial attention and awareness[55,56].

The fact that independent lesions of either V1 or parietal-temporal regions can greatly impair conscious vision indicates that no single visual area is sufficient for visual awareness. Whereas several parietal-temporal regions have been implicated in the ability to attend and respond to visual events, V1 seems to be the only single cortical visual area that is crucial for visual awareness.

Neural correlates of visual awareness
Whereas lesion studies can show whether the removal of a critical region leads to selective or global disruption of visual awareness, electrophysiological and neuroimaging techniques can investigate which visual areas contribute to awareness when the network is intact. A powerful approach is to investigate the neural correlates of visual awareness under ambiguous conditions in which the physical stimulus remains constant while perception changes from moment-to-moment or trial-to-trial. Neural responses corresponding to the subject's reported perceptual state cannot be attributed to changes in the physical stimulus and must instead reflect conscious perception.

Binocular rivalry. Many studies have capitalized on the compelling bistable phenomenon of binocular rivalry to investigate the neural correlates of visual awareness[60]. When different monocular patterns are simultaneously presented to the two eyes, they rival for

a Rivalry **b** Stimulus alternation **c**
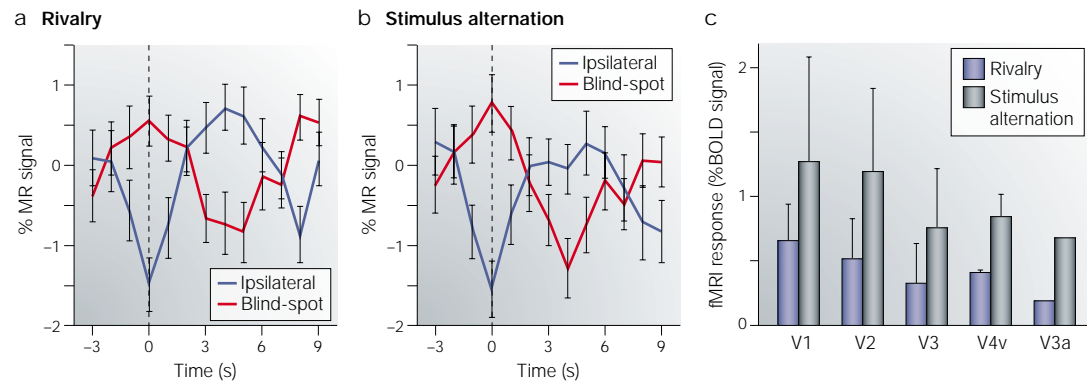
Figure 3 | **Functional magnetic resonance imaging correlates of binocular rivalry in human primary visual cortex.** Average functional magnetic resonance imaging (fMRI) responses from the monocular primary visual cortex (V1) representation of the blind spot of a representative subject during **a** | binocular rivalry and **b** | stimulus alternation. Positive responses occurred for reported switches to the preferred grating shown to the ipsilateral eye (blue line); negative responses occurred for switches to the non-preferred grating shown to the blind-spot eye (red line). The vertical line at 0 ms indicates the time of the subject's report of a switch. fMRI response amplitudes were equally high for rivalry and stimulus alternation for all four subjects, indicating that rivalry was fully resolved in this region of monocular visual cortex. Reproduced, with permission, from *Nature* REF. 68 © (2001) Macmillan Magazines Ltd. **c** | Amplitude of fMRI responses for rivalry (blue bars) and stimulus alternation (grey bars) between a high-contrast grating and a low-contrast grating. In this study, rivalry modulations were about half the strength of those evoked by stimulus alternation for all areas V1 through V4, indicating that rivalry effects that were evident in V1 were not further resolved in higher visual areas. The weaker rivalry modulations observed here, compared with the cortical blind-spot representation[68], might reflect the greater incidence of incomplete or piecemeal rivalry reported by subjects. Reproduced, with permission, from *Nature* REF. 69 © (2000) Macmillan Magazines Ltd.

exclusive dominance such that perception alternates between one monocular image and the other every few seconds[61]. Early studies in humans revealed robust electroencephalogram (EEG) modulations from occipital sites during rivalry[62,63]. By contrast, single-unit studies in awake, behaving monkeys found that only a minority of neurons in areas V1, V4 and MT showed significant modulations in activity that corresponded to perception during rivalry, and some neurons fired at increased rates when their preferred stimulus was suppressed[64,65]. Only in the inferotemporal cortex did most neurons show statistically significant activity changes corresponding to the monkey's reported perception[66]. These findings led to the proposal that binocular rivalry results from pattern competition in high-level extrastriate areas[65] rather than from interocular competition between monocular neurons in V1 (REF. 67).

