

# Belief states as a framework to explain extra-retinal influences in visual cortex

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The activity of sensory neurons is modulated by non-sensory influences, but the role of these influences in cognition is only partially understood. Here we review how the large-scale recording of neuronal activity within and across brain regions allows researchers to examine the interactions between simultaneously recorded neurons as they are jointly influenced by fluctuations in an animal's mental state. We focus on studies on the visual cortex of non-human primates to examine the relationship between extra-retinal influences and beliefs about the state of the sensory world. We explore how these influences can be understood within theoretical frameworks that propose how the continuous updating of belief states supports perceptual inference.

## Addresses

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## Introduction

It is well known that the responses of neurons in early visual cortical areas, including the primary visual cortex (area V1), are affected by factors other than the pattern on an observer's retina (e.g. [1–7]). Here we will focus on these extra-retinal signals because they provide insight into the interactions between neurons that enable cognitive functions. Similar influences have been observed for other modalities (e.g. [8]) but we will here focus on the visual system of the non-human primate. We will refer to signals as 'top-down' if they originate anywhere but the

ascending pathway of the visual processing hierarchy preceding the visual area from which neural activity is recorded. As neural circuits are highly recurrent, a strict dichotomy of 'bottom-up' (feed-forward) and 'top-down' (feed-back) signals is simplistic, yet it offers a useful first approximation of the computational role of different influences on the responses of sensory neurons. We will consider the following 'top-down' effects: (1) cognitive influences on the neuronal firing rates in sensory areas, (2) changes in the structure of correlations between the firing rates of pairs of neurons and their implications for signals related to behavioral choice and (3) cognitive influences on the tuning properties of neurons in sensory areas. We here review emerging theories based on data that suggest that these effects fit within a single, unified framework when it is assumed that 'top-down' effects carry information about the animal's beliefs about the stimulus back to sensory cortex.

## Visual neurons are modulated by 'top-down' phenomena at precise time-scales

Our insights into the 'top-down' influences on sensory neurons has benefitted enormously from recent advances in techniques for manufacturing and implanting electrode arrays. The new methods enable monitoring of large populations of neurons within and particularly across brain areas in the behaving animal.

One of the most extensively studied 'top-down' signals is related to the allocation of attention [9–12]. One example task associated with attention shifts is curve-tracing ([13<sup>\*</sup>], [Figure 1b](#)). The authors of this study required monkeys to mentally trace a curve that starts at a fixation point to determine the endpoint of this curve, because the circle at the end was the target for an eye movement. During this task, the neuronal responses in V1 elicited by a traced line were stronger than those elicited by the distractor ([Figure 1b right](#)). This response modulation was thought to be caused by the spread of object-based attention over this curve [14]. Importantly, V1 was only one of a number of cortical areas where activity was modulated during the curve-tracing task. It also occurred, for example, in the frontal eye fields, an area in frontal cortex involved in planning of eye movements. The authors then compared the timing of the attentional selection signal between the two areas by computing the latencies of the modulation. Although it is generally not easy to determine the precise moment of the onset of the attentional response modulation, the analysis suggested that the timing of selection of the

relevant curve in frontal and visual cortex was similar, which may indicate that the task calls upon reciprocal interactions between visual and frontal cortex. Interestingly, the authors found one exception to this simultaneous selection process. If the monkeys made an error and chose the wrong curve, the erroneously selected curve elicited extra activity, both in V1 and in the frontal eye fields. However, now selection in frontal cortex preceded selection in visual cortex as if the frontal cortex imposed its erroneous decision onto visual cortex [13]. In addition, the authors observed correlations between frontal and visual cortex that were strongest for the attended curve. These findings are compatible with fluctuations of attentional modulation in both areas that reflect the monkey's momentary interpretation of the stimulus and task.

