2013

Top-Down Control of Lateral Interactions in Visual Cortex

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TOP-DOWN CONTROL OF LATERAL INTERACTIONS IN VISUAL CORTEX

A Thesis Presented to the Faculty of

The Rockefeller University

in Partial Fulfillment of the Requirements for

the degree of Doctor of Philosophy

by

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June 2013

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The Rockefeller University 2013

V1 neurons are capable of integrating information over a large area of visual field. Their responses to local features are dependent on the global characteristics of contours and surfaces that extend well beyond their receptive fields. These contextual influences in V1 are subject to cognitive influences of attention, perceptual task and expectation. Previously it's been shown that the response properties of V1 neurons change to carry more information about behaviorally relevant stimulus features (Li et al. 2004). We hypothesized that top-down modulation of effective connectivity within V1 underlies the behaviorally dependent modulations of contextual interactions in V1. To test this idea, we used a chronically implanted multi-electrode array in awake primates and studied the mechanisms of top-down control of contextual interactions in V1. We used a behavioral paradigm in which the animals performed two different perceptual tasks on the same stimulus and studied task-dependent changes in connectivity between V1 sites that encode the stimulus.

We found that V1 interactions-both spiking and LFP interactions-showed significant task-dependent changes. The direction of the task-dependent

changes observed in LFP interactions, measured by coherence between LFP signals, was dependent on the perceptual strategy used by the animal. Bisection task involving perceptual grouping of parallel lines increased LFP coherence while vernier task involving segregation of collinear line decrease LFP coherence. Also, grouping of collinear lines to detect a contour resulted in increased LFP interactions. Since noise correlations can affect the coding accuracy of a cortical network, we investigated how top-down processes of attention and perceptual task affect V1 noise correlations. We were able to study the noise correlation dynamics that were due to attentional shift separately from the changes due to the perceptual task being performed at the attended location. Top-down influences reduced V1 noise-correlations to a greater extent when the animal performed a discrimination task at the recorded locations compared to when the animal shifted its attention to the location. The reduction in noise correlation during the perceptual task was accompanied by a significant increase in the information carried about the stimulus (calculated as Fisher information). Our analysis was also able to determine the degree to which the task dependent change in information was due to the alteration in neuronal tuning compared to changes in correlated activity. Interestingly, the largest effects on information were seen between stimuli that had the greatest difficulty of discrimination.

ACKNOWLEDGEMENTS

I thank Dr. Charles Gilbert and Prof. Wu Li for their guidance and mentorship. I am also grateful to Dr. Justin McManus for lively discussions and assistance in data analysis. I thank Valentin Piëch and Hiroshi Abe for their helpful suggestions.

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1. INTRODUCTION

The traditional view of visual information processing is a bottom-up view of analysis, whereby increasingly complex features of a visual scene are processed progressively in a hierarchy of cortical structures. In such a model, primary visual cortex (V1) is often viewed as a set of filters that serve to extract low-level features of the scene, such as local orientation or color or the depth position. It is unlikely, however, that feedforward inputs alone can achieve flexible and invariant pattern recognition in a complex and rapidly changing environment. Recent studies show that the function of any area of the cerebral cortex, including that of primary visual cortex, is subject to top-down influences of attention, expectation, and perceptual task. Perceptual experience allow us to acquire Internal representations of the world and consequently affect our brain's strategy for analyzing visual scenes. Thus, vision is an active process, and the function of any cortical area is not fixed—each area runs different 'programs' according to context and to the current perceptual requirements. This is evident even in earlier stages of visual processing, and emerging studies of contextual influences and top-down control suggest that primary visual cortex (V1) is a dynamic module influenced by both sensory context (global features within the scene like contours, figure-ground segregation) and behavioral context (like attention, perceptual task and expectation) (see Gilbert and Sigman, 2007 for review). And at any given instant confluence of bottom-up processes of sensory

features and top-down influences of behavioral states define the function of primary visual cortex.

1.1. CONTEXTUAL INTERACTIONS

The responses of neurons in V1 are dependent on the precise geometric relationships between line segments or texture elements within the receptive field and contours and surfaces that extend for considerable distances outside the receptive field. Thus, V1 cells' responses to features in the visual scene are highly dependent on the context within which those features are placed (Albright and Stoner 2002, Gilbert 2000). Such contextual influences play a central role in V1's capability to integrate information over a large area of visual field and capture global scene features such as perceptual saliency and pop-out, figure-ground segmentation. Many compelling visual illusions, that provide helpful insights as to how the visual cortex processes incoming visual scene, are also dependent on contextual interactions (Eagleman 2001).

The idea that the global characteristics of a visual scene shape neuronal responses to local features is in accord with the basic principle of Gestalt psychology. In the early 19th century, Gestalt psychologists offered a set of rules to characterize the interactions between sensory elements underlying "perceptual organization." They emphasized that the perception of objects was based on holistic patterns rather than by an assembly of the parts of objects (Wertheimer 1923). The principle of *good continuation* provides perceptual rules by which the visual system integrates oriented lines present in a scene, into a perceived

object. It suggests that line segments that are collinear and have similar orientation and not making an abrupt change in direction are easily linked to form a perceptual group (Fig. 1.1). This can be seen in contour saliency, where contours composed of line segments that have a gradual change in orientation tend to easily pop out from complex backgrounds made up of randomly oriented and positioned line elements; on the other hand, contour composed with line elements having random jitter in their orientations are difficult to discern in a complex background (Fig. 1.1).

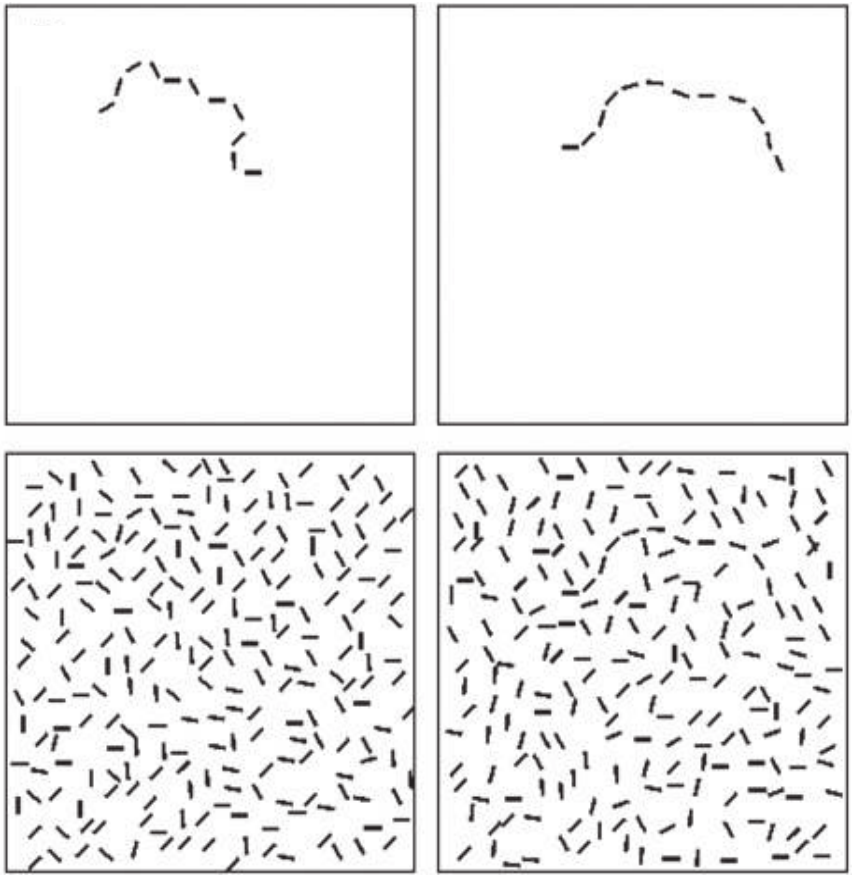

Figure 1.1 Gestalt theory of perceptual grouping. The law of *good continuation* states that we tend to link line segments that are collinear and have similar orientation and not those with sharp and abrupt changes in direction. This priniciple is demonstrated in contour saliency, the degree to which a contour, made up of line segements, pops-out in a background of random oriented elements. The top panels in the figure mark the position of the contours in the bottom panels. The contour on the right which satisfies the law of good continuation readily pops-out of the complex background, while the contour on the left composed of elements with large differences in orientation and abrupt changes in direction does not pop-out and needs an extensive search to find. Adapted from Field et al., 1993 and Gilbert and Sigman, 2007.

The rules of perceptual organization and saliency are widely reflected in the stimulus contextual interactions observed in various areas of the visual cortex. The effects of stimulus elements outside the receptive field of a cell on the core stimulus within its receptive field are termed contextual influences or interactions. The contribution of such contextual effects to various stages of perceptual processes is widespread throughout the primate visual brain (Albright and Stoner 2000, Allman et al. 1985). Peripheral influences on responses within the receptive field were originally found in the retina (Mcllwain 1964) with influences coming from positions as far as 90° from the receptive field center. In V1, modulatory influences of stimuli from outside the receptive field of a cell have been extensively characterized by a number of studies (Allman et al. 1985, Gilbert and Wiesel 1990, Knierim and Van Essen 1992, Nelson and Frost 1978, Maffei and Fiorentini 1976, Orban et al. 1987). These modulatory influences can be facilitative or suppressive depending on the relationship between the core and contextual stimulus attributes, that is, how the stimulus within the receptive field of a cell relates to the surrounding stimuli outside the receptive field. For example, a V1 cell's response to an optimal stimulus is suppressed if it is surrounded by stimulus of similar orientation, but the suppression reduces when the surrounding stimulus is orthogonal in orientation (Fries et al. 1977, Gilbert et al. 1990, Knierim and Van Essen 1992, Kapadia et al. 1995, Li et al. 2000, Li et al. 2001, Maffei and Fiorentini 1976, Nelson and Frost 1978, Sillito et al.1995). Similar contextual effects on stimulus motion have been found in middle temporal

(MT) visual area. Cells in MT respond to direction of motion and show facilitatory or suppressive interactions when surrounded by other stimulus motions (Allman et al. 1985, Xiao et al. 1997). When the surrounding stimulus motion matches the direction of motion within the receptive field, MT cells are suppressed; the cells are facilitated when the surround motion is in opposite direction (Allman et al. 1985). Evidence from such studies suggest that the effects of surrounding stimuli on the stimulus within the receptive field correlate with the perceptual saliency of the presented stimulus. Visual segments that are marked by contrasting features (e.g. motion, color or orientation) from the surrounding regions are perceived easily and thus more salient than the regions that are homogeneous with the background (Treisman and Gelade 1980, Julesz 1981, Treisman and Gormican 1988). Such figure-ground interactions between visual elements are similar to the stimulus contextual interactions described above—suppressed (and less salient) responses in the presence of similar background and enhanced (and more salient) responses in the presence of contrast (orthogonal stimuli) surround. The nature of the contextual interactions between the core and the surround stimulus, such as their strength, time course and spatial extent, have been comprehensively studied in the visual areas (Allman et al. 1985, Kapadia et al. 1995, Knierim and Van Essen 1992, Lamme 1995, Lee et al. 1998, Kapadia et al. 2000, Li et al. 2006, Walker et al. 1999, Zipser et al. 1996).

