Top-down influences on visual processing

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Abstract | Re-entrant or feedback pathways between cortical areas carry rich and varied information about behavioural context, including attention, expectation, perceptual tasks, working memory and motor commands. Neurons receiving such inputs effectively function as adaptive processors that are able to assume different functional states according to the task being executed. Recent data suggest that the selection of particular inputs, representing different components of an association field, enable neurons to take on different functional roles. In this Review, we discuss the various top-down influences exerted on the visual cortical pathways and highlight the dynamic nature of the receptive field, which allows neurons to carry information that is relevant to the current perceptual demands.

Re-entrant or feedback pathways
Processing strategy in which the product of an ongoing computation at one cortical level is analysed by the next level. The resultant information is then sent back to the initial level to influence its further computation. This is also sometimes referred to as countercurrent processing streams.

The functional properties of cortical neurons are not fixed. Rather, they can be thought of as adaptive processors, changing their function according to the behavioural context, and their responses reflect the demands of the perceptual task being performed. Cortical neurons are subject to top-down influences of attention, expectation and perceptual tasks. 'Top-down' refers to cognitive influences and higher-order representations that impinge on earlier steps in information processing. Such influences represent a reversal of the central dogma of sensory information processing, which is based on feedforward connections along a hierarchy of cortical areas that represent progressively more complex aspects of the visual scene. However, superimposed on the feedforward pathways, there are re-entrant or feedback pathways that convey higher-order information to antecedent cortical areas. The top-down signal carries a rich amount of information that facilitates the interpretation of the visual scene and that enables the visual system to build a stable representation of the objects within it despite rapid and continuous eye movements. It facilitates our ability to segment the complex arrangement of multiple objects and backgrounds in the visual scene. In addition, the top-down signal has a role in the encoding and recall of learned information. The resulting feedforward signals carried by neurons convey different meanings about the same visual scene according to the behavioural context. This idea is in stark contrast with the classical notion of a visual cortical hierarchy in which information is conveyed in a feedforward manner to progressively higher levels in the hierarchy, beginning with the analysis of simple attributes, such as contrast and orientation, and leading to more complex functional properties from one stage to the next. As we analyse visual scenes, we set up countercurrent streams of processing, with the resulting percept reflecting the set of functional states of all the areas in the visual cortical hierarchy. In this Review, we consider the receptive field properties that are subject to top-down influences, the nature of the information that is conveyed by re-entrant pathways and how the information carried by neurons depends on behavioural context. Over longer time periods, receptive fields can change to accommodate alterations in visual experience. These lines of evidence point towards an evolving view of the nature of the receptive field, which includes contextual influences, and emphasizes its dynamic nature, with neurons taking on different properties in response to experience and expectation.

Top-down influences are conveyed across a series of descending pathways covering the entire neocortex and are relayed through thalamic nuclei (FIG. 1). The feedforward connections define a hierarchy of visual cortical areas, beginning with the primary visual cortex (V1) and ascending through two primary pathways: a ventral pathway, which is involved with object recognition, and a dorsal pathway, which is involved with visually guided movements and attentional control. For every feedforward connection, there is a reciprocal feedback connection that carries information about the behavioural context.

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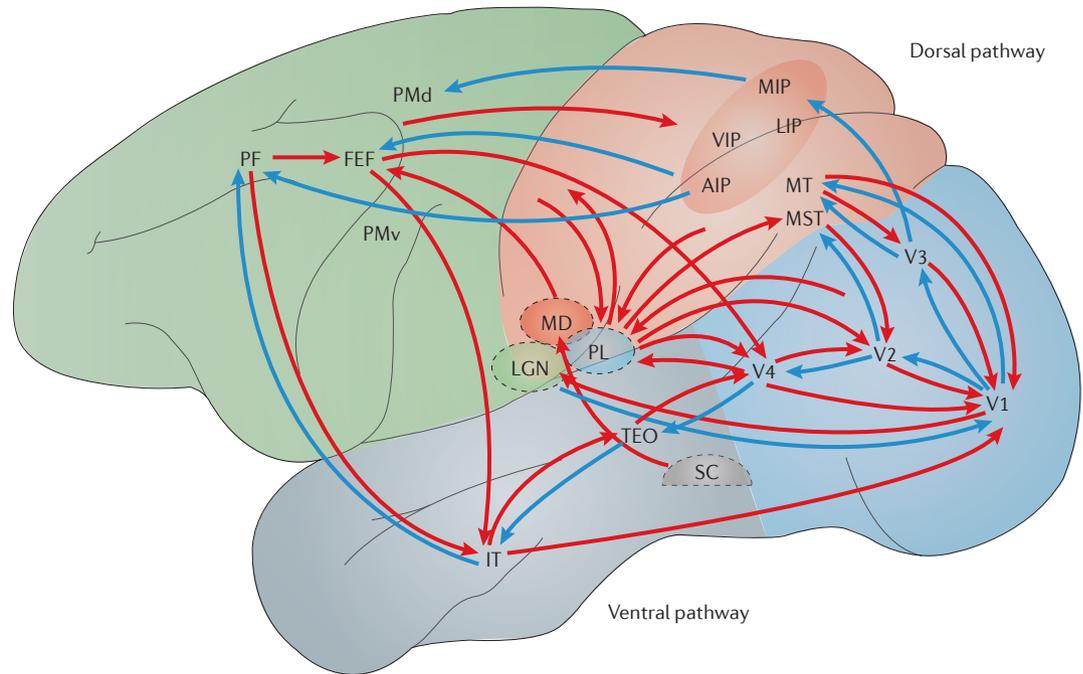
Figure 1 | **Feedback pathways carrying top-down information.** Processing visual information involves feedforward connections across a hierarchy of cortical areas (represented by the blue arrows). The visual cortical pathways begin in the primary visual cortex (V1), which receives subcortical input from the lateral geniculate nucleus (LGN). The feedforward connections extend through a ventral pathway into the temporal lobe and through a dorsal pathway into the parietal cortex and prefrontal cortex (PF). Matching these feedforward connections are a series of reciprocal feedback connections (represented by the red arrows), which provide descending top-down influences that mediate re-entrant processing. Feedback is seen in direct corticocortical connections (those directed towards area V1), in projections from area V1 to the LGN and in interactions between cortical areas mediated by the pulvinar (PL). Information about motor commands, or efference copy, is fed to the sensory apparatus by a pathway involving the superior colliculus (SC), medial dorsal nucleus of the thalamus (MD) and frontal eye fields (FEF). In addition to direct reciprocal connections, for example from area V2 to area V1, feedback can cascade over a succession of areas, for example, from the PF to FEF to area V4 to area V2 to area V1. As outlined in this Review, diverse information is conveyed across these pathways, including attention, expectation, perceptual tasks and efference copy. AIP, anterior intraparietal area; IT, inferior temporal area; LIP, lateral intraparietal area; MIP, medial intraparietal area; MST, medial superior temporal area; MT, medial temporal area; PMd, dorsal premotor area; PMv, ventral premotor area; TeO, tectum opticum. Figure is modified, with permission, from REF. 147 © (2012) McGraw-Hill Companies.

