Article

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Distinct Feedforward and Feedback Effects of Microstimulation in Visual Cortex Reveal Neural Mechanisms of Texture Segregation

Highlights

- Microstimulation of visual cortex evokes local excitation followed by inhibition
- Microstimulation of V1 causes feedforward excitation and inhibition in V4
- Microstimulation of V4 only causes feedback-based reductions in V1 firing rates
- When V4 is suppressed by microstimulation, V1 figure-ground segregation is reduced

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In Brief

Klink et al. probe interactions between visual cortical areas V1 and V4 with electrical microstimulation. Microstimulation effects reliably propagated in the feedforward direction. In the feedback direction, they depended on visual stimulation and figure-ground segregation. These results reveal the driving and modulatory roles of feedforward and feedback connections, respectively.

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Distinct Feedforward and Feedback Effects of Microstimulation in Visual Cortex Reveal Neural Mechanisms of Texture Segregation

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SUMMARY

The visual cortex is hierarchically organized, with low-level areas coding for simple features and higher areas for complex ones. Feedforward and feedback connections propagate information between areas in opposite directions, but their functional roles are only partially understood. We used electrical microstimulation to perturb the propagation of neuronal activity between areas V1 and V4 in monkeys performing a texture-segregation task. In both areas, microstimulation locally caused a brief phase of excitation, followed by inhibition. Both these effects propagated faithfully in the feedforward direction from V1 to V4. Stimulation of V4, however, caused little V1 excitation, but it did yield a delayed suppression during the late phase of visually driven activity. This suppression was pronounced for the V1 figure representation and weaker for background representations. Our results reveal functional differences between feedforward and feedback processing in texture segregation and suggest a specific modulating role for feedback connections in perceptual organization.

INTRODUCTION

Visual stimuli elicit a complex pattern of neuronal activity that spans a large number of cortical areas. In primary visual cortex (V1), the first cortical stage of visual information processing, neurons encode elementary features such as the orientation of line elements. After V1, activity is propagated to higher visual areas that represent more complex aspects of the visual world (Felleman and Van Essen, 1991; Salin and Bullier, 1995). How do neurons across different areas interact with each other when we interpret what we see? Feedforward connections drive neurons in higher areas so they can combine information and construct more complex receptive field (RF) properties. Higher-level neurons are silent when upstream activity in lower areas is blocked (Schmid et al., 2010). There is a similarly dense set of feedback connections from higher areas down to the lower areas. These connections are thought to modulate visually driven activity but to be less capable of evoking activity in the absence of stimuli (Hupé et al., 1998; Moore and Armstrong, 2003; Nassi et al., 2013; Roelfsema, 2006), which implies a functional asymmetry between feedforward and feedback effects (Crick and Koch, 1998; Lamme and Roelfsema, 2000; Sherman and Guillery, 1998). Accordingly, top-down effects on V1 activity are stronger when a stimulus is visible than when it is kept in working memory (van Kerkoerle et al., 2016). Anatomical information from monkeys further supports such an asymmetry, with feedforward connections targeting neurons in input layer 4 of higher cortical areas and feedback connections avoiding layer 4 and instead targeting the superficial layers and layer 5 of lower cortical regions (Felleman and Van Essen, 1991; Salin and Bullier, 1995).

Here, we used electrical microstimulation to study the interactions between a lower and higher area of visual cortex by perturbing neuronal activity in one area and measuring its distal effects in feedforward or feedback directions. There is an extensive body of work investigating how intracortical electrical microstimulation affects neuronal activity in the vicinity of the electrode (Clark et al., 2011; Histed et al., 2013; Tehovnik, 1996; Tehovnik et al., 2006). The prevailing view is that microstimulation directly activates a pool of neurons near the tip of the stimulation electrode, probably through initiation of action potentials in their axons, which are highly excitable. There have also been many previous studies that examined how microstimulation influences behavior (Cicmil and Krug, 2015; Clark et al., 2011). Microstimulation of the V1, for example, can produce reportable phosphenes, artificial percepts of light at the location of the RF of the stimulated neurons (Bartlett et al., 2005; Schiller and Tehovnik, 2008; Schmidt et al., 1996; Winawer and Parvizi, 2016). Furthermore, microstimulation of small groups of neurons in sensory