In addition to perceptual saliency, neural correlates of perceptual fill-in processes, where the visual system tries to recover 'missing' information in a scene by interpolating or filling-in the information from nearby areas, have been

observed in the primate visual cortex. One line of evidence for cortical representation of these fill-in processes come from studies involving the 'blind spot.' The blind spot refers to the region of retina lacking photoreceptor cells, where the optic disk exits the retina. Experiments studying cortical neurons that represent these blind spot zones indicate that perceptual filling-in of the blind spot results from an active neuronal process fed by informational content present in surrounding regions of the visual field (Fiorini et al. 1992, Komatsu et al. 2000). For example, in alert behaving monkeys, uniform rectangles with edges placed well outside the blind spot region elicit responses in V1 cells that represent the blind spot areas (Komatsu et al. 2000). Another visual tool used to study perceptual fill-in mechanisms is an 'artificial scotoma'. The artificial scotoma is achieved by having a homogenous gray patch within a patterned stimulus, thus temporarily removing localized visual information to the cortex (Ramachandran and Gregory 1999). Neuronal basis for the fill-in effects due to artificial scotomas have been found in monkey visual cortex: cells in the areas V1, V2 and V3 have been shown to respond when their receptive fields are placed within an artificial scotoma (Das and Gilbert 1995, Gilbert et al. 1996, Pettet and Gilbert 1992, De Weerd et al. 1998). V1 cells' receptive fields expand beyond their original limits, increasing up to fivefold in size, when placed within an occluder or artificial scotoma (Das and Gilbert 1995, Gilbert et al. 1996, Pettet and Gilbert 1992). Neurons deprived of information within their receptive field, extend their sensitivity to surrounding area of visual space. This enlarged field could serve to perceptually fill-in the scotoma with information from the surrounding spatial field.

'Illusory' or subjective contours is another perceptual fill-in process wherein a complete object is perceived even though only segments of the objects are physically present in a visual scene (e.g., Kanizsa figures; see Kanizsa 1976). Researchers have found direct neural correlate of such phenomena in V2, where neurons have been reported to respond illusory contours (von der Heydt et al. 1984) and some have found evidence for the same in V1 too (Grosof et al. 1993, Lee and Nguyen 2001).

Besides perceptual saliency and fill-ins, there exists another class of context-driven perceptual process, in which the perceived visual attribute (such as color or orientation or luminance) of a local region is influenced by the nearby surrounding stimulus. For example, in 'tilt illusion,' the perceived orientation of aline segment is altered by the surrounding elements of different orientation (Gibson and Radner 1937, Westheimer 1990). In V1, line segments outside the receptive field influences the orientation tuning of a cell to a line segment placed within its receptive field and this effect has been related to the tilt illusion (Gilbert and Wiesel 1990). In the perceptual process of 'brightness induction,' luminance in the surrounding regions can affect the perceived brightness of a surface. For example, a gray patch on a bright background will appear darker than the same gray patch on a darker background. Paradiso and colleagues (Rossi et al. 1996, Rossi and Paradiso 1999, MacEvoy and Paradiso 2001) studied neural mechanisms of brightness induction in V1 and have found that a substantial fraction of V1 neurons exhibit responses that correlate with the changes in perceived brightness of a stimulus within their receptive fields. The chromatic

analogue to brightness induction is 'color appearance'—the dependency of perceived color on the color of adjacent regions, and neural representation of this process have been found in V1 (Zeki et al. 1983, Wachtler et al. 2003) and V4 (Schein and Desimone 1990).

Along with the aforementioned visual processes, many other context-dependent percepts have been found to have neural counterparts. A subset of V4 neurons may encode 'color constancy,' the invariance of the perceived color of an object under different illuminating conditions is terms as color constancy (Zeki et al. 1983). 'Border ownership' cells, that assign objects to one or the other side of an image boundary, have been found in early visual areas (V1, V2, V3; Baumann et al. 1997, Zhou et al. 2000, Chang et al. 2001).

Pertinent to the current study are the contextual influences observed in V1 involving perceptual organization—grouping and segmentation—of oriented line segments in a visual scene, leading to contour saliency and pop-outs and extraction of figure-ground information. It's well known that a single oriented line segment within a V1 cell's receptive field will elicit a brisk response. When such a line is flanked by an iso-oriented line, the cells response is facilitated, while an orthogonal flank inhibits the cells response (Kapadia et al. 1995). Similarly, when an oriented line within a cell's receptive field is embedded within a complex background of randomly oriented and positioned line elements, the cell's response is greatly reduced. If some of the random elements are changed so that a contour, composed of collinear line segments, becomes visible, the cell's

response is enhanced and is termed as 'collinear facilitation' (Kapadia et al. 1995, Kapadia et al.1999, Li et al. 2006). When the length of the contour is increased by adding more collinear elements, the contours become readily visible and such salient contours further facilitate the V1 neuronal responses (Kapadia et al. 1995, Li et al. 2006).

In addition to the perception of contours, the influence of lines of contrasting orientations on the responses of V1 cells may play a role in the perception and segmentation of textures within a visual scene. When a V1 cell's receptive field is located within a stimulus pattern of oriented lines, which is surrounded by a contrasting pattern—for example, lines of another orientation—its response is facilitated relative to that seen when the field has a uniform texture (Knierim and Van Essen 1992). When activated by a grating of the optimal orientation within the receptive field, V1 cells are disinhibited and sometimes facilitated by a large grating of the orthogonal orientation in the receptive field surround (Sillito et al. 1995). The presence of a texture boundary in the visual field can activate some cells even when that boundary is located well outside the classical receptive field (Lamme 1995). Besides encoding orientation-based texture elements, V1 neurons show robust contextual modulation when disparity, color, and luminance cues define a textured figure centered on the receptive field (Zipser et al. 1996). These observations suggest that the responses of V1 cells are influenced by global texture elements and argue for the role of V1 in extraction of figure-ground information from a visual scene.

1.2. HORIZONTAL CONNECTIONS AND CONTEXTUAL INTEGRATION

It is debatable whether the contextual interactions seen in early areas such as V1 are mediated by local cortico-cortical connections or by feedback connections from higher cortical areas. One school of thought suggests that the long-range horizontal connections between neurons within the same cortical area, mediate functional interactions between the neurons and give rise to the contextual effects observed in early visual cortices (Gilbert and Sigman 2007). Others suggest that the feeback connections from visual areas higher in the hierarchy are responsible for these contextual effects, and that the computations performed in the higher areas are fed-back to the early visual areas such as V1 (Angellucci et al. 2002, Lamme et al. 1998, Shmuel et al. 2005). We suggest that the context-integrative properties of V1 neurons are caused by dynamic interactions between the horizontal, intrinsic connections and feedback projections (Gilbert and Sigman 2007; see below, *A Model of Top Down Control in V1*).

There is evidence that the contextual interactions involved in contour integration are mediated at least in part by long-range horizontal connections within V1. Horizontal connections formed by the axon collaterals of pyramidal neurons in superficial layers of V1, extend for long distances parallel to the

cortical surface (Gilbert and Wiesel 1979, Gilbert and Wiesel 1983, Gilbert and Wiesel 1989, Rockland and Lund 1982, Rockland and Lund 1983, Martin and Whitteridge 1984). In V1, a distance of ~1.5 mm separates cells with non-overlapping receptive fields, considering magnification factor, receptive field size, and scatter (Hubel and Wiesel, 1974). Thus horizontal connections spanning 6-8 mm allow communication between cells with widely separated receptive fields and enable V1 cells to integrate information over a larger part of visual space than that covered by their receptive fields. The connections formed by horizontal connections exhibit modular specificity, preferentially linking columns of neurons with similar response characteristics, such as preferred orientation (Ts'o et al. 1986, Bosking et al. 1997, Sincich and Blasdel 2001, Gilbert 1992, Gilbert and Wiesel 1989, Tanigawa et al. 2005, Schmidt et al. 1997, Stettler et al. 2002). The long-range projections also exhibit axial specificity connecting areas with receptive fields that lie along collinear axis (Bosking et al. 1997, Chisum et al. 2003). The visuotopic representation of intrinsic horizontal connections, at parafoveal eccentricities, originates from sites as far as 2° from either side of the target neurons (Stettler et al. 2002). This spatial extent exactly matches the maximum distance estimated over which collinear contour segments can be perceptually grouped (Li and Gilbert 2002). Thus the system of intrinsic connectivity within V1 selectively link neurons with co-oriented, co-axially aligned receptive fields and has been suggested to be at least partially responsible for mediating V1 contextual interactions that underlie contour integration and saliency (Gilbert 1992, Gilbert and Sigman 2007). The clustered intrinsic

connections have been seen in other visual areas, including V2, V3, and MT (Gilbert and Wiesel 1979, Gilbert and Wiesel 1983, Rockland and Lund 1982, Zeki 1976, Weller et al. 1984, Gilbert and Kelly 1975), in somatosensory and auditory cortex (DeFelipe et al. 1986, Jones et al. 1978, Imig and Brugge 1978) and in frontal cortex (Goldman and Nauta 1977).

The fact that some observed contextual influences in V1 show delayed effects has led to suggestions that feedback projections from V2 may play role in these contextual interactions (Angelucci et al. 2002, Shmuel et al. 2005). The underlying assumption is that influences from higher cortical areas, such as V2 and V4, would involve longer delays from the onset of a cell's response compared to influences arising from within the same cortical area (Lamme 1995). However, experiments involving measurements of conduction velocities show that feedback inputs from cortical areas are faster than that of intrinsic connections (Hupe et al. 2001, Bair et al. 2003, Pascual-Leone and Walsh 2001). This may suggest that intrinsic horizontal connections are the cause of the delayed contextual interactions. These observations suggest that it may be too simplistic to equate delayed influences to slow conduction velocities. Rather, such delays may reflect the time required for the cortical network to settle into a stable state, a process involving both intrinsic connections and feedback (Gilbert and Sigman 2007).

1.3. TOP-DOWN INFLUENCES IN VISUAL CORTEX

Besides the sensory context, neurons in primary visual cortex are also influenced by cognitive signals carrying the behavioral context and such cognitive influences are termed ad top-down control (for review see Gilbert and Sigman 2007). The general idea of top-down control is that complex behavioral information, such as attention, task or perceptual expectation, that is represented at higher stages of processing influences sensory processes occurring at lower stages. Thus, top-down influences can be viewed as one of the mechanisms within the brain that binds its computational state to behavioral requirements: higher order areas—where behavioral input is present—exert control over other cortical areas to select an appropriate algorithm that best serves the behavioral necessity. Some of the well characterized top-down influential factors include attention, anticipation and task-dependence.

One of the most common form of top-down control studied involves attending to a particular component of the visual scene. Attentional influences found in various cortical areas are diverse and varied depending on the nature of the attention engaged and the experimental paradigms utilized (Gilbert and Sigman 2007). Early attentional studies predominantly focused on spatial attention and analyzed neuronal properties when focus of attention was shifted into and out of their receptive fields or when attention was moved around different areas within the receptive field. A typical visual scene contains a great deal more information than we can process in a limited time and attention

serves to facilitate and select behaviorally relevant information. Perceptually, spatial attention can improve the processing of stimulus present at a given visual location (Posner et al. 1980) and neurophysiologically enhances neuronal responses evoked by a single stimulus appearing within the receptive field, an effect observed in neurons throughout the visual system (McAdams and Maunsell 1999a, Motter 1993, Mountcastle et al. 1987, Spitzer et al. 1988, Treue and Maunsell 1996). More importantly, attention also performs a selection role in extracting behaviorally pertinent stimuli from competing distractors (Desimone and Duncan, 1995) and neural correlates of such attentional selection have been observed in primate visual areas (Moran and Desimone 1985, Chelazzi et al. 1993, Chelazzi et al. 2001, Luck et al. 1997, Motter 1993, Reynolds et al. 1999, Reynolds and Desimone 2003). These studies found that, in monkeys trained to attend to one of the two stimuli presented within a receptive field of a neuron, the attended stimulus exerts preferential control over the neuronal response. Earlier spatial attention studies reported significant attentional influences in higher cortical areas like posterior parietal cortex (e.g., Goldberg and Wurtz 1972) and V4 (e.g., Moran and Desimone 1985, Haenny et al. 1988) and failed to convincingly demonstrate attentional effects in V1. But evidence from later studies, in which spatial attention was engaged within a complex and large context, suggested that V1 is equally susceptible to attentional influences (Motter 1993, Ito and Gilbert 1999, Crist et al. 2001, Li et al. 2006)(for reviews see Treue 2001, Posner and Gilbert 1999). For example, Motter demonstrated that V1 neurons show considerable spatial-attentional influences in the presence of

multiple competing stimuli in the visual field and that the degree of attentional modulation of V1 increase with the number of competing stimuli (Motter, 1993).