The receptive field

Top-down influences take into account the nature of stimulus-dependent properties in any sensory cortical area. There is an emerging view that in the early stages of visual cortical processing, rather than doing a local analysis of simple features, neurons can integrate information over large parts of the visual field and that neurons in these areas can show selectivity for complex stimulus configurations. The integrative properties of cortical neurons are reflected in their selectivity for stimulus context. Contextual influences refer to the ways by which the perceptual qualities of a local feature are affected by surrounding scene elements and the way in which global scene characteristics affect the responses of neurons to local features. They have important roles in perceptual grouping, perceptual constancies, contour integration, surface segmentation and shape recognition. The most profound effects of top-down control are exerted on contextual influences. This has led to a change in our thinking about the role and prevalence of top-down influences across

the visual cortical hierarchy, from initial studies suggesting that they are negligible at early stages of cortical processing to current studies showing substantial changes in neural responses with attention, expectation and perceptual tasks.

Understanding how such cognitive influences affect neuronal function requires an understanding of the character of the receptive field. The visual receptive field is the part of the retina in which a stimulus can cause the neuron to respond with a train of action potentials. The characterization of the receptive field is dependent on the nature of the stimulus that is used to measure it. A simple stimulus, such as an oriented line segment, will activate a neuron over a small part of the visual field (this is known as the 'minimum response field', which is on the order of 0.5 degrees in diameter for superficial layer V1 parafoveal receptive fields), but similar stimuli outside this area, which by themselves will not activate the neuron, can greatly affect the neuron's response when presented jointly with a stimulus in the centre of the receptive field. These modulatory

Visual cortical hierarchy
The hierarchy of cortical areas in the classical model of the cortical representation of visual information beginning with the primary visual cortex and ascending through two pathways: a ventral pathway extending into the temporal lobe, which is involved with object recognition, and a dorsal pathway extending into the parietal lobe, which is involved with visually directed movement and spatial attention.

influences can be either facilitatory or inhibitory, and the direction and size of the effect depends on the position of the flanking stimulus relative to the receptive field core[1]. As a consequence, neurons' responses are as dependent on the characteristics of global contours and surfaces as they are on the attributes of local features within the minimum response field, and these contextual influences can extend over relatively large regions of the visual field. Contextual influences in areas V1 and V2 have been implicated in intermediate-level vision, including contour integration (the assembly of contour elements into global shapes) and surface segmentation (the separation between object surfaces and their backgrounds)[2–8]. The extent of these contextual influences varies according to the level of stimulus complexity and attentional state[9]. One has to keep contextual influences in mind when considering the role of top-down influences in altering a neuron's response properties.

The function of a neuron is also characterized by its tuning to a range of stimuli, such as different line orientations, directions of movement or colours. One can extend this to any stimulus space and determine the responsiveness of a neuron to stimuli in different points within that space. This notion has been applied to determine a neuron's selectivity for the shapes of complex objects or for the configuration of complex stimuli consisting of multiple line segments. Beyond examining the shape of a neuron's tuning, one can use other measures to characterize a neuron's stimulus selectivity and to relate that selectivity to perception[10]. One measure is mutual information — the degree to which a neuron's response predicts stimulus identity, which is quantified in bits. Another is ideal observer analysis, which allows one to relate a neuron's discriminability in a stimulus space — its 'neurometric' curve — to the animal's discrimination performance — its 'psychometric' curve. Top-down influences also affect these measures of neuronal function, and as a result, change the nature of the information that neurons convey.

The cortical source and circuitry underlying contextual influences have been vigorously debated[5,11–17]. We have proposed that long-range intrinsic cortical connections provide a substrate for interactions across the visual field and have a spatial extent and columnar specificity that is consistent with the contextual influences and with the Gestalt rules of perceptual grouping[5,11,12,14]. Some researchers have argued that these influences originate from higher-order cortical areas on the basis of their timing relative to stimulus onset. It is not clear that timing is a reliable indicator of the source of a signal given the fast conduction velocities of feedback projections. An alternative explanation is that a signal delay is due to the time required for the network to shift from one stable state to another, with foreground and background interactions requiring time to evolve[18]. Delayed influences have been seen with stimuli involving texture segmentation and contour saliency[5,19], but for stimulus configurations without complex backgrounds, contextual effects have been observed from the onset of responses[20] (FIG. 2).

Effects of top-down influences

Top-down influences include different forms, such as attention, expectation and perceptual tasks. They are seen at all stages in the visual hierarchy, including area V1, and reaching as far back as the lateral geniculate nucleus[21,22]. The effect of these influences is to alter receptive field properties and the information carried by neural ensembles. As a consequence, vision can be thought of as an active process, requiring expectation or hypothesis testing in order to interpret the visual scene. Some contextual influences have been proposed to arise from a predictive coding strategy, by which higher levels in the cortical hierarchy make predictions about lower-level activity, and some neurons carry an error signal between the prediction and the stimulus-generated activity[23,24]. Top-down influences assume a number of forms, and there is a rich amount of information conveyed from higher-order to lower-order areas.

Spatial attention. Top-down control is traditionally associated with spatial attention. Its effect has largely been characterized in terms of gain control — which is the enhancement of neural responses — as well as suppression of responses outside the focus of attention[25,26]. Spatial attention allows us to select behaviourally relevant stimuli and to analyse specific parts of the visual field[27]. The consequent enhancement of neural responses is seen in a number of cortical areas, including V1, V2, V4, the medial temporal (MT) area and the inferior temporal (IT) area[5,26,28–40], and it provides a mechanism for selection of behaviourally relevant stimuli from competing distracters[41]. Whereas earlier studies have suggested that higher-order visual areas in the cortical hierarchy are more subject to attentional influences than earlier stages[42], the magnitude of attentional effects is highly dependent on the nature of the task and the configuration of the stimulus[20,26,35,38,43–46]. Attentional effects are more profound when there is competition between multiple stimuli[26,45]. In area V1, this is when contextual influences are involved[5,26,35,38,47]. One should therefore consider the effects of attention on lateral interactions instead of their influence on feedforward properties, such as the orientation of a line segment. For example, two collinear lines, one inside and one outside the receptive field, will produce a stronger response relative to that elicited by a single line centred within the receptive field. This facilitation depends on whether the lines are at an attended location and on the discrimination task being performed at that location, resulting in several-fold differences between responses obtained with 'attend to' and 'attend away' conditions[35]. Attentional influences become more evident with increasing stimulus complexity[26] and depend on the precise geometric relationships between stimulus components[5].

Object-oriented and feature-oriented attention. Rather than acting as a 'searchlight', attention can highlight the discriminability of features belonging to the same object (object-oriented attention) or components sharing similar properties (feature-oriented attention), such as colour, orientation or direction of movement. Feature-based attention highlights the components of a scene sharing

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Intermediate-level vision
Visual processing that involves contour integration and surface segmentation.