However, fMRI studies have demonstrated powerful effects of binocular rivalry in V1. One study probed a monocular region of human V1 that corresponded to the blind spot[68]. fMRI modulations during rivalry were as large as those evoked by physical alternation between preferred and non-preferred monocular stimuli (FIG. 3a,b), indicating that rivalry might be fully resolved in monocular visual cortex as a consequence of early interocular competition. In another study, rivalry between high- and low-contrast gratings led to equally robust fMRI modulations in visual areas V1 to V4, with no evidence that the effects of rivalry were stronger in higher visual areas[69] (FIG. 3c). Consistent with the proposal that visual signals are gated in area V1 (REF. 70), face- and house-selective areas in ventral extrastriate cortex showed equivalent responses during rivalry and stimulus alternation between a face and house, indicating that rivalry was already fully resolved by these levels
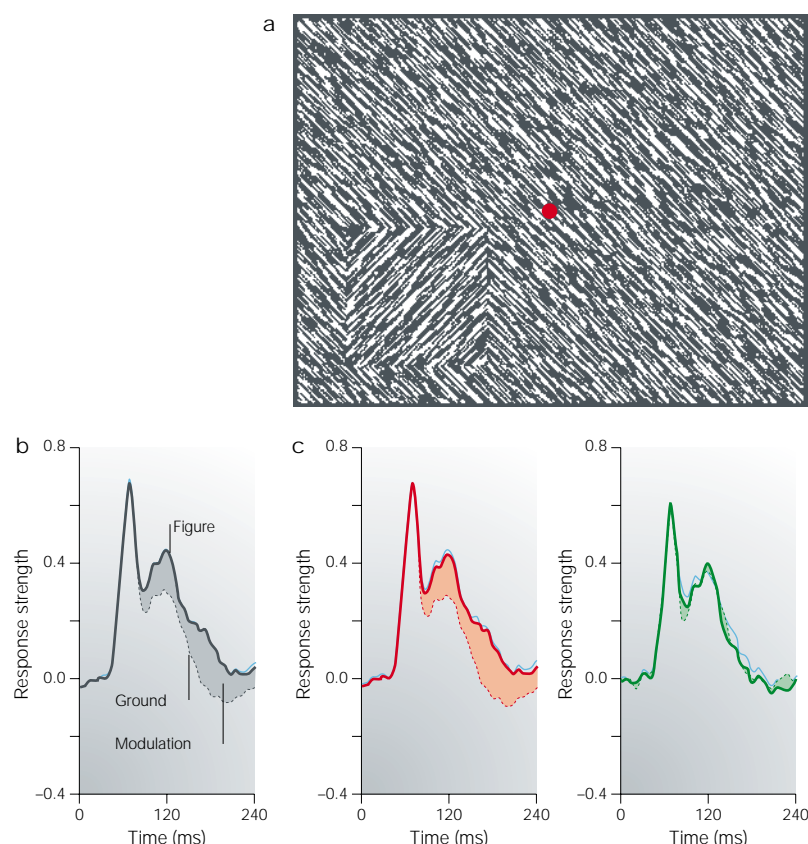
of processing[71]. Parietal and frontal attention-related areas were also activated during rivalry alternations, indicating that these areas might also be involved in the conscious detection and interpretation of ambiguous perceptual events[72].

It remains to be clarified why fMRI studies of human V1 yielded highly robust effects whereas few V1 neurons showed significant modulations in the monkey. However, re-analyses indicate that across all V1 units, neuronal population responses during rivalry were about one-third the size of stimulus alternation responses, indicating a smaller discrepancy between studies. Both V1 and extrastriate areas might contribute to grouping and segmentation processes in binocular rivalry, although the precise site(s) of inhibitory competition remain to be resolved[60]. With regard to awareness, the evidence indicates that population activity in human V1 is tightly linked to conscious perception during rivalry. These findings support the proposal that V1 activity might be essential for visual awareness. Alternatively, rivalry competition in V1 might disrupt awareness primarily by gating what information reaches higher-level extrastriate areas.