Evidence for fluctuations in attention were also observed in a study [15] in which monkeys were trained to detect an orientation change while their attention was cued toward a stimulus in the left or right visual hemi-field (Figure 1c). The authors recorded the activity of a population of neurons in V4 in both hemispheres and derived a neuronal measure for how strongly attention was directed to the left or right, on single trials. These estimates correlated strongly with how well the monkeys detected the orientation change in the left or right hemi-field (Figure 1c, right). Moreover, the value of the neuronal attention measure varied strongly from trial to trial, suggesting substantial fluctuations in attention. One possibility is that these fluctuations reflect random meandering of the mind. An alternative possibility is that they reflect the continuous updating and adjusting of 'top-down' influences for a computational purpose.

### **Inference and belief-updating may reveal the computational role of 'top-down' signals**

It has long been proposed (e.g. [16–18]) that perception reflects an inference process in which prior knowledge about the world is combined with the incoming sensory evidence to infer the most likely cause of the inputs. More recent theories have proposed how the required computations are implemented in neural circuits [19–31]. In these frameworks the response of a visual neuron is influenced both by the visual stimulus and a 'top-down' belief about the visual information available, which is based on prior knowledge and contextual information (Figure 2a). This belief is continuously updated based on additional incoming information. To account for the observed fluctuations in neuronal activity and attentional state described above we propose that this updating occurs on short timescales (during trials or between trials), but it likely also involves longer time-scales e.g. to reflect the process of learning novel task contingencies. This framework can explain a variety of seemingly disparate 'top-down' phenomena, some of which we will review here:

### **Spatial attention, feature-based attention and object-based attention**

Psychophysical and neurophysiological studies have shown that attention can selectively be directed at a particular location in space, a particular visual feature (e.g. motion in a particular direction) or an object to boost its representation in visual cortex [9–12,32]. One example is given by the curve-tracing task mentioned above. According to the inference framework, attentional modulation of neuronal activity can be explained by the belief that a particular spatial location, feature or object is relevant for the goal of the animal. Furthermore, in these types of tasks, the reward contingencies determine what is relevant and what not, and the framework therefore might also explain why the modulation of neuronal activity in visual cortex by rewards resembles the modulation by attention [33,34].

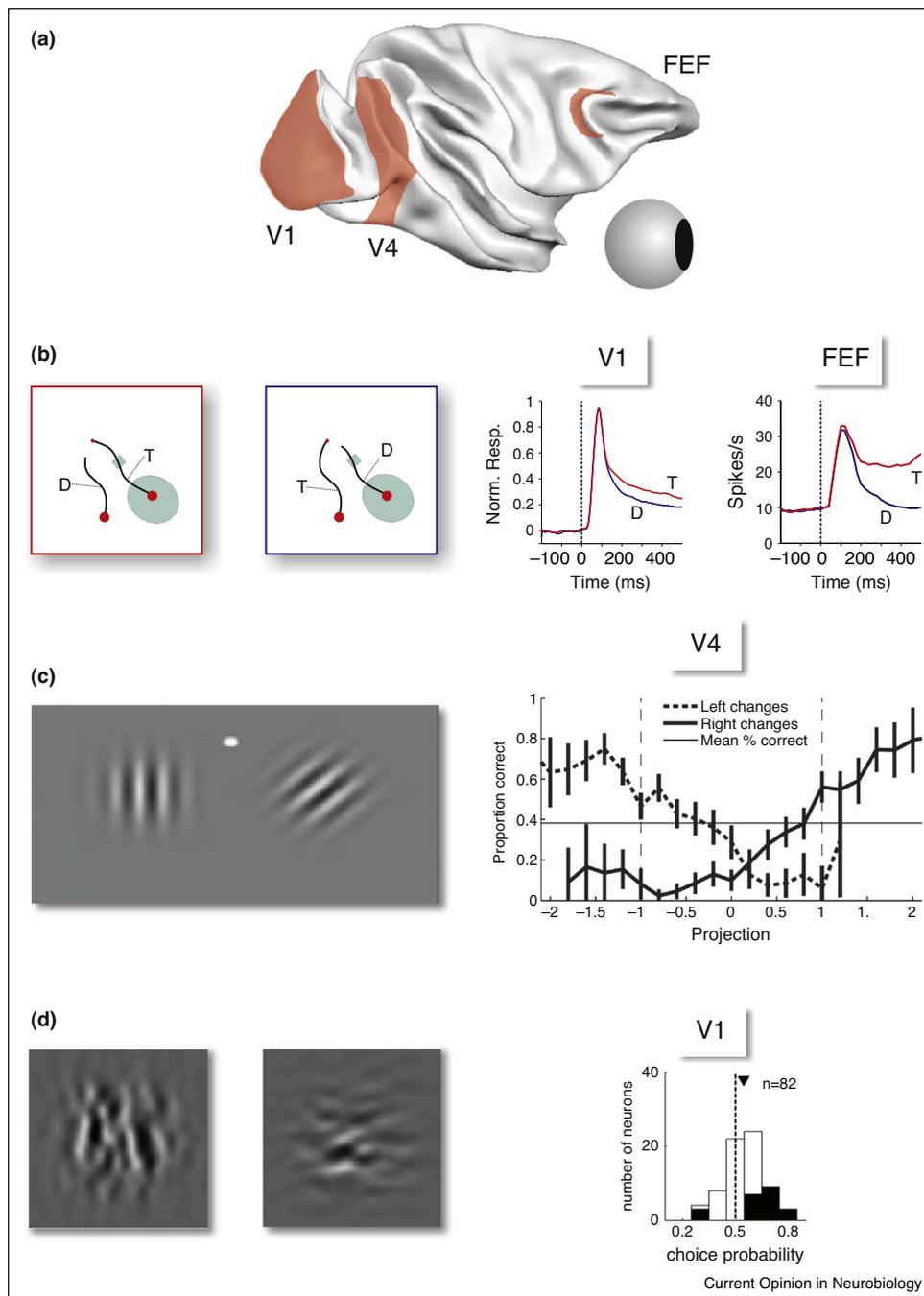
### **Updating of behavioral relevance**

