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Research Report

Influence of 'feedback' signals on spatial integration in receptive fields of cat area 17 neurons

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ABSTRACT

'Feedback' signals from mammalian extrastriate visual cortices are reported to exert primarily an excitatory influence on the classical receptive field (CRF) of neurons in the primary visual cortex (V1). However, given the much larger CRFs of neurons in extrastriate visual cortices it is not yet understood how feedback signals influence the spatial integration of visual signals by V1 neurons. To investigate this, we reversibly inactivated one of the 'form-processing' extrastriate visual cortices, the postero-temporal visual (PTV) cortex, and examined changes in responses of V1 neurons to drifting grating patches up to 28° in diameter. We found that during inactivation of PTV cortex the magnitude of the responses to CRF-confined stimuli and that to large stimuli inducing maximum suppression (i.e. minimum responses) was significantly reduced, while the spatial extent of the CRF remained largely unaffected. As a result, the relative strength of the surround suppression increased marginally. This effect was apparent in both simple and complex cells. It was also strong and consistent in cells located in supragranular and infragranular layers. For those cells exhibiting some relief from surround suppression or 'counter-suppression' when large stimuli patches were applied, the effect on counter-suppression was heterogeneous. Overall, the relative integrated responses to the 28° grating patches were also decreased when PTV cortex was inactivated. Thus, a substantial reduction in the CRF response and the largely unaffected spatial extent of the CRF as well as a weak surround effect observed in the present study are consistent with a multiplicative scaling effect.

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Abbreviations: CRF, classical receptive field; CSI, counter-suppression index; 2G, Difference of Gaussians model; eCRF, extra-classical receptive field; MT area, middle-temporal area; PMLS, posteromedial lateral suprasylvian area; PS, posterior suprasylvian area; PTV cortex, postero-temporal visual cortex; 3G, Supplementary Difference of Gaussians model; r_{opt}, the size of the CRF; r_{srd}, the estimated size of suppressive surround; R_{cs}, counter-suppression response; R_{ds}, response to stimulus grating patches of 28° in diameter; R_{max}, maximum response; R_{min}, minimum response; RIR, relative integrated response; SF, summation field; SI, suppression index

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1. Introduction

Excitatory inputs to individual neurons in the mammalian primary visual cortex (striate cortex, area 17, V1) are usually summed primarily over a small part of the visual field, known as the classic receptive field (CRF). As a result, the response of a neuron increases with an increase in stimulus size within the confines of the CRF. However, with further increases beyond the CRF or well into 'extra-classical receptive field' (eCRF), the neuron's response is often reduced (suppression), despite the fact that stimulation of the eCRF *per se* does not evoke any responses (Li and Li, 1994; Sengpiel et al., 1997; Walker et al., 2000; Akasaki et al., 2002; Sadakane et al., 2006; Bardy et al., 2009; Wang et al., 2009; see for reviews, Allman et al., 1985; Fitzpatrick, 2000; Seriés et al., 2003). In some V1 neurons, the magnitude of their responses may partially 'recover' from near surround suppression or show signs of so-called 'counter-suppression' when the stimuli are extended further, covering the part of the eCRF distal to the CRF (Li and Li, 1994; Wang et al., 2009). The maximum spatial extent over which V1 neurons pool visual signals is reported to exceed 12° of visual angle (cat: Maffei and Fiorentini, 1976; Li and Li, 1994; Mizobe et al., 2001; macaque monkey: Levitt and Lund, 2002). Given the limited spatial span of horizontal associational connections intrinsic to V1, Angelucci et al. (2002), in order to account for the full spatial range of centre-surround interactions observed in V1, invoked the influence of feedback projections from the higher-order, extrastriate cortices where neurons have much larger receptive fields.