Visual detection. V1 activity seems to be closely linked to the conscious detection of a visual target or pattern. Single-unit recordings in alert monkeys have shown that the late component of V1 activity, starting about 80–100 ms after response onset, is enhanced if the neuron's receptive field lies on a large textured figure that can be perceptually segregated from the background on the basis of orientation, disparity or colour cues[73] (but see also REF. 74). Crucially, V1 responses are enhanced only if the monkey successfully perceives the target; no enhancement occurs when the target is missed, indicating that

these neural modulations are tightly linked to the monkey's conscious perception[75] (FIG. 4). A related study found similar enhancements in V1 activity, which were correlated to the monkey's behavioural accuracy at detecting an odd-shaded target in an array of mirror-reversed distractors[76]. The late enhancement of V1 responses is consistent with the proposal that feedback is important for visual awareness, and this might reflect top–down attentional modulation of early visual activity (BOX 3).

Functional MRI studies also show that V1 activity is tightly linked to pattern perception. When subjects had to detect a faint, near-threshold pattern, V1 responses were equally large for successfully perceived targets and false alarms (when the subject erroneously believed a pattern to be present), and much lower on target-absent and missed-target trials[77]. In a separate study, V1 showed significant attentional modulation to an auditory tone in anticipation of a near-threshold visual stimulus, and the likelihood of correctly discriminating the presence or absence of the stimulus was positively correlated with the degree of attentional enhancement[78].

Bistable perception. Some studies of bistable perception have found that the correspondence between visual awareness and neural activity is greater in extrastriate areas than in V1. When monkeys reported the motion direction of an ambiguous rotating cylinder that was defined by moving dots, only 20% of V1 neurons were modulated by perception, compared with more than 60% of MT neurons[79]. Two fMRI studies found selective activation of extrastriate area MT during spontaneous alternations in bistable motion perception[80,81], and another study found activity increases in MT and concomitant decreases in V1 whenever subjects switched from perceiving incoherent motion to a coherent motion-defined form[82]. An fMRI study of reversible figures, such as the Necker cube and Rubin's face-vase, found activation of ventral extrastriate, parietal and frontal regions at the time of reported alternations that were accompanied by activity decreases in striate cortex[83]. These findings indicate a tight coupling between awareness and extrastriate activity, and also an unusual push–pull relationship between extrastriate activity and V1 activity during bistable perception. Unlike rivalry, which involves phenomenal fading of low-level features, these forms of bistable perception involve changes in the global organization of stable low-level features. Further research is required to clarify whether these V1 modulations reflect a role in perceptual grouping, shifts in attention to low- versus high-level stimulus properties or some other factor. Nevertheless, it seems that V1 activity is often correlated to these more complex forms of bistable perception.

V1 response properties and perception. Many studies have investigated the response properties of V1 under varying visual conditions. Although the studies described below cannot distinguish whether neural activity reflects properties of the physical stimulus or of conscious perception, they do address what types of perceptual information are likely to be represented in V1.

V1 seems to be necessary for high-resolution spatial processing of stimulus orientation and position[21]. Behavioural training on orientation discrimination can lead to sharpened orientation tuning in V1 neurons, indicating that V1 is involved in orientation learning[84]. V1 neurons are also highly sensitive to stimulus contrast and perceived brightness. Evidence of brightness constancy seems to emerge first in V1, rather than in the LGN or retina[85].

V1 might also be involved in perceptual grouping and filling in. Neurons in V1 respond more strongly when a bar outside the receptive field is aligned congruently to a bar that lies within the receptive field, suggesting a role in contour integration[86]. Responses in V1 to partially occluded objects have also been reported[87]. The processing of subjective contours, once linked primarily to area V2 (REF. 88), also seems to be evident in V1 (REF. 89). V1 neurons show some evidence of perceptual filling-in around the blind spot[90], and can exhibit dynamic displacements in their receptive fields minutes after retinal lesions have occurred[91]. However, presentation of an 'artificial scotoma' (a large grey patch surrounded by

Figure 4 | **Multi-unit activity in primary visual cortex correlates with conscious detection of visual figures on a background. a** | Figure–ground displays were generated using orientation-defined texture. Animals fixated on a central point and were required to saccade to the figure, which could appear in one of three locations. **b** | Average multi-unit responses across the recorded neural population for figure-present trials. Modulation is the difference between the response to figure (thick line) and the response to ground (dashed line) and is shaded. Standard error of the mean is shown by the blue line above the figure response. **c** | Figure and ground responses for 'seen' (red) and 'not seen' (green) figure-present trials. Reproduced, with permission, from *Nature* REF. 75 © (2001) Macmillan Magazines Ltd.

dynamic white noise), which leads to perceptual filling-in, causes increased activity in areas V3 and V2 but not V1 (REF. 92).