Besides attention to a visual location, attention can be directed to stimulus features to aid searching for a target in a visual scene. Feature-based attentional influences are seen in visual areas supporting the idea that top-down influences extend well beyond the notion of an attentional spotlight (Chelazzi et al. 1993, Chelazzi et al. 1998, Maunsell et al. 1991, Motter 1994, Treue and Trujillo 1999). When attention is directed towards a specific visual feature (e.g., color), cells with competing stimuli in their receptive fields show selective responses to the stimulus with the attended feature. Experiments on feature-based attention indicate that the top-down modulations are dependent on the feature encoded by the area, regardless of stimulus location: orientation or color (in area V4) or direction of movement (in area MT) (Bulthoff et al. 1998, Treue and Trujillo 1999, Reynolds et al. 2000, Giesbrecht et al. 2003). In addition to spatial and feature-based attention, psychophysical, imaging, and event-related-potential studies have demonstrated that attention can select whole objects. Directing attention to one feature of an object (e.g., its color) can cause all of the object's features (e.g., its orientation and motion) to be selected together, suggesting that attention to one feature spreads to other features of the same object (Duncan 1984, Egly et al. 1994, O'Craven et al. 1999, Blaser et al. 2000, Roelfsema et al. 1998, Reynolds et al. 2003, Yantis and Serences 2003). O'Craven et al. (1999) studied object-based attentional mechanisms, using fMRI, when subjects viewed stimuli consisting of a face transparently superimposed on a house, with one moving

and the other stationary. In different conditions, subjects attended to the face, the house or the motion. They found that attention to one feature of a stimulus (such as the motion of a moving face) enhanced the neural responses not only of that feature but also of the other feature of the same stimulus (for example, the face), compared with features of the other stimulus (for example, the house). Within V1, object-based attentional influences become evident during a curve tracing task (Roelfsema et al. 1998) or a perceptual discrimination task (Li et al. 2004). In monkeys trained for a curve-tracing task, V1 neurons responses were enhanced when the traced curve passed their receptive fields relative to when it did not (Roelfsema et al. 1998, Roelfsema et al. 2003).

Various models of top-down influences have been suggested to characterize the effects of attentional influences on neuronal responses. Studies showing enhanced attentional influences on neurons use a 'gain control' model to account for the observed multiplicative effect that is reminiscent of increasing the stimulus contrast (Treue and Trujillo 1999, Reynolds et al. 2000, Williford and Maunsell 2006). Alternatively, studies that involve competing stimuli within a receptive field invoke 'bias-competition' model, in which both the attended and unattended stimuli compete for the neuron's resources with the attended stimuli winning the competition (Desimone and Duncan 1995). But, neither of these models can explain the effects of top-down control in V1 where the resultant modulation in neuronal responses cannot be reduced to a simple gain alteration. In fact for V1, the strongest top-down influences are seen for the context-dependent integrative properties (Gilbert et al. 2000).

Top-down influences of attention, expectation and perceptual task show profound effects on the contextual interactions within V1. V1 neuronal responses to a contour embedded in a complex background are significantly stronger in attended condition compared to unattended condition (Li et al. 2006). Similarly, in a brightness discrimination task, V1 neurons responses to stimulus context are highly dependent on the attentional state of the animal (Ito and Gilbert 1999). Contextual facilitation is maximal when the monkey attends to the receptive field position and disappears when the animal distributes his attention or attends to positions away from the receptive field. In addition to spatial attention, contextual interactions in V1 have been shown to be under task-dependent top-down modulations. When an animal performs two different discrimination tasks on the same stimulus, context-dependent modulation of V1 neurons differ considerably dependent on whether the context is relevant for the discrimination task (Li et al. 2004). For example, V1 cells carry more information about positions of contextual parallel lines when the animal is engaged in a perceptual task (bisection task) involving the parallel lines, compared to when the animal performs a task unrelated to the parallel lines.

Contextual influences in V1 are also shaped by one's anticipation or expectation. For example, shape selectivity of V1 cells are modulated by the cue shapes presented to the animal (McManus et al. 2011). When the monkey is cued to look for a line, V1 cells are selective to collinear contours composed of co-aligned and iso-oriented line segments. On the other hand, when the monkey is cued to search for circles, the cells are selective to circular contours. Also, the

time course of the top-down influences seems to depend on expectation of the animal (Gilbert and Sigman 2007). In a discrimination task where the animal's expectation is set beforehand by cuing the type of the task, the differences in responses for different behavioral states can be seen from the first spike (Li et al. 2004). On the other hand, in a contour detection task where the location of the contour is unknown to the animal, the differences in the responses for attentional states develop after 100 ms (Li et al. 2006). Thus in V1, the strongest top-down influences are not seen on neuronal responses to simple stimuli, such as a single oriented line segment, but on responses to more realistic, complex stimuli, whereby neural activity and visual perception are shaped by contextual interactions.

1.4 A MODEL OF TOP-DOWN CONTROL IN V1

Given that the top-down control in V1 involves interactions between sensory context and behavioral contexts like attention or anticipation, it is still unclear what circuitry is involved in mediating such interactions. It has been suggested that in V1, top-down control could be mediated by interactions between feedback connections carrying the behavioral context and intrinsic horizontal connections providing the sensory context (Gilbert and Sigman, 2007). As mentioned before, long-range horizontal connections in V1 enable their targets to integrate information over larger area outside their classical receptive field (for reviews see Gilbert and Wiesel 1992, Gilbert 1992, Gilbert 1993). Even though the anatomical connectivity of the intrinsic connections is stable over

time, the functional efficacy of these connections can be under top-down influence provided by the feedback projections. That is, depending on the current task, the effective connectivity within the cortical network may be dynamically reset by behavioral context, thereby enriching the task-relevant information carried by neural responses. Our theory is that although a neuron may receive thousands of inputs from intrinsic connections, only a small fraction of these connections are expressed, or effective, under any particular behavioral context. Thus, behaviorally relevant sensory information can be extracted from V1 by creating ad-hoc, on-demand functional networks by selectively gating only appropriate horizontal connections between select set of neurons. This allows neurons to multiplex their function in a state-dependent manner, taking on different functional roles when the animal performs different perceptual tasks. In this manner, rather than performing a stereotyped operation on sensory input, each cortical area can be seen as an 'adaptive processor' running different algorithms under the instruction of feedback from higher order areas (Gilbert and Sigman, 2007).

Recent evidences of brain states have come from imaging and electro-physiological studies that reveal spontaneous fluctuations of depolarizations and hyper-polarizations that create distinct states (Fox et al. 2005, Petersen et al. 2003, Cossart et al. 2003). Experiments involving diverse techniques such as voltage-senstive dye imaging, fMRI and intracellular electrophysiological recordings have found large fluctuations in spontaneous fluctuations in neural activity even in the absence of sensory stimulus (Fox et al. 2005, Fox et al. 2006,

Arieli et al. 1996, Petersen et al. 2003, Stern et al. 1997, Lampl et al. 1999, Cossart et al. 2003, Haider et al. 2006). These default UP and DOWN states have been shown to have great impact on stimulus evoked activity and have been observed in awake animals (Anderson et al. 2000). Such discrete brain states may play a role in presetting the cortical state dependent on expectation or perceptual cuing (Kastner et al. 1999, Thut et al. 2006, Ress et al. 2000). While it's tempting to hypothesize that these different states can be viewed as equivalent to setting behavioral expectations, there is need for evidence to directly link dynamics of these brain states to behavioral task switching.

1.5 TOP-DOWN CONTROL AND PERCEPTUAL LEARNING

Experiments of top-down influences and perceptual learning provides us additional insight into the mechanisms of top-down control. Perceptual learning is an implicit type of learning that results in an improvement of a discrimination task with practice. The task involves learning to discriminate stimuli depending on their low-level attributes and can be found in all sensory modalities. For example, in touch modality, it can be the need to discriminate between various vibrating tactile stimulations (Recanzone et al. 1992); in sound modality, it can be the requirement to discriminate between various frequencies (Recanzone et al. 1993). In the visual system, perceptual learning has been to shown to occur for motion perception (Ball and Sekuler 1982), depth perception (Ramachandran and Braddick 1973), spatial frequency (Fiorentini and Berardi 1980), orientation discrimination, texture discrimination (Karni and Sagi 1991), brightness

discrimination (Kapadia et al. 1995, Ito et al. 1998) and spatial position discrimination (Fahle and Morgan 1996, Crist et al. 1997, Li et al. 2004) (for review see Gilbert et al. 2001). In most cases perceptual learning occurs with no or minimal feedback (Ball and Sekuler 1987, Karni and Sagi 1991, Fahle et al. 1995) and is highly specific to stimulus parameters used in training (Fiorentini and Berardi 1980, Ball and Sekuler 1987, Crist et al. 1997) and doesn't transfer to other similar discrimination tasks (Fahle and Morgan 1996). In early visual cortex, perceptual learning has been shown to result in sharpening of orientation tuning of V1 neurons in animals trained on an orientation-discrimination task (Schoups et al. 2001) and a change in contextual influences in animals trained on a shape-discrimination task (Crist et al. 2001, Li et al. 2004). Learning to search a target embedded in an array of distractors has been shown to be associated with a shift in the representation of the trained target from higher to lower retinotopically mapped visual cortical areas such as V1 and V2 (Sigman et al. 2005, Gilbert and Sigman 2000).

Researchers have found that the functional changes associated with perceptual learning are only expressed during the trained task. For instance the task-dependent differential tuning seen in V1 neuronal responses during 5-bar perceptual discrimination task is present, when the animal is engaged in the discrimination tasks, but not when the animal is passively fixating or engaged in an unrelated task (Li et al. 2004, Sigman and Gilbert 2007). This suggests that neurons are capable of multiplexing their function on a moment-to-moment basis, performing different analyses according to the behavioral context. It's also been

suggested that the changes induced during perceptual learning themselves require top-down influences (Sigman and Gilbert 2007). In the experiments involving target search, even though the subjects are exposed seven times more often to untrained orientations, the learning is present only for the target orientation (Gilbert and Sigman 2000), suggesting that learning of this task just do not result from perceptual exposure, but must involve top-down influences of attention. Thus, it would seem that both encoding and recall of the learned information are under top-down control.

Our model of top-down control discussed (see *A Model of Top-Down Control in V1*) above provides us within an alternate to Hebbian rule of learning. We have suggested that for a given task, feedback connections selectively gate subsets of horizontal connections so that behaviorally relevant stimulus information can be extracted effectively. Such a system then would be required to identify the subsets of horizontal inputs that are useful for performance of that task and to have those same connections expressed during the task. This is accomplished by training in the task, that is, learning a task would link appropriate intrinsic connections to the feedback connections specific for that task.

1.6 INFORMATION ENCODING MECHANISMS IN VISUAL CORTEX

We have argued that top-down control enables lower-order cortical areas, especially the primary visual cortex, to encode information about more complex stimulus attributes by selectively gating subset of neurons, dictated by behavioral

requirements and such selective gating allows for functional multiplexing of neurons in a behavioral state-dependent manner. This then raises the question: what is the nature of the neural mechanisms involved in such network state-switching? Does it involve responses of individual neurons or modulation of network interactions or both?