Feedback projections to V1 are known mostly to be glutamatergic and/or aspartatergic, thus excitatory to their target neurons (Johnson and Burkhalter, 1996; Pérez-Cerdá et al., 1996). Indeed, in the cat, during inactivation of higher-order visual areas, such as the extrastriate visual cortices – area 18 (V2), area 21a (V4) or postero-temporal visual (PTV) cortex (Mignard and Malpeli, 1991; Wang et al., 2000; Huang et al., 2004; Bardy et al., 2006, 2009; Huang et al., 2007) – the responses of V1 neurons are usually markedly reduced. Similarly, in macaque monkey reversible inactivation of V2 (Bullier et al., 1996) or the middle-temporal area (MT or V5, Hupé et al., 1998, 2001) resulted in a substantial reduction in the responses of V1 neurons to visual stimuli presented to their CRFs. Furthermore, in a subgroup of cat V1 neurons, specific receptive field properties such as orientation and direction selectivity, contrast response function (Wang et al., 2000, 2007; Huang et al., 2007) and spatial selectivity (Huang et al., 2004), are also affected by inactivation of ipsilateral extrastriate visual areas. However, very few studies have examined the effects of reversible abolition of feedback signals from the higher-order areas onto the silent surrounds of V1 neurons (Hupé et al., 1998; Bullier et al., 2001; Bardy et al., 2009). When testing the responses of V1, V2 and V3 neurons in macaque monkey to a moving bar over a stationary or moving checkerboard background, Hupé and colleagues (1998; cf. Bullier et al., 2001), demonstrated that during reversible inactivation of motion area MT there is a stimulus salience-dependent reduction in the strength of surround suppression induced by the moving background. However, the effect observed by them in V1 was not as pronounced as that in V2 and V3 (Bullier et al., 2001). We showed recently (Bardy et al., 2009) that reversible inactivation of cat PTV cortex, a higher-order form-processing visual area, can affect the strength of contextual modulation of some V1 neurons. The effects were not always consistent and varied with the relative orientation/direction differences between CRF and eCRF stimuli.

Based on the pattern of its connectivity within the visual cortex as well as earlier physiological studies and functional deficits induced by its deactivation in behaving animals, cat PTV cortex is considered to be the homologue of primate inferotemporal (IT) cortex (Markuszka, 1978; Symonds and Rosenquist, 1984a; Payne and Siwek, 1990; Baizer et al., 1991; Payne, 1993; Lomber et al., 1996a,b). Like other higher-order visual areas, for example, areas 18 (V2), 19 (V3), 21a (presumed homologue of primates V4, Payne, 1993) and the posteromedial lateral suprasylvian area (PMLS; presumed homologue of primates area MT or V5, Payne, 1993), PTV cortex sends direct projections to V1 from its subdivision, area 20a but not 20b (Symonds and Rosenquist, 1984a). Area 20a, in addition to being strongly and directly interconnected with area 20b, also projects to other cortical areas (e.g. areas 18, 19, 21a and PMLS), each of which, in turn, projects directly (as well as indirectly) to V1 (Symonds and Rosenquist, 1984a, Rosenquist, 1985; Dreher, 1986). Inactivation of PTV cortex has been shown to mostly reduce the responses of V1 neurons to CRF-confined stimulation (Huang et al., 2007; Bardy et al., 2009). However, it is not well understood so far, how the feedback signals from PTV cortex, one of the highest 'form-processing' areas, affects the integration of visual information from a large region surrounding the CRF of the 'lower-order' areas within the same information processing stream, such as V1.

In the great majority of V1 neurons, the integration by individual neurons of excitatory and inhibitory visual inputs appears most effective along the axis of preferred orientation — responses of V1 neurons peak at the cell's optimal orientation and in most cases, surround suppression is also strongest along the axis of the preferred orientation. Recent studies suggest that, similar to the spatial extent of the summation field (Sceniak et al., 1999), the strength of suppression (Song and Li, 2008; Wang et al., 2009) and counter-suppression (Wang et al., 2009) are also dependent on stimulus contrast. Thus, in the present study we used a series of iso-oriented sinusoidal grating patches (up to 28° in diameter) at low- and high-stimulus contrast to investigate the influence of feedback projections from ipsilateral PTV cortex on the spatial integration of visual signals by single V1 neurons. Consistent with previous reports we found that the magnitude of the response was, in general, significantly decreased during inactivation of PTV cortex (for separate data sets; see also Bardy et al., 2009) regardless of the size of the grating patch used. In most cases, the effects on the strength of surround suppression or counter-suppression of V1 neurons were rather small and/or not systematic. Our results indicate that, for the majority of V1 neurons, feedback projections exert a predominantly excitatory influence on CRF-generated responses but do not seem to strongly modulate the suppression induced by iso-orientation surround stimulation. Preliminary results have been published in abstract form (Wang et al., 2006).

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