A fundamental assumption of the framework is that beliefs are updated based on incoming information. What happens when monkeys have to update their belief about what is relevant and what not? Khayat *et al.* [35] used the curve-tracing task, and unexpectedly switched the identity of the relevant and irrelevant curve. The change in relevance caused an early increase in the activity elicited by newly relevant curve, followed by a decrease in activity for the curve that lost relevance, compatible with the view that this modulation of neuronal activity reflects the updated belief about the relevance of the respective curve. Neuronal modulation has also been observed during tasks that demand a sequence of cognitive steps, again compatible with rapid updating of beliefs. In one example experiment [36] monkeys had to trace a curve to identify the color of a marker at the end of the curve, and to then carry out a visual search for another disk with the same color. The successive increases in neuronal activity evoked by the task relevant items may reflect the monkey's progression in solving the task. The modulation of neuronal activity in these and other tasks that involved switching the relevant target [37,38] occurred at timescales of tens to hundreds of milliseconds, suggesting that beliefs about relevance can change on fast time-scales.

### **Task-dependent modulation of correlations between neurons**

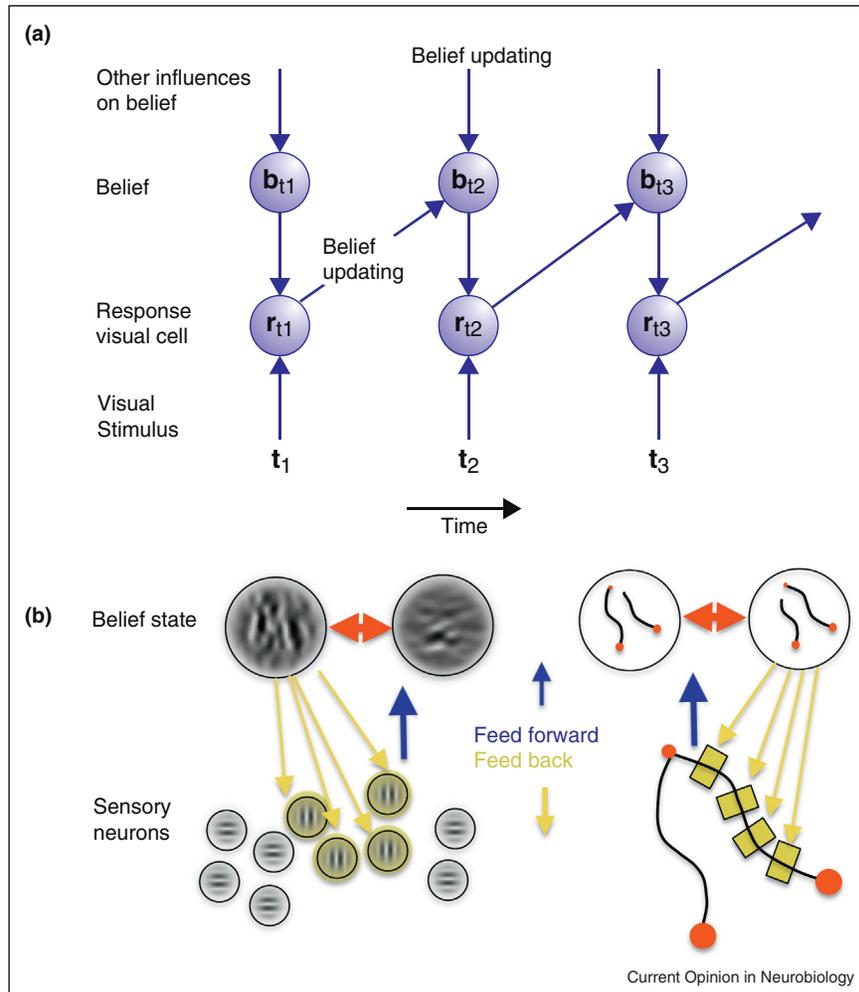
Sensory neurons respond variably to repeated presentations of an identical stimulus, and a component of this variability is typically shared between neurons. These interneuronal correlations are often referred to as 'noise-correlations' [39] as they occur in response to an identical stimulus, to differentiate them from 'signal correlations' that are caused by the similarity between the tunings of different neurons. While originally viewed as merely resulting from noise in divergent sensory afferents, more recent work has shown that these (noise) correlations

Figure 1



Example tasks associated with extra-retinal influences on activity in the visual cortex. **(a)** Lateral view of the brain of the macaque monkey. **(b)** Simultaneous recordings in V1 (48 contacts) and FEF (single electrodes) for a curve tracing task where monkeys had to mentally trace a target curve (T) while maintaining gaze on a small (red) fixation point. The animals had to ignore the distractor (D). Neuronal responses in V1 and the frontal eye fields (FEF) elicited by the target curve (red curve) were stronger than responses elicited by a distractor (blue). The green square in the left panels illustrates the location of a receptive field in V1; the green ellipse denotes a receptive field in FEF. Reproduced with permission from [13\*]. **(c)** Simultaneous recordings in left and right V4 ( $2 \times 48$  contacts) while monkeys had to detect small changes in the orientation in a stream of successively presented pairs of grating stimuli. The monkeys were rewarded for making a saccade to the stimulus that changed while attention was cued to the left or right stimulus. The authors derived a measure based on the activity of a population of neurons for the amount of attention directed to the left or right stimulus on a single trial. The panel illustrates the accuracy (y-axis) for detecting changes in the left (dashed line) and right grating (continuous line) as function of the single trial attention measure (called projection; x-axis). This attention measure predicted the animals' ability to detect changes in the left or right grating. Reproduced with permission from [15\*]. **(d)** Recordings in V1 using linear arrays (8 or 24 contacts) or single electrodes during an orientation discrimination task with stimuli composed of orientation band-pass filtered noise. The monkeys had to choose between one of two orthogonal orientations. The right panel illustrates the distribution of choice-probabilities, with a mean that was significantly larger than 0.5. For example, if neurons tuned to vertical were more active, the monkey was more likely to choose the vertical orientation. Thus, V1 neurons carried signals related to the animal's choice. Reproduced with permission from [53\*].