One way in which top-down signal encodes behaviorally relevant visual information is by the modulation of tuning properties of individual neurons. As mentioned before, spatial attention have been shown to facilitate neural responses similar to the effect seen when stimulus contrast is increased. These results have led some researchers to suggest that top-down influences operates by 'gain-control' model, wherein, attention co-opts the circuits that mediate contrast gain control and operates by increasing the effective contrast of the attended stimulus (Treue and Trujillo 1999, Reynolds et al. 2000, Williford and Maunsell 2006). But, the effect of top-down influences observed in V1 cannot be easily explained by this model. Top-down control can result in sharpening of tuning characteristics of V1 neurons (Schoups et al. 2001) or task-dependent modulations of the shape of the contextual tuning curves of the cells (Crist et al. 2001, Li et al. 2004). For example, a V1 cell's tuning for various positions of contextual parallel lines is more modulated (and hence more informative of the locations of the parallel lines), when an animal is performing a discrimination task involving parallel stimuli, compared to the modulation in the tuning when the animal is performing a task unrelated to the parallel lines (Li et al. 2004). The top-down influence here is not the gain control seen in other attentional studies,

since the shape change in the tuning curve cannot be explained by a multiplicative change in responses. Rather the tuning properties of the cells are affected in a complex, non-linear fashion so that the neurons carry more information about a behaviorally relevant stimulus attribute.

Another substrate for top-down influences of perceptual processes can be the functional interactions between neurons in a cortical network. The visual system rapidly groups diverse image features into coherent representations of objects and how this is accomplished in our brain is a matter of intense debate (Ghose and Maunsell 1999, Golledge et al. 1996, Gray 1999, Shadlen and Movshon 1999, Singer 1999). One proposed theory that synchronous neural activity provides a temporal code for grouping together parts of an object (Eckhorn et al. 1988, Gray 1999, Gray et al. 1989, Singer and Gray 1995, von der Malsburg and Schneider 1986). Numerous studies have experimentally evaluated this theory and researchers have found both evidence for (Gray et al. 1989, Fries et al. 2001, Engel et al. 1991, Castelo-Branco et al. 2000, Gail et al. 2000) and against (Lamme and Spekreijse 1998, Thiele and Stoner 2003, Palanca and DeAngelis, 2005; for review, see Gray 1999) this theory. Studies of top-down control have found some evidence for role of synchronous activity in extracting behaviorally relevant information. Synchrony has been suggested as a mechanism of selective attention (Fries et al. 2001, Steinmetz et al. 2000) and sensorimotor integration (Bland and Oddie 2001, Riehle et al. 1997, Roelfsema et al. 1997). Results from our current study further suggests that top-down control operates in V1 by coupling and decoupling neurons in an ensemble

network to encode salient visual information and that the perceptual strategy used to perform a visual task can dictate the direction of task-dependent changes in the neuronal interactions.

One of the main focus of systems neuroscience is to understand how populations of neurons encode information and guide behavior. It's well known that cortical neurons respond with variable strength to repeated presentations of identical stimuli. This variability is often shared among neurons, and such correlations in trial-to-trial responsiveness, termed noise correlations, can substantially affect the amount of information encoded by a neuronal population (Shadlen and Newsome 1998, Abbott and Dayan 1999, Averback et al. 2006, Zohary et al. 1994). If the noise in individual neurons is independent, averaging the responses of many neurons will lead to a very accurate estimate of the mean, no matter how noisy the individual neurons are. If, however, there are positive correlations in the trial-to-trial fluctuations of the responses of pairs of neurons, then the shared variability can never be averaged out, leading to a more variable and less accurate estimate of the mean activity in the population (Shadlen et al. 1996, Shadlen and Newsome 1998, Zohary et al. 1994). Attention and other forms of top-down control could alter the reliability of neuronal representations by modulating the amount of noise that is shared across a population of neurons. Recent studies have shown that shared variability in responses of cortical neurons can be affected by attention (Cohen and Maunsell 2009, Mitchell et al. 2009, Poort et al. 2009), perceptual tasks (Romo et al. 2003, Cohen and Newsome 2008, Vaadia et al. 1995) and perceptual learning (Gutnisky and

Dragoi 2008, Gu et al. 2011). It is more likely that the top-down influences improve the population code accuracy by decorrelating the noise in a neuronal network (Cohen and Maunsell 2009, Mitchell et al. 2009, Gu et al. 2011).

1.7. CURRENT WORK

In this study, we tested our hypothesis that the top-down control in V1 operates by modulating functional connectivity between V1 neurons, by studying task-dependent changes in V1 interactions in awake behaving monkeys. Two monkeys were implanted with chronic multi-electrode arrays in the superficial layers of V1 that enabled us to simultaneously monitor activity of multiple V1 neurons. Monkeys were trained to perform 5-line perceptual discrimination tasks and contour detection tasks. The 5-line perceptual tasks were spatial discrimination tasks involving judgement of relative offset of parallel or collinear bars (Li et al. 2004). The contour detection tasks involved searching a collinear contour embedded in complex background (Li et al. 2006). We used these perceptual tasks as they have been previously shown to engage top-down modulation of contextual interactions in V1 neurons (Li et al. 2004, Li et al. 2006). We recorded both spiking activity and local field potentials (LFPs) in V1. We estimated V1 interactions by measuring spiking correlations and coherence in LFP signals between V1 sites that encoded different stimulus components and studied changes in these interactions as a function of task.

Our results reinforce our earlier findings that the functional properties of cortical neurons are subject to top-down influences. This is not simply a matter

of enhancing responses but a change in the information carried by neurons that is relevant to the task at hand. The top-down control of behaviorally relevant sensory information in V1 was achieved by task-dependent changes in neuronal interactions, specifically LFP-LFP coherence and not by selective suppression of cells that encode for behaviorally irrelevant information. Both measures of neuronal activity, single unit recording of spiking activity and LFP measurements, showed the top-down modulation of contextual interactions. Interestingly, the direction of task dependent changes in coherence depended on the nature of the task, with increases in coherence between parallel sites for the bisection task and decreases between collinear sites for the vernier discrimination task. We propose that this may be related to the different perceptual strategies employed in the two tasks – perceptual grouping of side-by-side elements in 3-line bisection and perceptual segregation between the collinear elements for the vernier task (see Discussion for details). If this idea is correct, then one would expect an increase in LFP coherence between collinear sites that involves perceptual grouping. To test this idea we used a task requiring grouping of collinear elements, a contour detection task. Here, consistent with our hypothesis, the task induced an increase in coherence between collinear sites.

Top-down control in V1 also captured task-relevant stimuli information by decorrelating the noise in V1 neurons responses, thereby increasing the information content present in V1 network. The V1 neuronal ensemble was most informative for the stimuli with greatest discrimination difficulty. Also, both

changes in tuning characteristics and correlational structure were equally important in achieving the task-driven changes in the V1 information content.

2. TOP-DOWN CONTROL OF LATERAL INTERACTIONS IN VISUAL CORTEX.

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2.1 SUMMARY

Primary visual cortex(V1) changes its computation according to the perceptual task being performed. We propose that this cognitive modulation of V1 results from gating of V1 intrinsic connections. To test this idea, using behavioral paradigms that engage top-down modulation of V1 contextual interactions, we recorded from chronically implanted electrode arrays in macaques. We observed task-dependent changes in both spiking and LFP interactions. The direction of the changes in aggregate activity (LFP), depended on perceptual strategy: perceptual grouping increased LFP interactions between sites crucial for the task, while perceptual segregation lowered the LFP interactions. Using spiking activity as our measure, we found that the

behaviorally-driven changes in correlation structure between neurons dramatically increased the stimulus-related information they convey; this additional increase in encoded information at neuronal ensemble level equals that obtained from task-driven reconfigurations of neural tuning curves.The improvements in information encoding were strongest for stimuli with greatest discrimination difficulty.

2.2 RESULTS

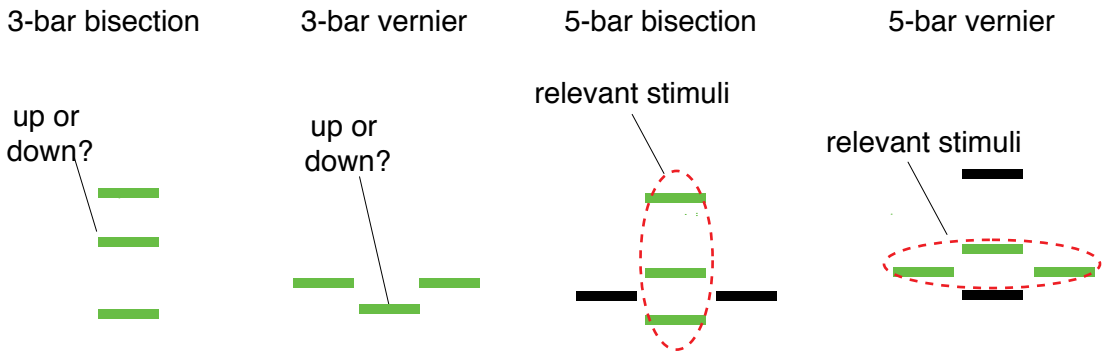
2.2.1 TASK-DEPENDENT MODULATION OF V1 CONTEXTUAL INTERACTIONS

To study the top-down control of effective V1 connectivity, we trained animals to perform two discrimination tasks—bisection and vernier—on a 5-bar stimulus (Fig. 2.1, top panel; see Stimuli and Task design for details). In the bisection task, the animals discriminated the relative distance between the parallel bars, while the vernier task involved discriminating the direction of offset of collinear bars. For a given 5-bar stimulus, the two tasks engaged different stimulus components: the bisection task involved the relative position of the parallel bars; the vernier task relied on the spatial offset of the collinear bars. Using chronically implanted multi-electrode arrays, we recorded from V1 cells whose receptive fields (RFs) were positioned over the various parts of the 5-bar stimulus (Fig. 2.1, bottom panel). During a recording session, the central bar was fixed in the RF center of an arbitrarily selected V1 neuron; all the bars were oriented to match the preferred orientation of this neuron. We then studied the

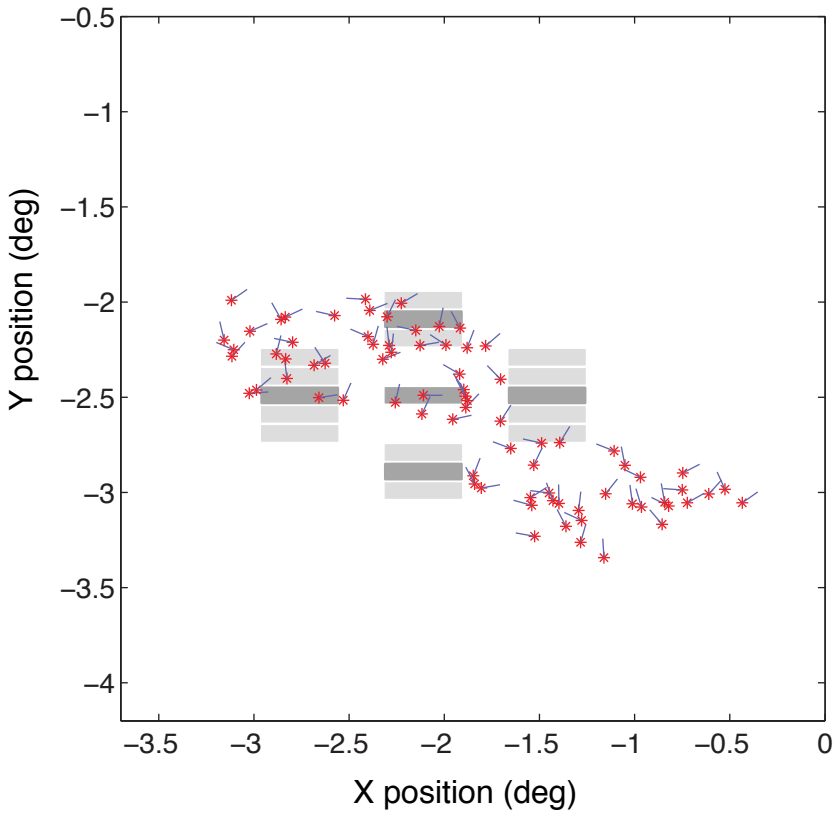
effect of top-down signals on individual neuronal responses and network interactions in V1, using both neuronal spiking and the LFP as measures of cortical activity.