Distracters
In a complex visual scene, some objects are attended (the targets) and others (the distracters) are unattended, but the distracters can compete with the target for attentional resources.
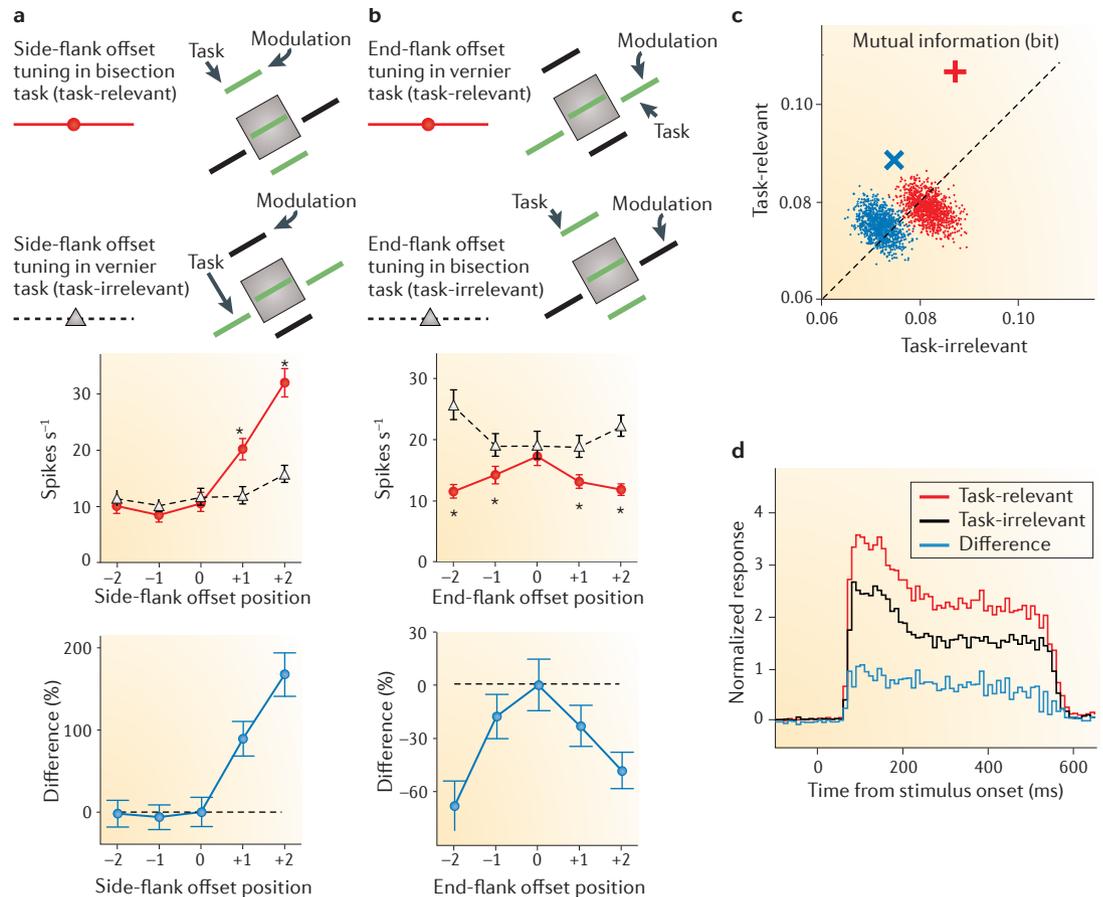
Figure 2 | **Task-dependent changes in neural tuning and information content in the primary visual cortex.** Monkeys were trained to perform two different tasks with a visual stimulus consisting of five lines — a central line flanked by two collinear and two parallel lines. Each of the pairs of flanking lines were presented in one out of five offsets relative to the central line fixed in the receptive field of a recorded neuron, forming a total of 25 stimulus conditions. From these stimuli, the animals were cued to perform either a three-line bisection task based on the relative positions of the three parallel lines or a vernier discrimination task based on the relative positions of the three collinear lines. The bisection task involves judging to which of the two flanking parallel lines the central line is closer, and the vernier task involves judging the direction of offset of the central line relative to the two collinear lines. **a** | The tuning of neurons to the offset of the side-flanks was measured when the animal performed either the three-line bisection task, in which the side flank position was relevant to the task (solid red line), or the vernier discrimination task, in which the side flank position was irrelevant to the task (dashed black line). The cell shown in this example was more modulated in its response to the side-flank offset position when the animal performed the three-line bisection task (the difference in response is shown in blue). **b** | The change in tuning of a primary visual cortex (V1) cell to the end-flank offset position when the animal performed the vernier discrimination task, in which the tuning was relevant to the task (solid red line), versus when it performed the three-line bisection task, in which the tuning was irrelevant to the task (dashed black line). **c** | The difference in tuning for task-relevant and task-irrelevant conditions was characterized in terms of mutual information, where the population of recorded neurons carried more information relative to side-flank tuning (blue x) or vernier tuning (red +) in the task-relevant condition than in the task-irrelevant condition. A series of Monte-Carlo simulations in which the responses were randomly assigned to the two different tasks are shown in the blue and red clouds, which are located on the diagonal and far from the experimental conditions. **d** | The difference in response between the task-relevant and task-irrelevant conditions arose from the outset of the neurons' responses, indicating that the cortical state for performing a given task was set in advance of stimulus onset. Figure is modified, with permission, from REF. 20 © (2004) Macmillan Publishers Ltd. All rights reserved.

the same attribute and, in contrast to the restricted spot-light of spatial attention, distributes cognitive resources broadly across the visual scene[31,48–50]. The effect of the distribution of cortical resources may be specific to cortical areas that deal with the attended feature, such as colour in area V4 and direction of movement in area MT[50–53], or to cortical areas that deal with the attended object, such as the fusiform face area or parahippocampal place

area[54]. Object-oriented attention increases the perceptual saliency of the components of an entire object rather than the features incorporated within a fixed spotlight. Attending to an object encompasses all of the features belonging to the object[3,54–61], and as measured with functional MRI (fMRI), the cortical effects of attention to a feature can spread throughout the visual field, even to regions lacking a visual stimulus[62,63].

The Gestalt psychology movement recognized the importance of the whole influencing the perceptual quality of the parts, essentially reversing the direction of information flow whereby the representation of the object precedes the representation of its components[64]. Object expectation may have an important role in the segmentation of the visual scene. Because of the complexity of the visual environment, the most difficult task of object recognition is not the identification of an object but the association of the contour elements and surfaces belonging to the object and separating these from the object's background. Thus, although object recognition itself can, in theory, be accomplished by feedforward mechanisms alone[65], top-down processes or a countercurrent stream of information flow are required for proper scene segmentation[66] in which objects have to be identified in complex scenes consisting of many objects. Models that incorporate recurrent processing can help to resolve an extremely challenging task for the visual system: grouping and segmenting elements within the visual scene.

Perceptual tasks. Even when attending to the same location and receiving an identical stimulus, the tuning of neurons can change according to the perceptual task that is being performed. This form of top-down control allows the network to engage stimulus components that are relevant to the task and to discard influences from components that are irrelevant to the task. The task-dependent change in the tuning of neurons can be analysed in terms of a change in task-relevant information in neuronal signalling. This implies that the functional roles of neurons are not fixed but instead that they are adaptive processors, running different programmes in differing behavioural contexts. By changing the perceptual task on the basis of the same visual stimulus, one sees responses that are influenced by different stimulus components[20]. As shown in FIG. 2, when presenting a central target line flanked by two parallel lines and two collinear lines, animals can perform either a three-line bisection task based on the parallel lines or a vernier discrimination task based on the collinear lines. Neurons change their tuning according to the task being performed, showing more modulation to changes in the position of the task-relevant components (the parallel lines when performing the three-line bisection task or the collinear lines when performing the vernier discrimination task) than to changes in the position of the task-irrelevant stimulus components.