Figure 2



The mental state of an animal can be characterized as a succession of belief states. (a) Sensory input is represented by sensory neurons and influences the belief through feedforward pathways. Sensory neurons, in turn, receive feedback from neurons representing the animal's belief about the sensory stimulus. (b) Belief states can account for the influence of the animal's choices on the activity of sensory neurons. *Left*, in an orientation discrimination task, the monkey's belief (e.g. its expectation about the stimulus or its decision about the stimulus) that the stimulus is vertical enhances the activity of sensory neurons coding for vertical. These top-down influences may be related to shifts in feature-attention. *Right*, in a curve-tracing task, the belief that one of the two curves is relevant causes enhanced activity for neurons that represent its contour elements. These top-down effects are likely related to shifts of object-based attention.

depend on cognitive factors such as attention [40], learning [41], task [42], and also on anesthetic state [43]. In an elegant study, Cohen and Newsome [42] required monkeys to discriminate between the direction of motion along two different axes (e.g. up-down or left-right). They observed that the relevant motion axis influenced the pattern of noise correlations in motion-sensitive area MT. When the axis was such that the pair of neurons supported the same decision, the noise correlation was stronger than when the axis was such that they supported different decisions. Thus, the noise-correlations depended on the animal's task. Using

simulations, the authors could explain this finding with a component of feature selective attention that fluctuated from trial to trial. This explanation is in accordance with the idea of fluctuating belief states (Figure 2a). Suppose that the animal has to discriminate between up and down. Now the belief will fluctuate between the upward and downward direction. These influences would induce a positive correlation between neurons that support the same decision along the up-down axes, but negative correlations between neurons that support opposite decisions along this axis. However, if the monkey discriminates between left and right directions, fluctuations in

belief would induce these correlations and anti-correlation along the left-right axis, similar to the pattern observed in MT. A recent theoretical proposal combined Bayesian inference with neural sampling [22,44,45] and produced exactly these results [46].

Such an effect on noise correlations also has implications on trial-by-trial correlations between neural activity and perceptual decisions in discrimination tasks, which may therefore be accounted for in the same framework. These correlations are frequently referred to as ‘choice-probabilities’ and occur in many perceptual tasks and in many visual areas [47–52]. Figure 1d shows recent results of a study reporting choice probabilities in V1 for an orientation discrimination task [53<sup>\*</sup>]. The animal’s task was to discriminate between two orientations 90 degrees apart in a noisy stimulus (orientation bandpass filtered noise). Choice probabilities quantify the correlation between neural activity and the animal’s choices. A choice-probability of 0.5 indicates no relation between neuronal activity and choice while values >0.5 indicate a positive correlation. The mean choice probability across the population of V1 neurons was slightly above 0.5 indicating a weak but systematic relationship between the neural activity and behavior (Figure 1d, right). Theoretical [54,55] and empirical [56,57] findings show a close relationship between noise correlations and choice-probabilities. Let us reconsider the fluctuations in feature selective attention mentioned above, which may reflect the variations in the animal’s belief. Suppose that on some trials the animal attends more to vertical and on others more to horizontal orientations, and that this modulation in feature selective attention affects neuronal responses. These fluctuations would therefore result in correlations among neurons preferring vertical or horizontal orientations, respectively (Figure 2b, left). It is plausible that these fluctuations in feature selective attention are also systematically associated with choice: when the animal attends to vertical (e.g. because it expects the next stimulus to be vertical) it is also more likely to respond that a noisy stimulus is vertical. On trials when the animal attends more to vertical this would increase the probability of the animal choosing the vertical target and boost the responses of a neuron preferring vertical orientations, thus result in a choice probability larger than 0.5 [58]. Such an expectation resulting from the previous stimulus (and the choice given) could also explain recent findings that an animal’s choice on a preceding trial correlates with the activity of visual neurons on the current trial [59]. A similar explanation can be given for ‘top-down’ effects in the curve-tracing task (Figure 2b, right). Erroneous beliefs about the identity of the target curve are reflected by neurons in frontal cortex, which may feed back to enhance activity of visual neurons whose receptive fields overlap with the erroneously selected curve, and give rise to significant choice-related modulation [60].