Figure 2.1. 5-bar perceptual discrimination task. ***Top,*** Stimulus design for 5-bar perceptual discrimination tasks. The *bisection task* required the animal to judge if the center bar was closer to the bottom or top parallel flank. In the *vernier task*, the animal had to judge if the center bar was above or below the collinear flanks. When performing these tasks with the 5-bar stimulus, the animal was cued to the task to be performed by color: green indicated which bars had to be used for discrimination. ***Bottom,*** Receptive field (RF) centers of the neurons near the electrodes in the array implanted in one monkey and the stimulus arrangement in one sample recording session. The red stars give the RF centers and the oriented line segments at each red star indicate the orientation preference of the neurons. The grey bars show the size and position of the 5 bars used in the stimulus.

Perceptual discrimination task



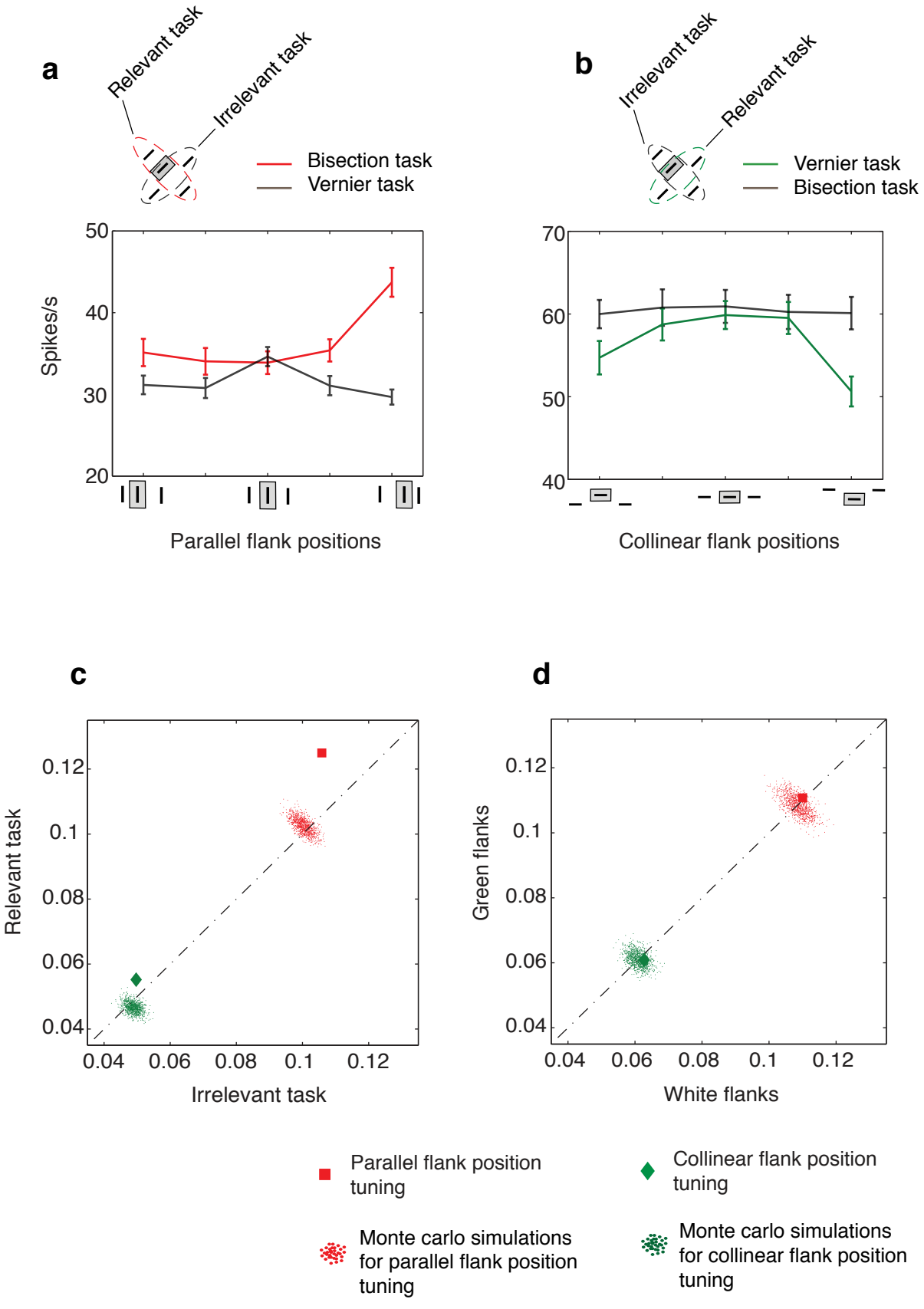
Sample recording arrangement



2.2.1.1 SPIKING ACTIVITY

As we showed previously (Li et al. 2004), the functional properties of V1 neurons, as measured by their spiking activity, were task-dependent. V1 neurons were differentially modulated by positional offset of either the parallel or collinear flanks (Fig. 2.2) when the animals performed different discrimination tasks. For example, the tuning curves for various parallel-bar positions (Fig. 2.2a) differed in a task-dependent fashion, whereby cells showed more modulation when the animals were performing the bisection task, in which parallel-flank position was the task relevant attribute, compared to the vernier task where the same parallel flanks were task irrelevant. In other words, the cell's tuning for the parallel-bar positions was more informative during the bisection task, when the animal had to use this information (see our mutual information analysis below). On the other hand, the cell's tuning was less modulated and hence less informative of the parallel-bar positions during the vernier task, when this information would be of no use for the animal. Similarly, the degree of modulation in tuning for collinear-flank position depended on its relevance to the task of vernier discrimination (Fig. 2.2b).

Figure 2.2. Task-dependent modulations of contextual interactions in V1 spiking activity. ***a,*** Responses of a sample V1 cell for various positions of parallel flanks under the relevant (red line) and irrelevant task conditions (black line). Higher modulation in the cell's response was observed when the animal performed a task involving parallel bars (relevant task, bisection task; mutual information, 0.1303) compared to when the animal performed a task involving collinear bars (irrelevant task, vernier task; mutual information, 0.0771). ***b,*** Responses of another sample V1 cell for various collinear flank positions under the two task conditions (green line, relevant, vernier task; black line, irrelevant, bisection task). The cell showed higher modulation for the relevant task condition (mutual information: vernier, relevant task, 0.0836 ; bisection, irrelevant task, 0.0072). ***c,*** Population averaged mutual information (bits) for the parallel (red square) and collinear (green diamond) flank position tuning under the two task conditions (N=57). The red and green clouds are the population mean mutual information for 1000 Monte Carlo simulations of the spike data. (see Methods for details). ***d,*** Similar to ***c***, except the animal performed a visual task in the hemifield opposite to that of the recorded RFs. Error bars in ***a*** and ***b*** represent ±s.e.m.


a
Relevant task
Irrelevant task
Bisection task
Vernier task
Spikes/s
50
40
30
20
Parallel flank positions
b
Irrelevant task
Relevant task
Vernier task
Bisection task
70
60
50
40
Collinear flank positions
c
Relevant task
0.12
0.1
0.08
0.06
0.04
0.04 0.06 0.08 0.1 0.12
Irrelevant task
d
Green flanks
0.12
0.1
0.08
0.06
0.04
0.04 0.06 0.08 0.1 0.12
White flanks
Parallel flank position tuning
Collinear flank position tuning
Monte carlo simulations for parallel flank position tuning
Monte carlo simulations for collinear flank position tuning

We used ‘mutual information’ between the spiking response and the stimulus to quantify the task-dependent modulations in the tuning curves of V1 cells. Mutual information provides us with a measure of how reliably an ideal observer could categorize a stimulus presented in a single trial based on the spike count of a cell during the trial. Over the population (N=57, Fig. 2.2c), the average mutual information for both the parallel-flank and collinear-flank position tuning was higher in the relevant task. Moreover, it was clearly higher than that calculated by Monte Carlo simulations of the data (the red and green clouds), where the data were randomly assigned to the two task conditions. Therefore, V1 responses carried significantly more information about a stimulus context when the context was task-relevant.

The animals were cued to the task by color: green was used for relevant bars and white for irrelevant ones. To exclude the possibility that the changes in mutual information could arise purely from this manipulation, we measured mutual information present in V1 cells’ responses during a control task in which the animal performed a visual task in the hemifield opposite to that of the 5-bar stimulus. We found no significant differences in the population mean mutual information during the control task: the values for average mutual information for both the parallel-flank and collinear-flank position tuning were close to the diagonal within the Monte Carlo simulations (Fig. 2.2d, N=57). These results suggest that the observed task-dependent changes in V1 neuronal responses were not due to the change in stimulus color but rather due to the change in the behavioral relevance of the stimulus.

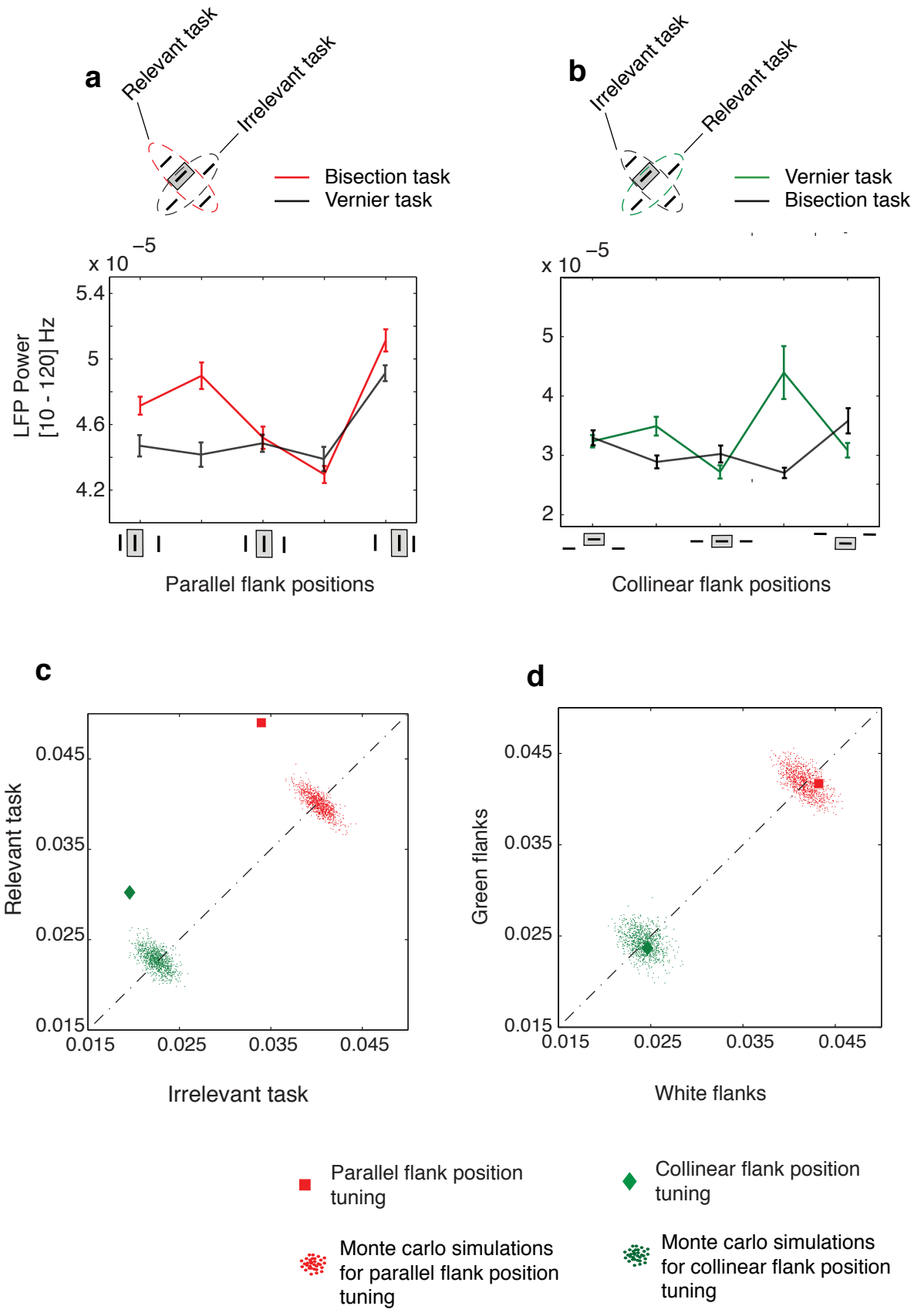
2.2.1.2 LFP RESPONSE

We performed a similar analysis based on LFPs, which reflect aggregate activity over a large population of neurons. Considerable task-dependent modulation of contextual effects was seen in the power present in LFP frequencies (Fig. 2.3). We measured the power in the frequencies 10-120 Hz from 100 ms after stimulus onset and analyzed its dependency on the flank positions under the two task conditions. LFP power tuning, in 10-120 Hz, for both the parallel-flank positions and the collinear-flank positions was more modulated in the relevant task than in the irrelevant task (Fig. 2.3a,b). Similar to spiking activity, the mean mutual information was significantly higher during the task where the flanks were task relevant, and clearly separated from Monte Carlo simulations (Fig. 2.3c, N=80). Moreover, there was no significant difference in the population-averaged mutual information during the control task (Fig. 2.3d). These results together indicate that V1 LFPs represent both stimulus context (parallel or collinear flank positions) and behavioral context (bisection or vernier task).