Another example of this task dependency is in a curve tracing task, in which neurons that have receptive fields lying along the attended contour show enhanced responses compared with neurons that have receptive fields lying along the unattended contour[3]. A task involving the detection of a contour in a complex background enhances the contour-related facilitation in the responses of neurons in area V1. The perceptual saliency (also called detectability) of such a contour increases with the number of collinear line segments, and this correlates with the increase in neuronal responses as the contour is lengthened. The facilitatory influence of the collinear line segments is much larger when the animal performs a contour detection task than when it carries

out an unrelated task[5]. Although we emphasize the specificity of the task in generating the enhanced neural responses, one might think that these observations fall under the rubric of object-oriented attention. Regardless of whether one calls this object-oriented attention or a task-dependent top-down influence, it is important to emphasize that the effect is to cause neurons to change their tuning to the characteristics of the stimuli within the area of visual space that is attended.

Recent electrophysiological studies have suggested that frontal eye fields are the cortical loci for attentional selection of a target among distracters[67,68]. Transcranial magnetic stimulation of human frontal eye fields has shown that the backpropagation of the induced signals from the prefrontal cortex to visual areas is dependent on the task being performed on a given stimulus, reflecting task-specific modulatory effects of expectation[69]. Anatomical studies have also shown segregated pathways projecting from the frontal cortex to areas V4 and MT, which may carry different top-down signals for processing different stimulus features[70].

The idea that neurons multiplex their function in a task-dependent fashion — that is, at different times, they select one out of a battery of functional properties — may be general to all areas of the cerebral cortex (for the auditory cortex, see REF. 71). Recordings in the prefrontal cortex have demonstrated that neurons can be tuned to multiple categorical distinctions, so that the same neuron can exhibit different categorical representations as the task changes[72] (FIG. 3). Establishing the generality of this phenomenon in other areas depends on using an experimental design in which neurons' selectivities are measured under different behavioural contexts (an example in which neurons' shape selectivity is determined while animals are searching for different shapes is described in the following section).

Object expectation. When animals are cued to look for a specific shape, the shape selectivity of neurons in area V1 changes to a form that approximates the cued shape or a portion of that shape. Evidence in support of object expectation in producing selectivity for specific geometric forms comes from an experiment in which animals were trained to identify a cued contour embedded in a complex environment. The cue consisted of a straight line, a circle or a wave shape. The shape selectivity of V1 neurons was measured before the correct and false targets were presented in complex backgrounds in either hemifield, at the time the animal made a saccade towards the correct target. The important findings of this experiment were, first, that neurons in area V1 showed selectivity for complex shape geometries (not just single oriented line segments), and second, that this selectivity could be altered for individual neurons and for the population of superficial layer neurons as a whole by changing shape expectation[8]. This process suggests that the expectation of an object creates a set of filters that are selective for the object's components, which requires the involvement of top-down processes in object recognition[73]. The idea is further supported by the transfer of perceptual learning between objects with shared components[74].

Hemifield
One-half of the visual field.
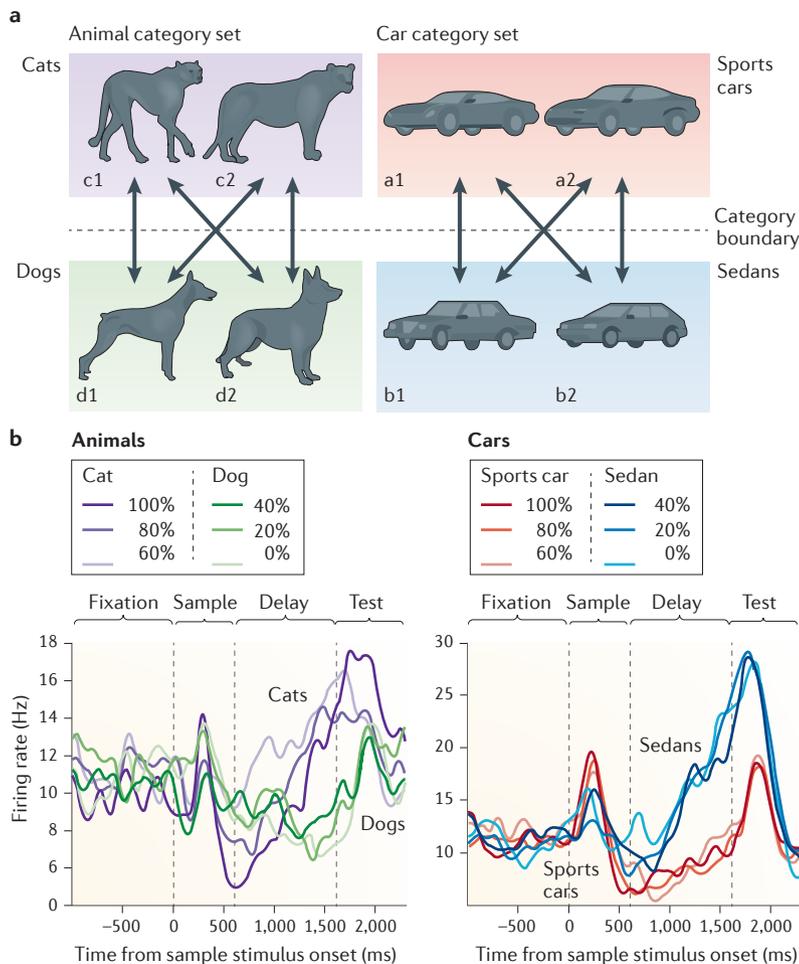
Figure 3 | **Neurons in the prefrontal cortex carry out different functions in accordance with the task. a** | Monkeys were trained to discriminate between images of a dog versus a cat (left panel) and between images of a sports car versus a sedan (right panel) in a delayed-match-to-sample task, as images were morphed from dog to cat prototypes, or as images were morphed from sports car to sedan prototypes. **b** | An individual neuron in the prefrontal cortex showed similar responses to images on one side of the category boundary and distinct responses to images on opposite sides of the category boundary. The differential responses during the delay period between the animal categories or the car categories support the idea of neuronal multitasking. Figure is modified, with permission, from REF. 72 © (2010) Elsevier.

These experiments demonstrate that even at the earliest stages in visual cortical processing, neurons are selective for more complex geometries than single oriented line segments and that their shape selectivity depends on object expectation. In effect, neurons become selective for components of expected objects, and object recognition involves a countercurrent stream of processing, with top-down anticipatory influences dynamically creating the appropriate set of lower-level filters, and the feedforward connections from these filters collectively creating the representation of the full object. This emerging view contrasts with the dogma of hierarchical, bottom-up visual processing.