Visual adaptation to a specific orientation, colour or motion direction leads to corresponding decreases in V1 activity, indicating that activity in V1 might be linked to the strength of visual impressions[93–95]. In studies of flash suppression, V1 neurons responding to an optimally oriented monocular grating undergo suppression if an orthogonal grating is subsequently presented to the opposite eye[96]. By contrast, facilitation occurs if the second grating matches the orientation of the first grating. This orientation-specific interocular inhibition can account for the phenomenal suppression reported by human subjects under such conditions and might also account for binocular rivalry. Competitive interactions in BACKWARD VISUAL MASKING also seem to occur at an early stage of processing in the LGN or V1 (REFS 97,98).

Dissociations between V1 activity and awareness
V1 activity is not sufficient for awareness. Although much of the evidence described above is consistent with a role for V1 in awareness, other studies show that V1 activity might be necessary but is not sufficient for perceptual awareness. For example, the responses of V1 neurons can follow flickering colour gratings at temporal rates that are too fast to be perceived[99]. Behavioural studies indicate that orientation-specific adaptation, which presumably takes place in V1, can occur for high-spatial-frequency gratings that are too fine to be perceived[100]. Similar visual after-effects ascribed to V1 have been observed under conditions of rivalry suppression[101]. These findings indicate that visual processing can proceed in V1 in the absence of awareness, indicating that V1 activity alone is not sufficient for awareness.

However, activity throughout the ventral extrastriate pathway also does not seem to be sufficient for awareness. Blindsight patients, for example, can show considerable extrastriate activity in the absence of awareness[42]. Monkeys with gross lesions of non-visual frontal, parietal and temporal cortex have chronic blindness despite the sparing of V1 and extrastriate cortex[102]. Likewise, patients with right parietal lesions show preserved activity in striate and ventral extrastriate areas, even though they fail to detect left-sided stimuli during bilateral stimulus presentation[103,104]. These and related findings indicate that neither ventral extrastriate activity nor V1 activity is sufficient for awareness, and that parietal attention-related areas might also be necessary for normal conscious vision[14,105,106]. It is impossible to exclude V1 or any other visual area from a possible role in awareness on the basis of lack of sufficiency, given that no single cortical area seems to be sufficient for mediating visual awareness.

Internally generated visual experiences. Neuroimaging studies have found that some internally generated forms of visual experience can occur in the absence of measurable changes in V1 activity. Visual hallucinations in schizophrenic patients lead to significant increases in fMRI activity in ventral extrastriate areas but not in striate cortex[107]. Positron emission tomography (PET)

studies have found that extrastriate activity is greater during rapid eye movement (REM) sleep (when vivid dreaming occurs) than in waking periods, whereas the opposite pattern is observed in V1 (REF. 108) (perhaps similar to the decreased V1 activity found during bistable perceptual alternations[82,83]). In one migraine patient, visual auras were associated with the onset of retinotopic waves of activity in V3A well before these effects propagated to V1 (REF. 109). In one study, colour SYNAESTHESIA evoked by spoken words led to an increase in activity in the colour-sensitive area V4/V8 but not in V1 (REF. 110), whereas another study did find significant effects in V1 (REF. 111). Some studies of visual imagery find evidence of V1 activation but others do not, indicating either poor sensitivity at measuring these changes or that visual imagery might not always reliably activate V1 (REF. 112). These findings provide some support for the hierarchical view by showing that activity in V1 can be dissociated from visual awareness. One possible interpretation is that V1 is necessary for normal aspects of visual awareness but not for atypical forms such as hallucinations, visual auras, dreams and visual imagery. Internally generated experiences share some, but not all, of the phenomenal properties of actual perception; to the extent to which they differ, the underlying neural correlates might differ as well. Alternatively, some studies might have failed to detect significant changes in V1 activity because of inadequate statistical power or the use of baseline conditions in which some V1 activity remained. Further studies that measure electrophysiological activity directly from the cortex might help to address whether V1 is active during alternative forms of visual experience.