To explore frequency dependence of the task-dependent modulation, we analyzed the LFP power in the 0-30 Hz band separately from the power in 31-120 Hz ranges. LFP power in both the frequency bands showed similar task-dependent effects of mutual information, suggesting that in V1 both low and high frequencies represent information about behavioral context.

Given that V1 activity reflected the task-dependent contextual interactions, this requires that top-down signals carrying task information induce the network to process behaviorally relevant sensory information. This could be achieved either by suppressing the activity of neurons encoding information that is irrelevant to the task, or by altering the effective connectivity between cortical sites representing stimulus context that are either relevant or irrelevant to the task.

Figure 2.3. Task-driven changes of contextual interactions in V1 LFP power. ***a,*** LFP power tuning (10-120 Hz; 100-500 ms after stimulus onset) of a sample V1 site for various positions of parallel flanks under the relevant (red line) and irrelevant (black line) task conditions. LFP power was highly modulated and informative when the animal performed a task involving parallel bars (relevant task: bisection; mutual information, 0.0870) compared to when the animal performed a task involving collinear bars (irrelevant task: vernier; mutual information, 0.0563). ***b,*** Another sample V1 site's LFP power tuning for various collinear flank positions under the two task conditions (green line, relevant, vernier task; black line, irrelevant, bisection task). LFP power at this site showed higher modulation for the relevant task condition (mutual information: relevant task 0.2352, irrelevant task 0.1398). ***c,*** Population averaged mutual information (bits) for the parallel (red square) and collinear (green diamond) flank position tuning under the two task conditions (N=60). The red and green clouds are the population mean mutual information for 1000 Monte Carlo simulations of the LFP data. (see Methods for details). ***d,*** Similar to ***c***, except the animal was performing a visual task in the hemifield opposite to that of the recording visual field. Error bars in ***a*** and ***b*** represent ±s.e.m.

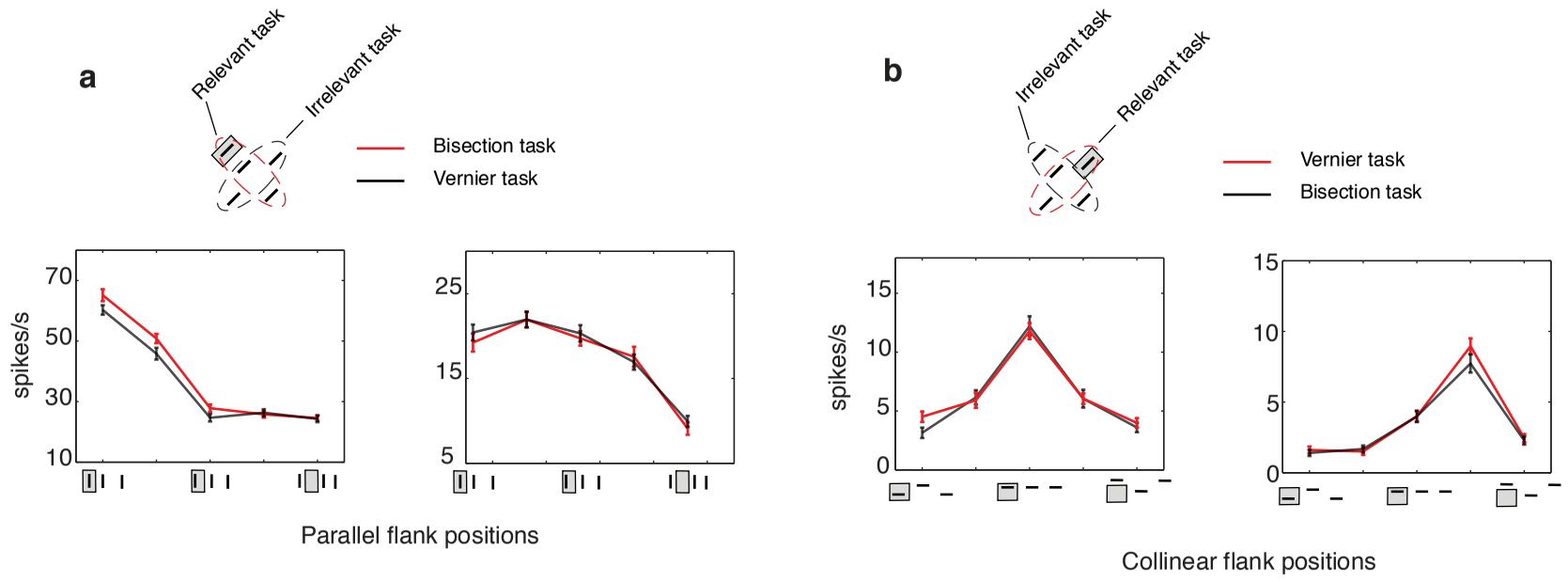

a
Relevant task
Irrelevant task
Bisection task
Vernier task
x 10 −5
5.4
5
4.6
4.2
LFP Power [10 - 120] Hz
Parallel flank positions
b
Irrelevant task
Relevant task
Vernier task
Bisection task
x 10 −5
5
4
3
2
Collinear flank positions
c
0.045
0.035
0.025
0.015
Relevant task
0.015
0.025
0.035
0.045
Irrelevant task
d
0.045
0.035
0.025
0.015
Green flanks
0.015
0.025
0.035
0.045
White flanks
Parallel flank position tuning
Collinear flank position tuning
Monte carlo simulations for parallel flank position tuning
Monte carlo simulations for collinear flank position tuning

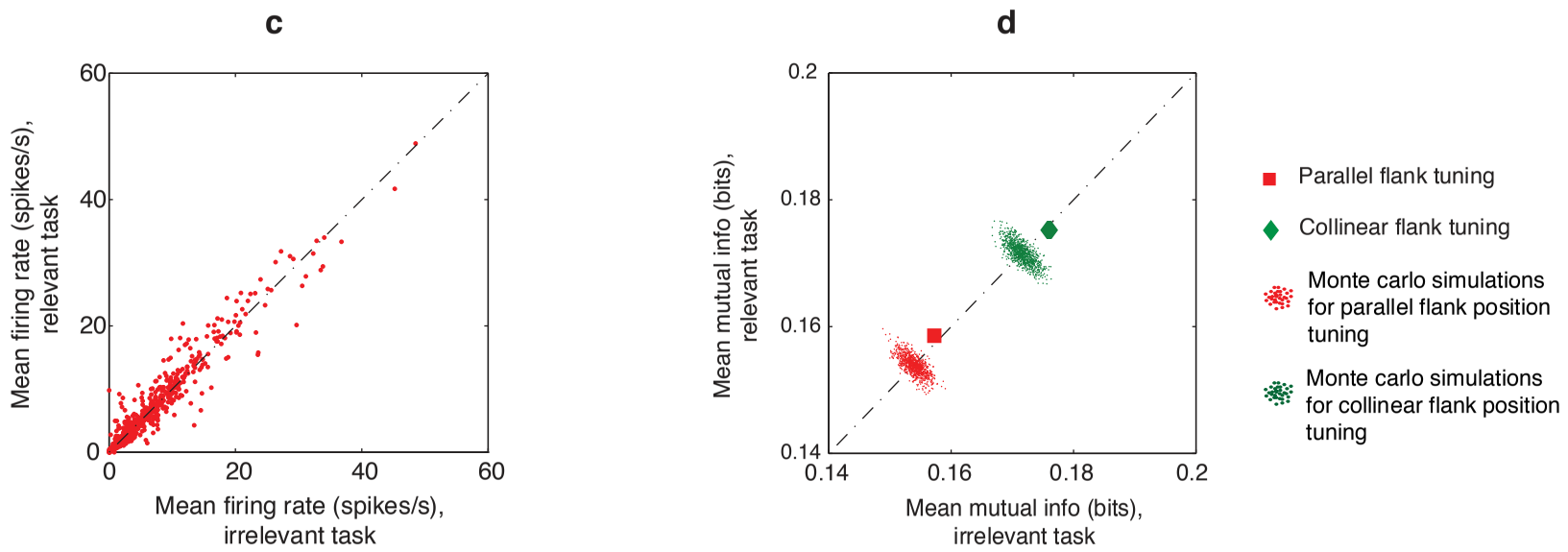
2.2.2 NEURAL REPRESENTATION OF THE FLANKS

First, we tested the possibility that the top-down control of contextual modulation works by suppressing or enhancing the V1 neurons that encode the various stimulus context. We compared the response properties of cells whose RFs were over the parallel or collinear flanks, when the animal performed the bisection or vernier discrimination task (Fig. 2.4). The flanking sites did not show significant task dependent changes in their responses for various positions of the flank stimuli in their receptive fields. For example, V1 spiking neurons (Fig. 2.4a) that encoded parallel flank stimuli did not change their responses according to whether the information about the parallel flanks was required for the discrimination task. Similarly, the sites that represented the collinear flank stimuli (Fig. 2.4b) did not show task-dependent changes in their responses.

The same trend is seen over the population that represented the flankers: the mean firing rate of V1 cells (Fig. 2.4c, N=729) showed no significant task-dependent changes. Though the responses of these sites encoded the various flank positions, there was no task-dependent changes in the encoded mutual information (Fig. 2.4d; the mean mutual information for both parallel and collinear flank sites was away from the Monte Carlo clouds but the mean values lie on the diagonal). This suggests that top-down influences did not operate by suppressing or facilitating V1 neurons that encode the stimulus context.