Efference copy. We see the world as stable, even as our eyes scan the visual scene, causing movement of scene features across our retinas. This is because a copy of the motor instruction to execute an eye movement, which is known as the efference copy or corollary discharge, is sent to the sensory apparatus to 'subtract' the movement signal, thereby cancelling out any sensation of object movement that is due to eye movement. In the past few years, the efference copy pathway, involving the superior colliculus, the medial dorsal nucleus of the thalamus and frontal eye fields, has been elucidated[75,76]. The effect of this signal is to shift the position of the receptive field (for neurons in the parietal cortex) in the direction of the eye movement[77]. An alternative mechanism for perceptual stability involves predictive mapping of attention to selected targets[78], although the shift in the locus activation of neurons is nonetheless powerful evidence of top-down influence on receptive field properties based on motor planning. Shifting cortical receptive fields in anticipation of eye movements has been seen in areas of the parietal cortex and frontal eye fields[79–84]. Thus, for some neurons, even the property of receptive field location is not fixed, and shifting receptive fields play a valuable part in perceptual stability.

Working memory, associative memory and perceptual learning. The way a cortical area responds to a stimulus depends on prior experience and the current task. An excellent example of this is when animals were trained to associate a pattern of moving dots with a stationary arrow. Ordinarily, neurons in area MT respond to stimuli moving in a particular direction and are not responsive to stationary stimuli. But in animals trained in this associative task, MT neurons respond well to the stationary stimulus, indicating that their activity reflects not just the external stimulus but also cognitive state, visual imagery and stimulus associations[85] (FIG. 4). Another example is when neurons in frontal eye fields retain 'memory responses' in the absence of a visual stimulus but represent locations of intended saccades[86] or attentional selection[87]. Longer term influences of learning, particularly perceptual learning, have been shown to alter response properties as early as area V1 (for a review, see REF. 13). Although perceptual learning is outside the scope of this Review, top-down influences have an important role in its mechanism. They are required for the encoding of the learned information as well as its recall, as the neuronal properties associated with learning are only present when the animal is performing the trained task[6,20,38].

Dynamic encoding at the network level

A useful way to think about the effect of top-down influences is in terms of the information they convey and impart on their target neurons. Information theory provides a measure of the extent that an ideal observer can categorize a stimulus on the basis of the spike count from a recorded neuron during one trial. Top-down influences affect neuronal tuning in a way that enables neurons to carry more information about the stimulus being discriminated. Neurons can increase the degree of modulation of their responses over a set of stimuli, making these responses more informative about stimulus identity.
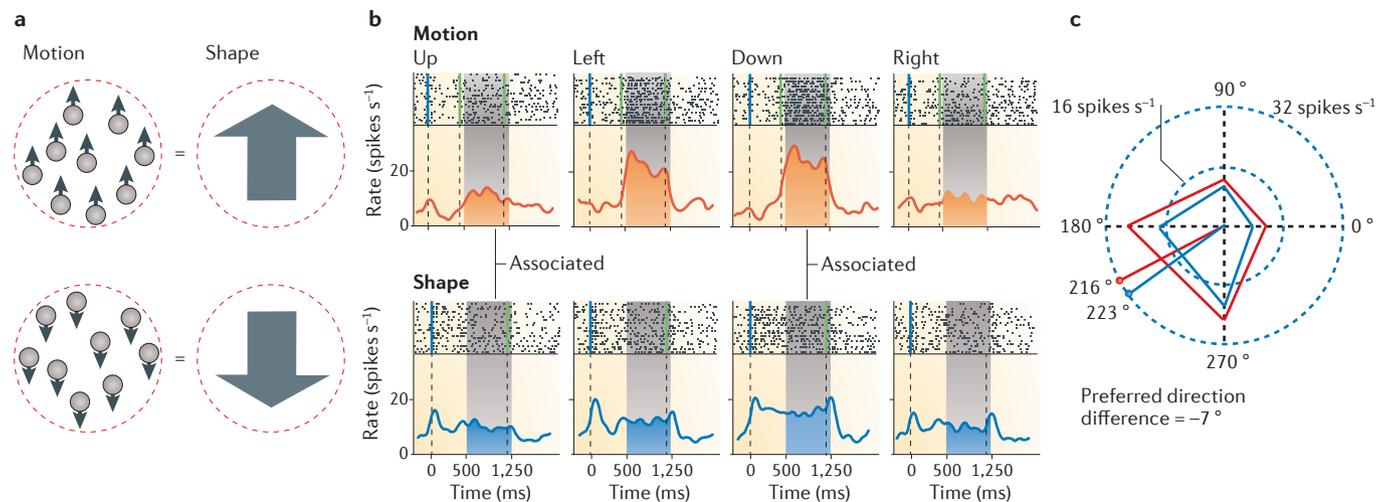
Figure 4 | Learned association generates recall-related activity in the medial temporal area. a | The medial temporal (MT) area normally responds to moving stimuli. However, when trained to associate a moving stimulus (a set of dots moving in a particular direction) with a static stimulus (an arrow), neurons become activated by the static stimulus. **b |** A neuron in area MT responds to and shows directional tuning to both the moving dot stimulus (red line in top panels) and the static arrow stimulus (blue line in bottom panels). **c |** For this neuron, a polar plot showing tuning to direction of movement (red) and to arrow orientation (blue) is shown. Figure is modified, with permission, from REF. 85 © (2007) Elsevier.

The idea that a neuron is an adaptive processor, changing the calculation it performs in accordance to the top-down instruction received from higher-order cortical areas, has attendant with it that the neuron's line label is not fixed. The line label idea suggests that when a neuron fires, it is signalling the presence of a stimulus with an attribute close to its preference (orientation preference, for example), and the strength of its firing indicates the closeness of the stimulus to that attribute. But if the top-down signal causes neurons to change the meaning of the information they carry, then these neurons are effectively changing their line label. How can this not distort the analysis of the visual image if neurons are constantly changing their function? The answer lies in the fact that the higher-order areas sent the instruction for these neurons to perform a particular calculation, so the return signal is 'interpreted' by these areas as the result of that calculation and is not confused with other operations those neurons perform.

Beyond the effect of top-down influences on the functional properties of individual neurons, neuronal ensembles can be induced to carry more information by altering their correlation structure: that is, the spatial and temporal distribution of correlated activity over the network of neurons within and across cortical areas. Neurons are variable in their responses to a given stimulus, and as more neurons participate in encoding the stimulus, the variability can be averaged out to provide better signal-to-noise ratios. But this depends on the ability of neurons to be independent from one another. The optimal information content would require zero or low noise correlations. There is, however, a significant amount of noise correlation[88–91], so a decrease in noise correlations induced by top-down influences would increase the amount of information encoded by the neuronal ensemble[92–95]. Decorrelation in the trial-to-trial variability of responses can allow groups of neurons to average out

this variability and improve the signal-to-noise ratio. This benefit depends on whether neurons are similarly tuned, as noise correlation between differently tuned neurons can increase coding efficiency[92,93,96].

Attention and perceptual learning have been shown to reduce noise correlations, although this has been an area of some debate[97–100]. Even more task-specific effects are seen on noise correlations between cortical sites that are relevant to the task being performed, and these changes are larger than those associated with merely attending to the stimulus[101]. In area MT, noise correlations between a pair of neurons receiving identical visual stimuli can either increase or decrease depending on which of two orthogonal axes the monkey is cued to perform a motion detection task[102].

