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Vision and vigilance on the go

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Abstract

Moving purposefully through the world requires the seamless coordination of a wide variety of sensory, motor, and motivation systems. Recent experiments suggest that mouse visual cortex may offer a particularly well suited forum for experimental investigation of this coordination.

Vision is an active and fluid process: it provides information to guide our actions and behavioral states, which in turn shape the visual information that we receive. One of the most pervasive examples in the animal kingdom of this interplay is in the realm of active navigation through an environment. Vision guides movements during navigation, but every movement, such as rounding a corner, generates new visual information. Similarly, what we see (e.g., an imminent danger), can raise our vigilance, which in turn increases our visual sensitivity. The inherent interplay between sensation, action, and vigilance during navigation poses a challenge for neurophysiologists. How does one disambiguate the tightly correlated sensory, motor, and arousal signals underlying navigation to understand its neural basis? Recent discoveries suggest that the mouse might offer a solution.

Mice would seem to be an odd choice for studying visually guided behaviors. Their lack of a cone-dense foveal region, makes their visual acuity extraordinarily poor compared to the classic experimental models for vision, cats and monkeys. However, in the case of the analyzing the motion patterns that are created by movement through an environment, this is not a significant concern. However, self motion produces distinctive patterns of motion across the entire retina, including the periphery, known as flow fields, and thus is not dependent on the foveal acuity. Moreover, the mouse model offers some unique experimental advantages. The animal's diminutive size makes it relatively easy to construct virtual reality environments in which mice actively "move" on a spherical treadmill while visual stimuli are presented. And the pathways underlying active navigation can be selectively activated or deactivated by illuminating genetically targeted neuronal populations in which microbial opsins can be expressed.

A recent study by Erisken et al. [1] has begun the leverage these advantages by studying how the signals from populations of visual neurons are altered during mouse locomotion. In

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accordance with a previous study [5], they found that the responsiveness, but not selectivity, of individual neurons in mouse visual cortex increased during active locomotion [5]. This pattern of response modulation, called a gain change, has been proposed to be a general mechanism for the enhancement of sensory signals and has been observed in studies of attention in primates. Consistent with a prominent role of arousal during locomotion, the authors found similar changes among cells within the dorsolateral geniculate nucleus (dLGN), the thalamic body that conveys retinal signals to visual cortex, and these changes were correlated with pupil dilation, an established correlate of arousal. Perhaps most significantly, they found that the correlations between visual cortex neurons were reduced during locomotion, consistent with the reductions observed in primates with variations in task difficulty [8]. As noted by the authors, this decorrelation is particularly notable because one might expect correlations to increase with the increased firing rate associated with locomotion.

Although the Erskine study shows a potential role for arousal, a remaining issue is the extent to which other factors affect visual processing. Their study shows that arousal, as quantified by pupil dilation, is highly correlated with run speed. Thus if arousal was the sole contributor to locomotion-related signals in visual cortex, one would expect visual cortex responses to uniformly rise with run speed even when there is no visual input. However, in the dark, visual cortex neurons have a wide diversity of run speed tuning, with some neurons preferentially responding to low run speeds [9]. This suggests that visual cortex, in addition to be altered by arousal, also receives more specific proprioceptive and motor signals during locomotion.

The computational question of how all of these signals actually help animals navigate also remains to be resolved. Depending on the algorithms used to read out neural activity and the particular task employed, decorrelation can either help or hurt behavioral performance [7]. Studying the impact of changes in correlation structure, such as those found in locomotion, therefore requires a well-defined behavior for which we have a good idea of the neural population that is actually sampled. For example, it is important to treat an external object looming toward you [10] differently from an object that moves on the retina due to self-motion. In the primate, this problem is likely to be solved by cells that are selectively responsive for both the visual flow fields associated with movement and the vestibular cues created by self-movement. Such cells can be divided into two broad categories: those in which the direction selectivity to visual and vestibular signals are congruent and those in which these selectivities are incongruent. The existence of both congruent and incongruent multimodal cells, and the relatively poor correlations observed between cells of different congruency, allows for a decoding algorithm to disambiguate the retinal signals associated with self and external motion [2].

Mouse visual cortex clearly receives extraretinal information during locomotion, and cells that are congruent and incongruent with respect to their visual and locomotive responses have been found [3, 9]. Such populations could potentially be used to disambiguate retinal motion signals. However, we have no idea how the arousal effects reported—in particular, changes in correlation structure and reliability—are distributed between these two groups of neurons and the extent to which these effects enhance the perception of self and external

motion. The robustness of behavioral and physiological responses to looming stimuli suggests a potential paradigm by comparing the physiological and behavioral responses to different motion stimuli which in terms of retinal motion are identical, but with respect to locomotion correspond with either external or self motion. The effects of putative arousal inputs on the encoding of visual information or the decoding of neuronal responses can be studied in the same task by the selective optogenetic activation or deactivation of those inputs. Thus, although primates have traditionally been used for such studies of multimodal integration and behavioral state, the success of studies such as Erisken *et al.*, combined with the inferential power of optogenetic manipulations, suggest that the mouse may play a leading role in solving the puzzle of navigation.

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