Figure 2.4. Flank channel responses. ***a***, Spiking responses of two sample neurons, with receptive fields over one of the parallel flanks, under the bisection (red line) and vernier task (black line). For various positions of parallel flanks within their RFs, these cells showed no difference in their responses for the two task conditions. ***b,*** Two sample collinear flank channel responses under the vernier (red line) and bisection task (black line), showing no task-driven changes in their responses for different collinear flank positions. ***c,*** Population plot for mean firing rate of the flank channels (both parallel and collinear flanks) under the relevant and irrelevant task conditions, demonstrating no significant changes in their firing rate (N=729). ***d,*** Population plot for mean mutual information encoded by the flanking sites (red, parallel flanks; green, collinear flanks) under the relevant and irrelevant task conditions. These sites showed no significant task-dependent changes in the encoded mutual information (N=729). Error bars in ***a*** and ***b*** represent ±s.e.m.


a
Relevant task
Irrelevant task
Bisection task
Vernier task
spikes/s
70
50
30
10
25
15
5
Parallel flank positions
b
Irrelevant task
Relevant task
Vernier task
Bisection task
spikes/s
15
10
5
0
15
10
5
0
Collinear flank positions


c
Mean firing rate (spikes/s), relevant task
60
40
20
0
0
20
40
60
Mean firing rate (spikes/s), irrelevant task
d
Mean mutual info (bits), relevant task
0.2
0.18
0.16
0.14
0.14
0.16
0.18
0.2
Mean mutual info (bits), irrelevant task
Parallel flank tuning
Collinear flank tuning
Monte carlo simulations for parallel flank position tuning
Monte carlo simulations for collinear flank position tuning

2.2.3 TOP-DOWN MODULATION OF SPIKING CORRELATIONS

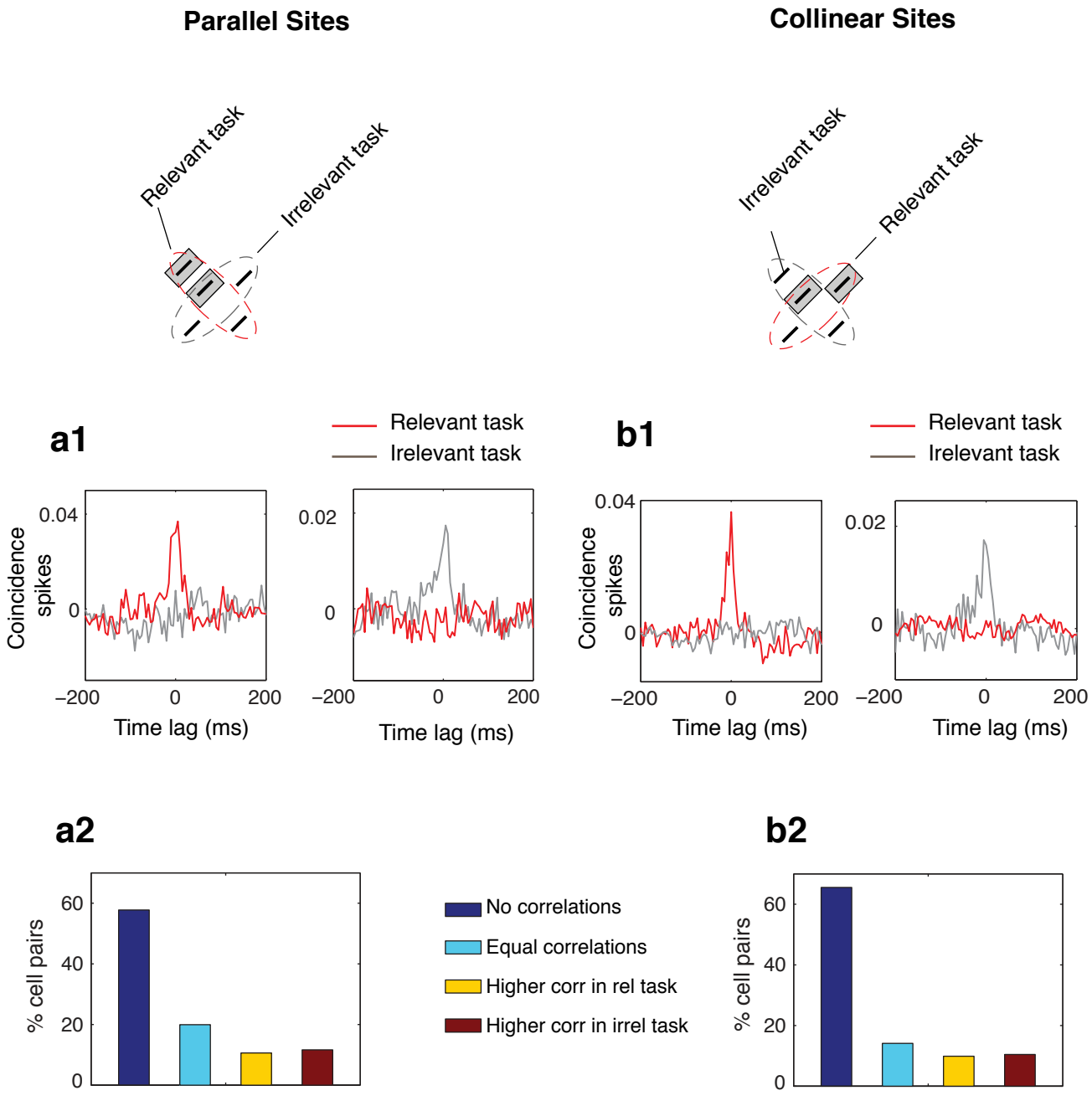
To test the alternate possibility that the task-dependent V1 contextual modulations is caused by the top-down driven changes in functional connectivity, we studied the spiking interactions between sites that encoded different stimulus contexts (see Fig. 2.5 for recording sites configuration). The interactions were calculated by cross-correlation analysis, which provides a measure of effective connectivity by calculating the probability, at different time intervals, of a spike in one cell given the occurrence of a spike in a second cell.

We did observe task-dependent changes in spiking cross-correlations. Figure 6a1 shows the normalized cross-correlations observed in two sample pairs of V1 neurons. In each pair, one neuron's RF was located at the position of the center bar and the other neuron's RF was positioned over one of the parallel flanking bars. The two correlograms were calculated under the two task conditions (red, relevant task; grey, irrelevant task). Though both cell pairs showed significant task-driven differences in their correlations, the direction of changes were not consistent. The cell-pair on the left, representing side-by-side bar positions (Fig. 2.5a1), showed a peaked correlogram when then animal did the bisection task (red curve) and noise level correlations when the animal did the vernier task (grey curve). The cell-pair on the right showed opposite trend in their interactions: higher correlations during the irrelevant, vernier task.

Similar results were observed for collinear V1 sites (Fig. 2.5b1). Some collinear cell pairs showed higher correlations during the relevant task, that is, when the animal performed the vernier task using the collinear bars (Fig. 2.5b1, left panel) while some other cell pairs showed higher correlations during the irrelevant, bisection task involving the parallel bars (Fig. 2.5b1, right panel).

Over the population of recorded V1 cell pairs (Fig. 2.5a2, b2; N=395 parallel pairs; 362 collinear pairs), 40% of the cell-pairs showed significant correlations, and of these, a subset (50%) showed task dependency of correlation strength. Though this reflected a significant task dependence of effective connectivity, stronger correlations could be observed either under the task relevant or task irrelevant conditions.

Figure 2.5. Top-down modulations of spiking correlations. Spiking correlations showed task-dependent changes. ***a1,*** Normalized cross-correlograms of two sample V1 cell pairs with parallel RFs under different task conditions. The red curves give the correlations when the animal performed the bisection task, where the flank positions were task-relevant, and the grey curves show correlations when the animal performed the vernier task, where they were irrelevant to the task. One cell pair (left) had higher correlations during the relevant task and the other (right) had higher correlations during the irrelevant task. ***b1,*** same as a1, except for two sample collinear V1 sites. Here the relevant task was the vernier task (red curves) and the irrelevant task was the bisection task (grey curves). Again, one cell pair showed stronger correlations for the relevant task while the other for the irrelevant task. ***a2,b2***, Distribution of cross-correlations of all the recorded parallel (N=395) and collinear (N=362) cell pairs respectively.


Parallel Sites
Collinear Sites
Relevant task
Irrelevant task
Irrelevant task
Relevant task
a1
b1
Relevant task
Irelevant task
Coincidence spikes
0.04
0
0.02
−200
200
Time lag (ms)
a2
b2
% cell pairs
60
40
20
No correlations
Equal correlations
Higher corr in rel task
Higher corr in irrel task

2.2.4 TOP-DOWN MODULATION OF LFP INTERACTIONS

The finding of task dependent changes in spike correlations motivated us to obtain a measure of cortical interactions reflecting the integrated connectivity over multicellular ensembles. To measure functional interactions between cortical sites at the population level, we calculated LFP coherence between V1 sites representing different stimulus components under the two tasks. We found significant task driven changes in LFP coherence for both parallel (Fig. 2.6a1-a4, N=382) and collinear sites (Fig. 2.6b1-b4, N=296). We computed the coherence between parallel sites during bisection task involving parallel bars (Fig. 2.6a1, dark red curve, relevant task) and the coherence between the same sites during vernier (irrelevant) task involving collinear bars (Fig. 2.6a2, darker grey curve, irrelevant task). Since the animals were cued to the task by the flanks' color, we determined the contribution of color to LFP coherence: we measured coherence during a control task performed in the hemifield opposite to the recorded RF locations, and the stimuli were identical to those used for the experimental task (the lighter red and grey curves in Fig. 2.6a1,a2). Subtracting the coherence under the control condition from the task condition provided an accurate estimate of coherence changes due purely to the nature of the task being performed (Fig. 2.6a3, red curve, relevant task; black curve, irrelevant task). The coherence between parallel sites was higher in the bisection task when the animals were using the stimulus (parallel bars) encoded by these sites compared to the vernier task, where these sites were irrelevant to the task. These task-driven changes

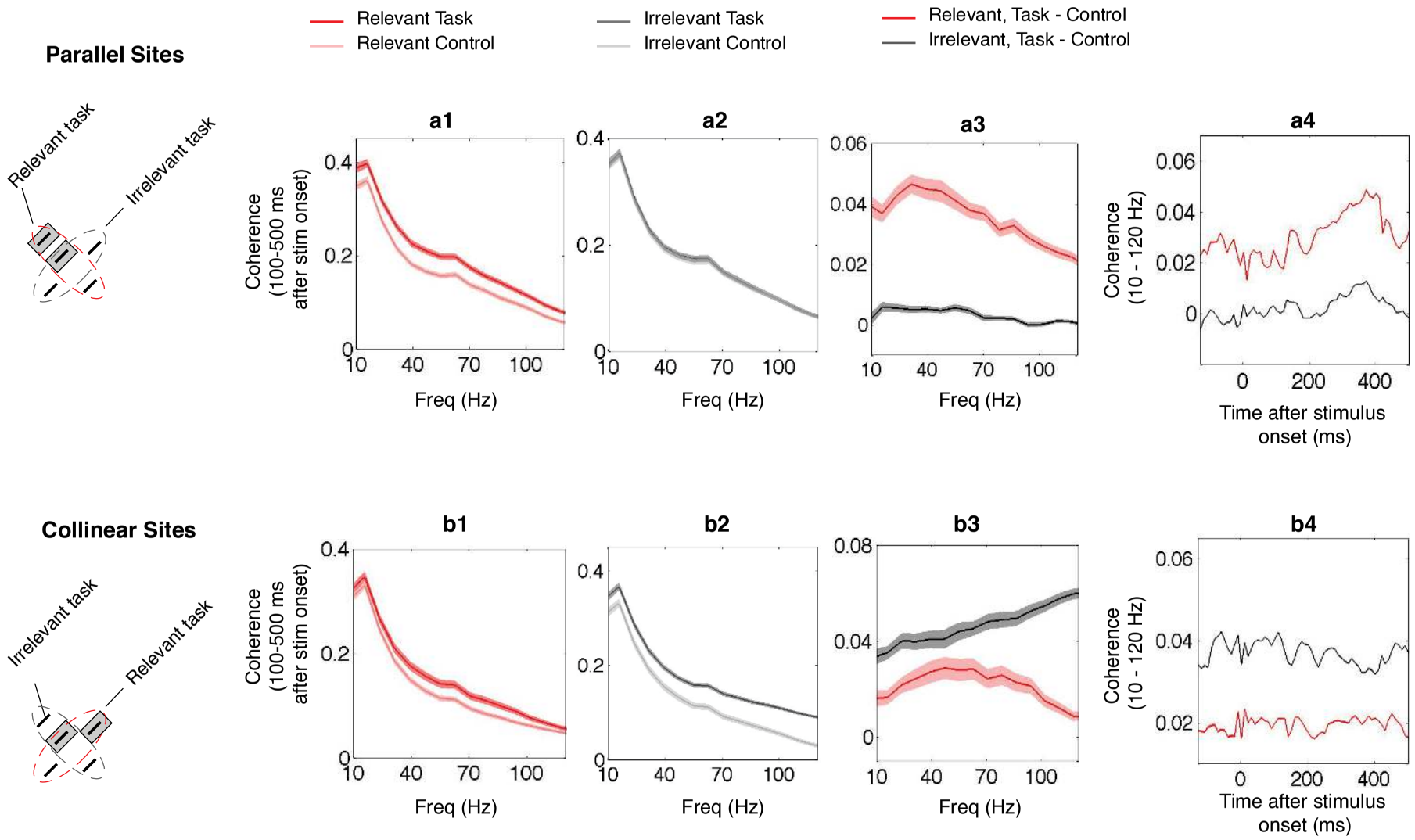
were present in both lower and higher frequencies, ranging from 10-120 Hz and for the entire trial period (Fig. 2.6a4). Interestingly, these differences emerged even before the stimulus onset, suggesting that task expectancy can preset computational state of visual cortex (see Discussion).

