



Contextual signals in visual cortex

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Vision is an active process. What we perceive strongly depends on our actions, intentions and expectations. During visual processing, these internal signals therefore need to be integrated with the visual information from the retina. The mechanisms of how this is achieved by the visual system are still poorly understood. Advances in recording and manipulating neuronal activity in specific cell types and axonal projections together with tools for circuit tracing are beginning to shed light on the neuronal circuit mechanisms of how internal, contextual signals shape sensory representations. Here we review recent work, primarily in mice, that has advanced our understanding of these processes, focusing on contextual signals related to locomotion, behavioural relevance and predictions.

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Introduction

The classical model of information processing in the brain is based on a hierarchical organization of feedforward connections from one brain region to the next. In the visual system, information from the retina is relayed via the dorsolateral geniculate nucleus (dLGN) in the thalamus to the primary visual cortex (V1), and from there through a hierarchy of increasingly higher-order cortical areas [1]. In this hierarchical model, visual cortex neurons are mainly seen as feature detectors that signal the presence of a specific visual stimulus in the environment, while feedback connections have a minor, modulatory influence. This view remains a cornerstone of our understanding of visual processing.

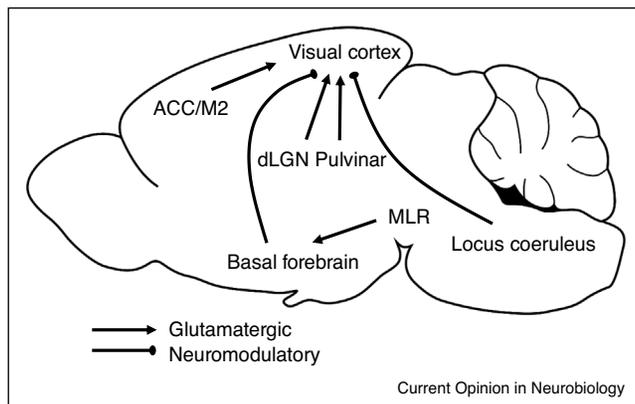
However, we understand only a small fraction of activity even in V1 [2], and many aspects of visual responses cannot be predicted by feedforward models [3]. This is not surprising given that less than 10% of synapses received by cortical neurons stem from feedforward projections [4]. It is now well established that in behaving animals, visual responses can be strongly influenced by contextual cues, such as visual scene context, attention, self-movement, task requirements, spatial location and expectations [5–9,10*,11]. Visual processing therefore is likely to be an active process, involving internal models of the world and dependent on the behavioural and perceptual needs of the animal.

At the circuit level, contextual influences are thought to be conveyed via top-down projections from higher brain areas, intra-areal horizontal connections or neuromodulatory inputs. However, circuit mechanisms of contextual modulation have often been difficult to identify, and hence our understanding of the sources of specific contextual signals and how they are integrated with feedforward sensory information is still very limited. Advances in genetic tools for labelling specific cell types and circuits, and monitoring or manipulating their activity in behaving rodents are beginning to advance our understanding of how contextual and visual signals are combined during active vision. This review focuses on a few specific areas which have witnessed particularly interesting developments in recent years: contextual signals related to locomotion, behavioural relevance and predictions.

Effects of locomotion on visual cortex activity

Behavioural state has a strong influence on cortical processing [12,13]. For instance, visual responses in V1 are stronger, more reliable, and less correlated when mice walk or run compared to when they are quietly resting [14–16]. These effects show similarities to modulation of responses by arousal or attention [9,17–20]. Locomotion-related response modulation in visual cortex is thought to be at least partly conveyed by cholinergic input from the basal forebrain, which is activated by projections from the mesencephalic locomotor region during running [21,22*] (Figure 1). The cholinergic signals have been shown to strongly act on vasoactive intestinal peptide (VIP) expressing inhibitory interneurons [21]. These inhibit somatostatin (SOM) expressing interneurons, which can lead to disinhibition and thus increased activity of excitatory pyramidal neurons. This disinhibitory motif involving VIP and SOM cells was also found in other cortical areas [23,24,25] and could provide a more general mechanism for state-dependent gain