Creating and disrupting visual experiences
It has long been known that electrical stimulation of the occipital lobe can elicit subjective visual sensations or 'phosphenes'[113]. Subdural cortical stimulation of V1 in blind or HEMIANOPIC patients typically elicits the impression of a small point of light, even in patients with severed connections between LGN and V1 (REFS 114,115). These findings indicate that subcortical activity before area V1 is not necessary for conscious experience.

Phosphenes can also be generated by stimulation of higher visual areas such as V2 (REF. 115). Stimulation of MT can bias motion perception in monkeys[116] and elicit MOTION PHOSPHENES in humans, but feedback to V1 might be important for these evoked impressions[117]. Consistent with this possibility, neurophysiological studies have shown that electrical stimulation of V2 and MT can lead to ORTHODROMIC ACTIVATION of V1 neurons[118,119]. Stimulation of occipital areas evokes vivid impressions of basic visual sensations (points of light, motion, colour and so on), whereas stimulation of the temporal lobe can elicit hallucinations of people, scenes or objects, which have a more dreamlike or recollective quality[120].

Perception can be reliably disrupted when TRANSCRANIAL MAGNETIC STIMULATION (TMS) of the occipital pole is applied 80–120 ms after a briefly flashed stimulus[121,122] and over areas corresponding to V1 and/or V2. This might reflect the disruption of feedback signals from higher areas to V1 (REF. 123). For example, TMS applied to

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BACKWARD VISUAL MASKING
The reduced perception that occurs when a weak or brief stimulus is followed immediately by a stronger stimulus.

SYNAESTHESIA
An unusual 'mixing of the senses' in which a stimulus in one sensory modality (for example, a sound) elicits a percept in another modality (such as visual perception of a colour).

HEMIANOPIA
Loss of vision over half of the visual field, typically resulting from damage to the optic radiations that project to V1 or damage to V1 itself.

MOTION PHOSPHENES
Moving visual images that can be induced by stimulating parts of the visual system that are sensitive to motion.

ORTHODROMIC ACTIVATION
Activation of a target neuron by stimulation of an input neuron that synapses onto the target; action potentials are propagated in the normal direction along the input axon.

TRANSCRANIAL MAGNETIC STIMULATION
(TMS). A technique that is used to induce a transient interruption of normal activity in a relatively restricted area of the brain. It is based on the generation of a strong magnetic field near the area of interest, which, if changed rapidly enough, will induce an electric field that is sufficient to stimulate neurons.
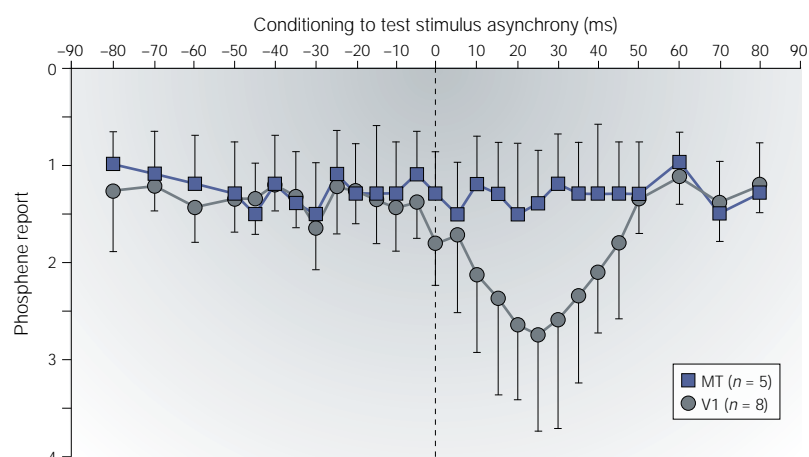
Figure 5 | **Relationship between timing of primary visual cortex disruption and visual awareness.** Transcranial magnetic stimulation (TMS) was applied to area MT to elicit a motion phosphene while a conditioning pulse was applied to either primary visual cortex (V1) or MT at different relative times. The conditioning pulse was set to subthreshold levels for evoking a phosphene. Subjects reported whether they perceived: 1, a clearly moving phosphene; 2, a weakly moving phosphene; 3, a stationary phosphene; or 4, no phosphene. TMS applied over V1 between 5 and 45 ms after TMS over MT disrupted the perception of the phosphene, whereas a conditioning pulse applied to MT had no disruptive effect at any time interval. These findings support the proposal that feedback connections from MT to V1 might be necessary for awareness of motion. Reproduced, with permission, from REF. 125 © (2001) American Association for the Advancement of Science.

area MT produces maximal disruption of perception if given at the time of motion onset, but when TMS is applied to V1, maximal disruption occurs considerably later, 70–80 ms after motion onset[124]. Such findings are difficult to reconcile with hierarchical feedforward models in which information propagates from V1 to MT for further processing and conscious representation.

