

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.

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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^{*}], 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

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