Figure 1



Schematic depicting the pathways conveying locomotion-related signals to V1. ACC/M2, anterior cingulate cortex and secondary motor cortex; dLGN, dorsolateral geniculate nucleus of the thalamus; MLR, mesencephalic locomotor region of the brainstem.

modulation [26]. However, other studies found that SOM cells were activated rather than suppressed by locomotion when animals were exposed to light or visual stimuli [27–29]. These seemingly disparate findings recently could be reconciled by two cortical circuit models that included interactions between excitatory and multiple inhibitory cell types [28,30*].

Neuromodulation by cholinergic and noradrenergic signalling likely contributes to locomotion-related activity changes in cortex [21,27], probably due to increased arousal during locomotion [22] (but see [31]). However, some locomotion-related signals in visual cortex are inconsistent with unspecific gain modulation, but instead provide specific information about self-motion. Pyramidal cells in V1 are active during running in the dark and their firing is modulated by running speed [16,29,32,33]. These motor signals could be inherited from the visual thalamus where locomotor-related activity has been observed both in the dLGN as well as in the higher-order pulvinar complex [16,34*]. In addition, anterior cingulate and neighbouring secondary motor cortex (ACC/M2) convey strong motor signals to V1. These projections specifically activate running-modulated V1 cells and silencing ACC/M2 decreases locomotion-triggered V1 responses [35**]. Such motor signals could represent an efference copy that informs visual processing of the animal's self-motion (see below).

Locomotion has further effects on visual responses in V1, including decreased surround suppression and increased spatial sensitivity [16,36,37]. Together, the described changes might adapt visual processing to the needs of an animal moving through its environment.

Learning the behavioural relevance of visual stimuli

When a sensory stimulus becomes behaviourally relevant, its representation in sensory cortical networks is enhanced, including expanded cortical representations, increased or more reliable and selective responses, changes in stimulus tuning and decreased response correlations. Many of these changes are already visible at the earliest stages of cortical processing. Repetitive practice in a perceptual task can further improve sensory responses. These can facilitate the read-out and interpretation of sensory signals relevant to the task to better inform behavioural decisions, and may even directly couple to behavioural output through projections to the striatum [38]. Previous reviews have comprehensively covered the effects of behavioural stimulus relevance and learning on visual cortical areas, focusing on various contributing factors, including perceptual learning, different forms of attention, reward expectation, and flexible circuit adaptations to the requirements of a task [8,9,39–41]. Here we focus on recent studies that have started to elucidate the circuit mechanisms of learning-related changes in visual circuits as well as the role of top-down signals from higher brain areas.

Two-photon imaging of genetically encoded calcium indicators enables tracking the neuronal responses of identified neurons over the time-course of learning [42]. Using this method, Poort *et al.* found that when mice learned a visual discrimination task, V1 population responses became increasingly better at discriminating the task-relevant stimuli. This improvement in stimulus encoding resulted from an increase in the number of selective neurons and greater day-to-day stability of selective responses [43**]. Visual response selectivity decreased when trained mice engaged in a non-visual task, but was still higher than before learning, even under anaesthesia. This suggests that learning the behavioural relevance of sensory stimuli engages task-dependent top-down influences which act in concert with more permanent circuit modifications in V1 [43**,44]. Local circuit changes in V1 are associated with increased stimulus selectivity of parvalbumin-expressing interneurons [45*], which thereby provide more selective inhibition during processing of behaviourally relevant stimuli.

Top-down inputs potentially contribute to learning-induced neural response changes in several ways. Learning can change the strength and/or nature of signals conveyed to visual cortex from specific higher brain areas. For instance, axonal projections in V1 from retrosplenial cortex increase their activity as mice learn to react to a visual input in order to escape an aversive stimulus, thereby altering visual responses of layer 2/3 cells [46*]. Anterior cingulate cortex (ACC) is another major source of long-range input to V1 [47], and has been shown to convey task-dependent, contextual signals during

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