A recent study provided new evidence to support the role of feedback connections in visual awareness[125] (FIG. 5). Motion phosphenes were reliably elicited by applying TMS to area MT, and a second TMS pulse was applied to either V1 or MT at various times before or after the phosphene-eliciting pulse. Perception of the motion phosphene was selectively impaired when V1 stimulation occurred shortly after MT stimulation (10–40 ms later) but not beforehand, indicating that feedback projections from MT to V1 might be necessary for conscious perception. It is possible that rapid feedforward signals from V1 to MT interrupted the late component of the MT response, although a second pulse applied to MT had no disruptive effect. The authors concluded that MT activity alone might be insufficient to support awareness of motion, and that feedback activity to V1 might be necessary for visual awareness. These findings provide direct support for the proposal that recurrent connections between V1 and higher areas are important for maintaining a visual representation in awareness.

The disruptive effects of TMS closely parallel studies of backward visual masking, in which a target stimulus can be rendered invisible by a subsequent visual mask. Most models of masking assume that the visual mask disrupts neural activity that corresponds to the target at a low-level site of processing, possibly V1 or LGN[98], but the precise mechanism remains controversial. One proposal is that the mask disrupts re-entrant activity from higher visual areas[126]. Other models assume that transient V1 responses to the mask disrupt a late component of the feedforward activity, either the sustained parvocellular response[127] or the off-response to the target[97]. Given the long integration times of the visual system, it has proven difficult to tease apart feedforward and feedback accounts of visual masking.

A preliminary TMS study of a blindsight patient, GY, provides some evidence in favour of the feedback re-entrant account[117]. In GY, stimulation of MT elicited motion phosphenes only when applied to the side with intact V1, but not when applied to the side with damaged V1 cortex. By contrast, motion phosphenes were successfully elicited in all normal subjects tested, as well as in a retinally blind patient. Further tests of the interactive model should pursue whether direct cortical stimulation of extrastriate areas can elicit phosphenes in patients with V1 damage. Studies of non-human primates undergoing temporary V1 inactivation would also be revealing if animals can be trained to report the location or perceptual characteristics of electrically generated phosphenes.

Concluding remarks

Considerable evidence indicates that V1 is necessary for normal visual awareness, and recent studies indicate that V1 activity is tightly correlated with awareness under various conditions. There is growing evidence that the late component of V1 activity reflects feedback contributions from higher areas, and that this feedback activity might be crucial for conscious vision. Although activity in V1 is not sufficient for awareness, the same is also true of other visual areas. In the absence of V1, visual signals can still reach many extrastriate areas but seem incapable of generating normal conscious experiences. However, it remains to be determined whether V1 contributes to awareness directly or whether its disruption leads to degenerate activity in higher visual areas, thereby disrupting awareness indirectly.

The neural basis of conscious vision is an intriguing area for future research. Many questions remain to be addressed. What are the contributions of individual visual areas to awareness? What are the relative contributions of feedforward and feedback pathways? How do multiple visual areas bind disparate forms of information into a coherent percept? How do distinct areas or neural populations resolve 'disagreements' about conflicting information? And to what extent is visual information represented in dynamic or distributed circuits as opposed to individual neurons? Along these lines, there seems to be a shift towards studying the interactions between multiple visual areas rather than focusing on processing in individual areas. Improved techniques for manipulating or monitoring neural activity in multiple areas will be important for this line of research. Identifying the source of causal relationships in an interactive network will be a major challenge, requiring detailed analysis of the timing of

activity across multiple visual areas and the ability to selectively excite or disrupt neural activity at specific levels of the visual pathway. Neural interactions will have to be linked directly to the conscious report of humans or the perceptual report of trained animals. After all, the goal of this endeavour is not to understand brain activity in isolation, but to clarify how it corresponds to phenomenal aspects of the mind.

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