Top-down influences go well beyond specifying the locus of spatial attention and changing neuronal firing rates. The recurrent pathways that convey these influences must be capable of conveying much more information than the locus to be attended. By the same token, top-down influences cause neurons at the antecedent stages in the cortical hierarchy to alter the nature of the information in their signals. This is not simply a matter of gain control but involves alterations in tuning that enable neurons to carry more information about stimulus components that are relevant to the task at hand, to take on selectivity for features that are components of expected objects and to maintain a stable representation of the world in the face of continual eye movements. The increase in task-relevant information is contributed to in part by changes in the tuning of individual neurons and in part by changes in the structure of correlations across the neuronal ensemble.

Different forms of top-down influences have been documented in different cortical areas, and these effects are relevant to the functional properties of these areas.

Line label
The property or information represented by a neuron. Different neurons represent different values, and the strength of their firing indicates how close the stimulus is to that value.

Noise
The variability in neurons' responses to a given stimulus. If different neurons with similar functional properties have independent noise, an ensemble of such neurons can carry more information about a stimulus than a single neuron.

But all cortical areas, and even the thalamus, can exhibit profound top-down influences. On the basis of early findings on the lack of attentional effects in area V1, along with findings of strong effects in areas V4 and MT, it has been suggested that attentional influences get progressively stronger along the visual pathway[42]. However, more recent findings, which are based on more complex stimuli and behavioural paradigms, have called this idea into question and have suggested that all areas in the hierarchy are equally subject to top-down influences. It is becoming increasingly evident that attention effects are seen early in the visual pathway[21,22,26,35,43,44,46,103]. The way in which these influences are manifested depends on the functional role of each cortical area: contour integration in area V1, responses to movement direction in area MT, modulation by eye position in parietal areas, and so on.

Circuit mechanisms of top-down control

Many studies on top-down influences have focused on the enhancement or change in gain of responses induced by attention, which is equivalent to the stimulus being increased in contrast[50,52,104,105]. The influence of attention on stimuli within the receptive field has been described in the 'biased competition' model[41]. In this model, objects in the visual field compete for computing resources, and an object can 'win' on the strength of its saliency ('bottom-up' attention or pop-out) or behavioural relevance (top-down control). Related to the idea of biased competition is a normalization model of attention, which involves a multiplicative scaling of responses to multiple stimuli in the receptive field, and attention affects the strength of the normalization[106,107]. These models assume that attention does not affect the stimulus selectivity of neurons. But top-down influences can alter the information carried in neuronal signals, which is distinct from gain control. For example, changes in a neuron's tuning to the specific components of the stimulus that are relevant to the task being performed, rather than a generalized increase in response to attended stimuli, have been observed[20,38]. Attention can change stimulus selectivity in addition to changing gain of responses[108]. It is therefore useful to have a model that can account for the specificity of top-down influences for different contextual components and for a neuron's ability to select a subset among all of its inputs in order to exhibit different functional properties. According to this model, although a neuron receives thousands of inputs from intrinsic connections, only a fraction of these are expressed under a particular behavioural context. Interactions between re-entrant connections from higher-order cortical areas and intrinsic circuits enable the network to gate the connections that are appropriate for the task at hand, with different functional networks operating under different task conditions. As a consequence, neurons multiplex their function in a state-dependent manner and constitute adaptive processors running different operations under the instruction of feedback from higher-order cortical areas[109].

The contextual influences that mediate higher-order, complex receptive field properties in area V1 involve lateral interactions across a topographically organized region, and they have the consequence of perceptual grouping, such as that involved with linking line segments to global contours. The interactions follow precise geometric rules, showing facilitatory influences for neurons with receptive fields lying along collinear or co-circular contours. This mode of interaction is known as the 'association field'[110]. This is a general entity that has been identified in area V1 but is likely to have an analogue in all cortical areas. The idea underlying the association field is a linkage between elements that are systematically and topographically represented over each cortical area. Lateral interactions between these elements allow perceptual linkage or the association of pieces of information. The lateral interactions may be mediated by a plexus of long-range horizontal connections within area V1. These connections are formed by pyramidal neurons, whose axons extend for long distances parallel to the cortical surface, and link neurons with widely separated receptive fields[11,14,111–114]. Because of their extent and columnar specificity (they connect neurons of similar orientation preference[11,14,115,116]), they are ideal conveyors of the contextual influences that enable contour integration[12]. Although the horizontal connections provide an anatomical framework for a range of contextual interactions, the observation that these interactions are subject to top-down control suggests that feedback signals can alter the effective connectivity of horizontal connections.

We have proposed that re-entrant inputs dynamically modify intrinsic cortical connections, allowing the appropriate associations to be made under different behavioural contexts. A possible reason for the existence of horizontal connections is that they allow such changes in connectivity within the network, as opposed to each cell having a large receptive field generated by a fixed set of feedforward connections. This idea has been implemented in models of cortical circuitry, in which changes in the gain of horizontal connections by feedback allow subsets of neuronal inputs to be selectively expressed[18]. It also accounts for the time course of contextual interactions, in which delays in neuronal responses are due to the time required for the network to move from one stable state to another rather than due to the conduction time required to get information from a distant, more central source. Last, it provides a mechanism for contour integration and saliency[18]. The interaction between feedback and horizontal connections also suggests a mechanism for perceptual learning. During the encoding of learned information, the recurrent input acquires the appropriate mapping to intrinsic connections, and during the recall of the learned information, this relationship allows the appropriate inputs to be gated and the target neuron to assume the appropriate functional properties. In area V1, the association field mediates contour integration and saliency, and the top-down input allows for subcomponents of the association field to be gated, leading to the manifestation of different shape selectivities. In other areas, the association field would be defined by the properties and the kinds

of information that are topographically mapped in that area, and by the relationship between the long-range horizontal connections and that map.

Many of the task- and expectation-dependent effects described above can be explained by an input selection mechanism. By selecting components of the association field, neurons can express contextual influences that are relevant to the task being performed. A contour detection task enhances collinear interactions and suppresses influences from non-collinear elements in the background[5]. A shape discrimination task induces neurons to select collinear influences when the cue is a line and co-circular influences when the cue is a circle[8]. By selection of components of the association field over multiple nodes in the horizontal network, neurons in area V1 can take on selectivity for complex shapes, including wave-like shapes with reversals in curvature. The selective influence of parallel lines in a three-line bisection task and collinear lines in a vernier discrimination task[20] can be mediated by changing the effective connectivity of task relevant inputs. This idea is supported by an experiment involving recordings from an array of electrodes, in which the interactions between cortical sites are measured by cross-correlation analysis (based on the relative timing of spikes between pairs of neurons) or coherence between local field potentials (LFPs) measured at different sites. Changing the perceptual task with the identical visual stimulus strongly influences correlation strength. Perceptual grouping tasks enhance LFP coherence between parallel sites in a three-line bisection and between collinear sites in contour detection. Perceptual segregation decreases LFP coherence between collinear sites, as seen in a vernier discrimination task[101] (FIG. 5). This is similar to the expectation-dependent changes seen in noise correlations[102]. Although some measures of coherence suggest that attention decreases cortical interactions[117], the effect of top-down influences depends on the nature of the task and the way in which different cortical sites are engaged in the task. Further support of this idea comes from fMRI measures of coupling between distant cortical sites representing separated stimuli in a task requiring the integration of the two stimuli[118].