### Receptive field shifts in V1 which may underlie a size illusion

Visual cues about perspective to generate a 3D impression of a scene influence judgments about the size of an object [61]: an object for which the perspective cues suggest it is further away is perceived as larger than an object of the same size that seems closer. In a recent study [62<sup>\*</sup>] monkeys were trained on a size discrimination task in the presence or absence of perspective cues. The monkeys showed the same behavior as human subjects, judging the object that appeared further away to be larger. When recording the responses of V1 neurons in these animals the authors observed that in the presence of the perspective cues the receptive fields of the neurons were shifted systematically in a way that could support this size illusion. The authors suggested that these shifts reflected ‘top-down’ influences based on the perspective context that differed from previous findings of modulation by attention. For the inference framework this suggests that beliefs can exert rather complex influences on the responses of visual neurons depending on the prior or contextual information.

### Large-scale recordings are ideal to study ‘top-down’ phenomena as they open many windows simultaneously into the same mental state

While the control of the visual input allows experimenters to directly manipulate and explore visually driven responses of cortical neurons, the control of ‘top-down’ influences is indirect. It typically requires behavioral manipulations to systematically generate a mental state, e.g. an expectation that a stimulus will appear in the right half of the visual field, to measure the ‘top-down’ signals associated with this mental state. Because mental states fluctuate even when the same tasks are performed [15<sup>\*</sup>] control of these ‘top-down’ signals is less precise and repeatable than that of the visual input. Large-scale recordings offer a solution to this problem since all simultaneously recorded neurons are influenced by the same mental state. Simultaneous recordings from neuronal populations also allow for measurements of correlations between neurons, in the same or in different areas, which are crucial for an understanding of how the information available in visual neurons is used during perception.

New probes have also been developed that enable the recordings from the different layers of a cortical area, an approach used by (e.g. [63]). Monkeys had to detect figures defined by textures. When the figure was centered on the receptive field of a V1 neuron its responses were enhanced compared to when the same texture was presented inside the receptive field but was part of the background. At the boundary between a figure and the background, this extra activity occurred relatively early and it was largely stimulus driven [64], i.e. it could be

explained by orientation-tuned surround influences [65]. However, the extra-activity in the center of the figure did not occur if the monkey failed to perceive the figure [66] and was more pronounced if the animal directed attention to the figure [64]. This suggests that it reflected the monkey's belief about stimulus presence as well as its relevance. The advantage of the linear arrays is that they span the cortical thickness enabling a comparison of activity across the cortical layers. Interestingly, the response modulation was strongest in the superficial and deep layers and weaker in layer 4. The superficial and deep layers are the main targets of feed-back connections [67,68], suggesting that the modulation was likely to be mediated by feedback.

## Conclusion

One of the major challenges of contemporary neuroscience is to understand how visual cortex and other brain areas interact to construct an interpretation of the visual world and select the visual information that is relevant for behavioral goals. Here we have reviewed recent neurophysiological evidence for 'top-down' effects in the context of theories about belief states. These belief states could emerge from interactions between the sensory cortices and other brain regions with the sensory areas providing input for the more categorical representations in higher areas [69], and for the representation of behavioral — and emotional — relevance in other cortical and subcortical structures. These areas in turn provide feedback to influence activity in sensory cortices. An interpretation of these interactions as resulting from belief states provides a computational framework that may unify the task-related influences on firing rates and tuning properties in the sensory areas, the patterns of noise-correlations and their consequences for choice-related activity. We anticipate that the further development of technologies for the simultaneous recordings of neuronal activity within and particularly across brain regions will pave the way for testing predictions about belief states, as well as other ideas on how neurons in different areas coordinate their activity for the emergence of cognitive functions.

## Conflict of interest statement

Nothing declared.

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