Changes in effective connectivity mediated by top-down influences relate to the idea that neural synchrony is the neural code for perceptual grouping and segmentation[119–125], although some studies have failed to confirm this idea[102,126–129]. It has been proposed that perceptual grouping is achieved by synchronizing the activity of neurons representing the grouped features[130,131] and that neuronal synchrony has important roles in sensorimotor integration[132–134]. Synchrony in itself may be more a reflection of the dynamic connectivity leading to task-dependent alterations in neural tuning rather than the information being carried by the relative timing of action potentials per se. The two may in fact be related, with alterations in effective connectivity underlying the task-dependent changes in tuning. Selective attention can also provide a solution to the 'superposition problem', in which contour components belonging to one object have to be associated with one another and perceptually

separated from components that belong to the object's background. The role of attention in synchronization is seen in animals performing a colour change detection task, in which there is gamma-band synchronization between cortical sites encoding the behaviourally relevant stimulus[135]. Also, top-down influences can affect effective connectivity between cortical areas. Just as attention can increase gamma-band synchronization within area V4, it increases synchronization between the frontal eye fields and area V4 (REFS 136,137). This idea is supported in human subjects by fMRI-based correlations of blood-oxygen-level-dependent background connectivity between cortical areas, which are specific to the task and cortical area[138]. It is important to emphasize that top-down influences do not just alter effective connectivity in general, they can selectively and differentially change the effective connectivity between cortical sites that are task-relevant[101].

Signals that represent top-down influences are observed following the cue directing the task or expectation and before the stimulus presentation[99,101,139,140]. The pre-stimulus task-dependent activity suggests that subthreshold signals set the cortical 'state' for executing the calculation that is appropriate for the behavioural context and that a given percept results from the set of states assumed by the entire network of cortical areas. This view contrasts with the traditional idea that perception results from the activity of a small number of cells at the top of the visual hierarchy. Instead, the percept arises from the global set of cortical states and task-specific interactions between multiple cortical areas.

The connectivity mediating top-down instructions is likely to include corticocortical feedback connections. For area V1, for example, although the strongest feedback arises from area V2, there are a number of cortical areas that provide direct recurrent input to area V1, including those in the ventral pathway, such as areas V4 and IT, and areas in the dorsal pathway, including area MT[14,141–143]. The feedback projection from area MT to area V1 has been implicated in visual awareness[144]. The ventral pathway inputs could provide information about object expectation, and the dorsal pathway inputs could provide information about attentional locus or saliency maps. In addition, other areas, such as the prefrontal cortex, could provide executive control over a perceptual task, and the sites of transmission from the prefrontal cortex to posterior areas depend on the nature of the task[69]. Although the prefrontal cortex is not directly connected to area V1, it could exert its influence by a cascade of connections descending through the parietal lobe. Other non-cortical sources of recurrent input have been suggested, such as the pulvinar[145,146]. Multiple sources are likely to be involved in top-down control, but as indicated above, they must be capable of carrying the richness of information that is involved in not only spatial attention but also expectation and perceptual tasks (FIG. 1).

Summary

The existence of such a varied array of top-down influences and their profound effect on the functional properties of neurons (as well as on their interactions within

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Local field potentials
(LFPs). The electrical fields generated by a population of neurons, with signals having components spanning a spectrum of frequencies. LFPs originate from the integrated currents coming from synaptic activation and from action potentials in dendrites, cell somata and axons.
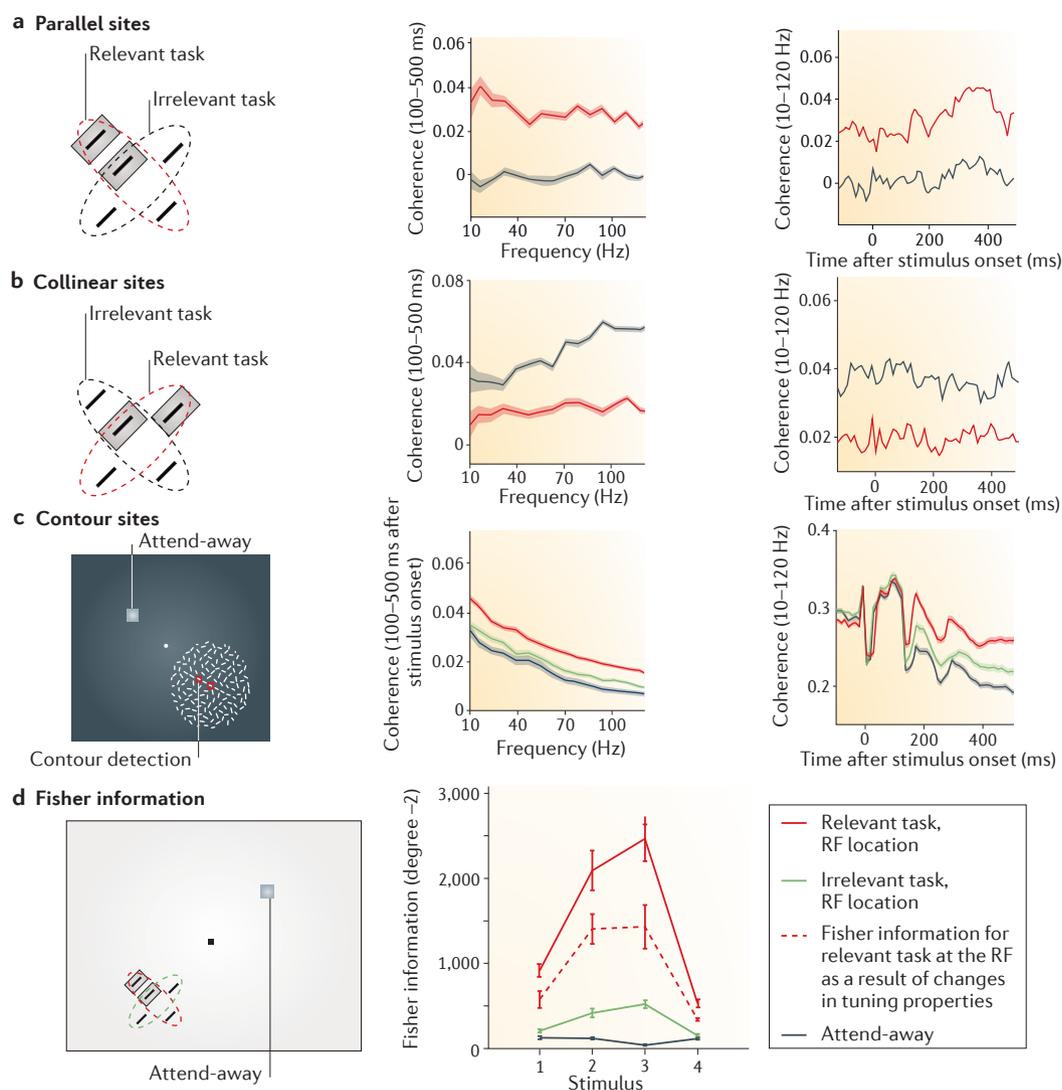
Figure 5 | Task-dependent changes in local field potential coherence and noise correlations in the primary visual cortex. Neurons were recorded with a 96-electrode array while animals performed different discrimination and detection tasks. **a,b** | Animals performed one of two tasks based on a stimulus configuration of five lines (left panel of part **a**): a three-line bisection task, where they had to judge to which of two parallel lines the central line was closer (part **a**), or a vernier discrimination task, where they had to judge to which side of two collinear lines the central line was offset (part **b**). **c** | A third task involved detecting a contour embedded in a background of randomly positioned and oriented lines (left panel of part **c**). In the bisection task, the side by side receptive field (RF) locations, represented by the grey rectangles in part **a**, are relevant to the task (red dashed oval), whereas the collinear sites (black dashed oval) are irrelevant to the task. Conversely, in the vernier task, the collinear RF locations (grey rectangles and red dashed oval) are task-relevant and the parallel locations (black dashed oval) are irrelevant to the task. In the contour detection task, collinear RF locations are relevant to the task. The effective connectivity between cortical sites representing parallel flanks (part **a**) and collinear flanks (part **b**) was measured by calculating the coherence between local field potentials (LFPs) at different frequencies. The graphs in the centre column of parts **a** and **b** represent LFP–LFP coherence during the response interval from 100 to 500 ms in the task-relevant (red) and task-irrelevant (black) conditions. The middle panel of part **c** represents LFP–LFP coherence in the contour detection task when the stimulus contained (red) or did not contain (black) a global contour, or in the attend-away condition (green) when the contour stimulus was task-irrelevant. Operations involving contour detection (part **c**) or grouping of parallel sites (part **a**) give stronger coherence in the task-relevant condition. Operations involving segregation of collinear sites (part **b**) produces weaker coherence in the task-relevant condition. The difference in coherence in the three-line bisection and vernier task was seen not only during the entire response period but also in the interval preceding stimulus presentation, indicating top-down setting of lateral cortical interactions in advance of the appearance of the stimulus (right panels of parts **a** and **b**). **d** | Attention- and task-dependent changes in neuronal information content — calculated as Fisher information — as a function of changes in the stimulus bar position for the three task conditions (solid red, green and black lines). The primary visual cortex network carried more information about the stimulus when the animal performed the task (solid red line) and roughly equal contributions to the increase in information came from the changes in neuronal tuning (dashed red line) and from changes in noise correlation (difference between solid and dashed red line). Figure is modified, with permission, from REF. 101 © (2013) Society for Neuroscience.
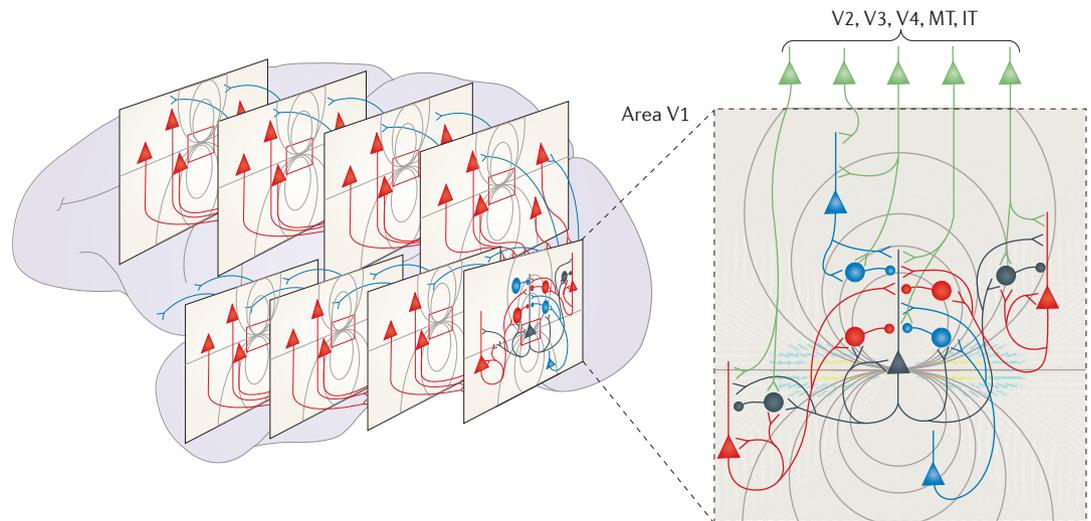
Figure 6 | **Top-down influences on effective connectivity within and between cortical areas.** Top-down influences dynamically change effective connectivity within and between cortical areas, allowing neurons to select inputs and take on functional properties that are appropriate for the immediate behavioural context. As a result, each cortical area and each neuron within that area is an adaptive processor, continuously changing its line label to serve different functions. The right panel shows long-range horizontal connections linking distant points in each cortical map, mediating an association field that provides a set of potential interactions. The association field in the primary visual cortex (V1) is represented by the grey co-circular and collinear lines and by the fields of oriented line segments on either side of the central black neuron. The underlying circuit is represented by the long-range horizontal connections formed by excitatory neurons (triangles) and disynaptic connections involving inhibitory neurons (circles). Depending on the top-down instruction, different sets of inputs can be gated according to the state of feedback (represented by the green connections coming from higher-order cortical areas), so that under different tasks the black neuron may select either the red or blue inputs. Because of the multiple sources of long range inputs coming from within the same cortical area and from many other cortical areas, and because these influences can cascade over multiple nodes, each neuron effectively becomes a microcosm of nearly the entire brain. In the brain on the left, multiple layers of such interactions operate across the entire visual pathway, with each cortical area containing its own gate-able association field, and top-down interactions cascade across the layers (feedforward pathways are represented by the blue connections between cortical 'planes' and feedback pathways are represented by the red connections) not just between nearby cortical areas but also by longer range connections that skip over multiple stages (not shown). Each cortical area is represented here as a two-dimensional network, but because of their laminar structure different layers tend to be responsible for feedforward connections (superficial cortical layers) and feedback connections (deep cortical layers).

neuronal ensembles) raises a host of questions for further investigation. What are the sources of the various types of top-down control and what are the pathways by which this control is exerted? What is the nature of the signal that is conveyed along these recurrent pathways? What are the synaptic and network mechanisms by which feedforward, recurrent and intrinsic cortical connections interact to enable adaptive changes in neuronal function? The challenge is to address these questions in the context of the intact, functioning system and to do so in behaving animals.

By selecting different sets of inputs, neurons take on different functions. The source of top-down influences can be widespread, either by direct connections from different cortical areas or by a cascade of inputs originating from many more areas. In effect, a large part of the cerebral cortex can exert influences over individual neurons within a particular area, with multiple descending inputs interacting with intrinsic cortical connections (FIG. 6). As such, each neuron is a microcosm of the brain as a whole, with synapses carrying information originating from far flung brain regions. This mode of operation has important implications for our understanding of the cortical mechanisms underlying all sensory modalities and behaviours, and its dysfunction may be the cause of behavioural disorders.

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FURTHER INFORMATION
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