The collinear sites also displayed task-dependent changes in LFP coherence (Fig. 2.6b1-b3). For these sites, the coherence was *lower* in the relevant vernier task compared to the irrelevant bisection task (Fig. 2.6b3). Similar to parallel sites, the difference in coherence between the collinear sites for the two tasks was observed in both lower and higher frequencies, and emerged during the pre-stimulus period and persisted for the entire trial period (Fig. 2.6b4).

The above results suggest that top-down control in V1 operated by modifying the connectivity among the sites. However, the direction of changes differed between the two classes of sites: strong increased connectivity under the relevant (bisection) task for parallel sites and decreased connectivity under the relevant (vernier) task for collinear sites. This difference may have resulted from the perceptual strategies employed for the two tasks: bisection involves grouping of the central and flanking bars using the Gestalt perceptual grouping law of proximity. Vernier discrimination however, involves segregation of the collinear bars, breaking the percept of continuity (see discussion). Thus, grouping of parallel bars increased LFP-LFP interactions between V1 parallel sites while segregation of collinear lines reduced interactions between the collinear sites. To

test this idea, we had the animal perform a task that required grouping, rather than segregation, of collinear sites: a contour detection task.

Figure 2.6. Top-down influences of LFP coherence in V1. (***a1-a3),*** Population averaged coherence plots of parallel V1 sites (as shown in the diagram on the left) under different task conditions (N=382). ***a1,*** Shift-corrected LFP-LFP coherence from 100 to 500 ms after stimulus onset, as a function of frequency. The dark red curve gives the coherence during the relevant, bisection task involving parallel bars. The lighter red curve gives the coherence between the same sites during a control task, when the animal performed a perceptual task on the opposite hemifield when the same 5-bar stimulus was presented over the recording location. ***a2,*** LFP coherence during the irrelevant, vernier task (dark grey) and the corresponding control stimuli (lighter grey). ***a3,*** Perception-related LFP coherence between parallel sites for the relevant (red) and irrelevant (black) task conditions. These curves were calculated as the difference between the curves in ***a1*** and ***a2***. These sites increased their coherence when the animal performed the task that was relevant to the sites. (***b1-b3),*** Population coherence plots of collinear V1 sites (as shown in the diagram on the left) under different task conditions (N=296). Same conventions as ***a1-a3***. Note that these sites reduced their coherence during the relevant task (***b3***). ***a4,b4,*** Time course of task-dependent modulations in LFP coherence between the parallel and collinear sites respectively. Here mean coherence in 10-120 Hz is plotted as a function of time after stimulus presentation. Task-driven differences in LFP coherence, for both parallel and collinear sites, were present for the entire trial period and emerged before stimulus presentation. The shaded area represent ±s.e.m .

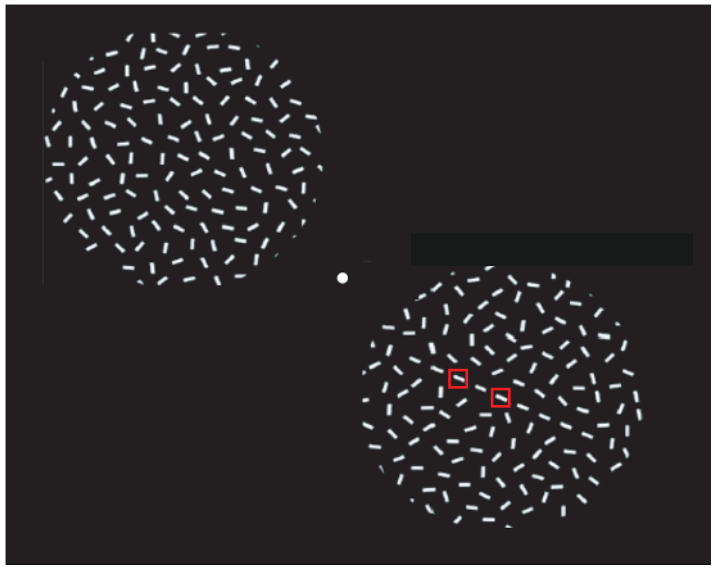

Relevant Task
Relevant Control
Irrelevant Task
Irrelevant Control
Relevant, Task - Control
Irrelevant, Task - Control
Parallel Sites
Relevant task
Irrelevant task
a1
a2
a3
a4
Coherence (100-500 ms after stim onset)
Freq (Hz)
Coherence (10 - 120 Hz)
Time after stimulus onset (ms)
Collinear Sites
Irrelevant task
Relevant task
b1
b2
b3
b4

2.2.5 CONTOUR DETECTION TASK

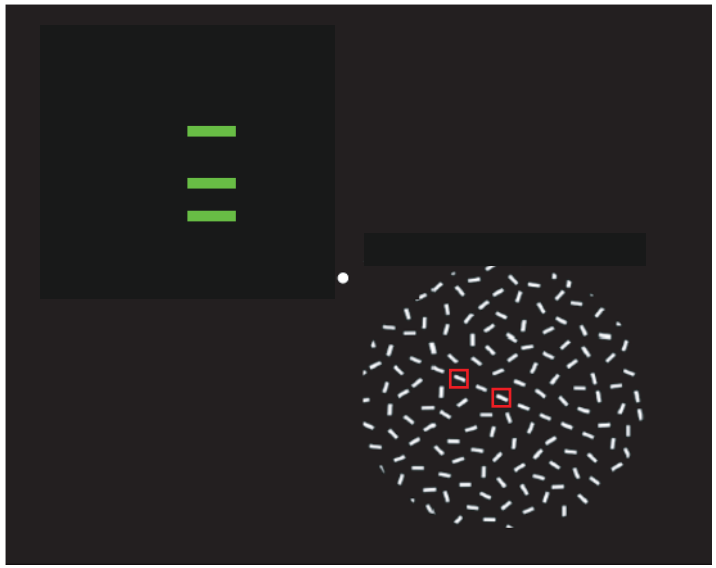
In this task, a contour composed of collinear bars was embedded in a complex background, and the contour saliency depended on the number of collinear elements. The animals were trained to detect the presence of the contour embedded in one of the two stimulus patches (Fig. 2.7a). Previous work in V1 has shown that more salient contours increases facilitation of spiking neurons and that the degree of collinear facilitation is subject to top-down influences: it is strongest when animals perform task involving contours (Li et al. 2006). To understand if V1 network properties could account for this task-dependent facilitation, we compared network interactions during the contour detection task and a control (attend-away) task unrelated to contour stimulus (Fig. 2.7b; see Materials and Methods). Both spike and LFP data were collected from V1 neurons that lay along the contour (Fig. 2.7a,b red squares represent the RFs of the recorded cells).

Figure 2.7. Contour detection task. ***Left (a),*** The animal was trained to detect the presence of a contour in one of the two patches of randomly positioned and oriented lines. ***Right, (b)*** Control task where the animal performed a perceptual task in the hemifield opposite to the visual field location of the RFs of the recorded neurons. During the control task, the contour stimulus embedded in the complex background was presented in the RF of the recorded neuron.

(a) Contour detection task



(b) Control (unattended) task

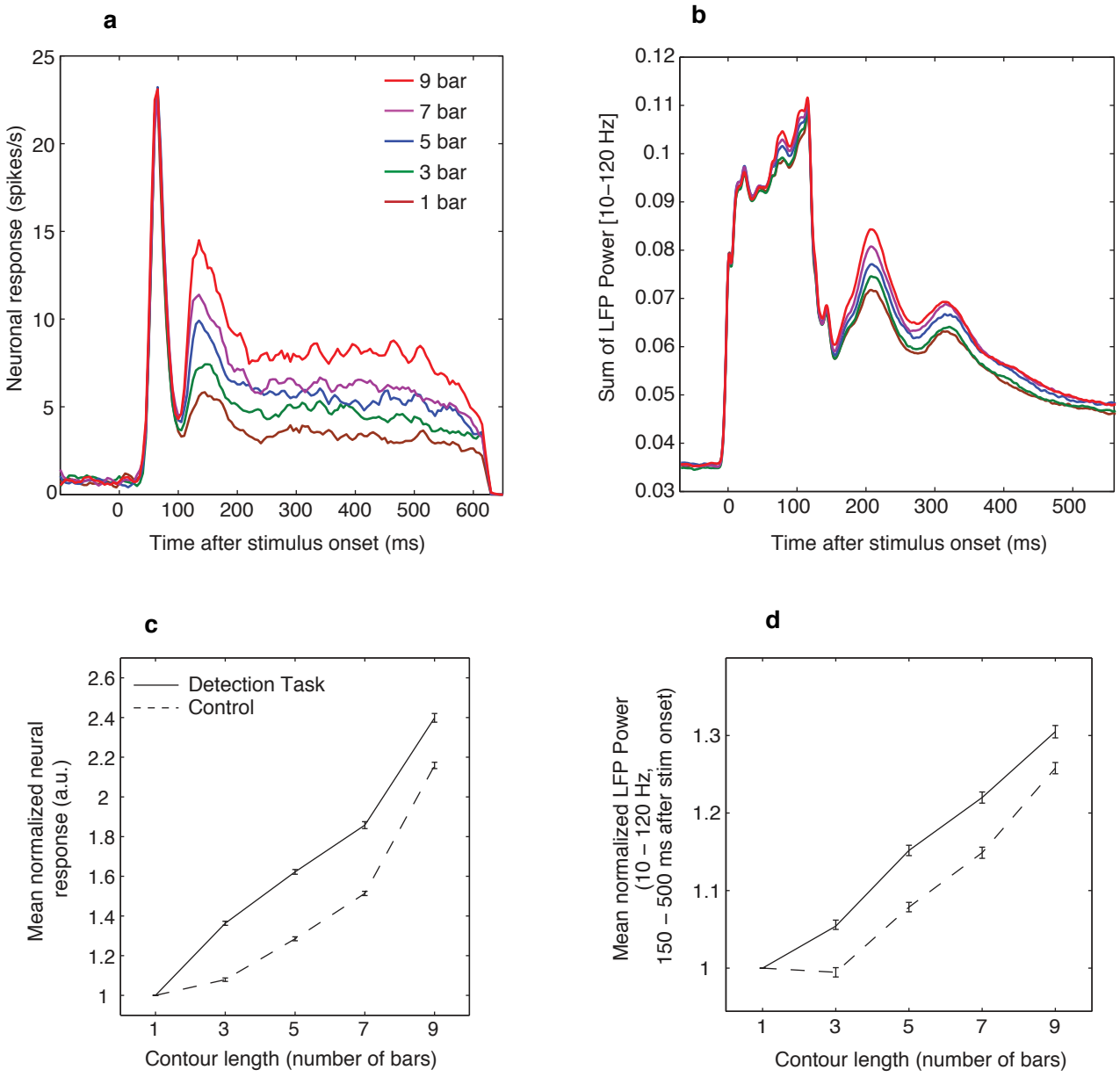


2.2.6 V1 CONTOUR INTEGRATIVE PROPERTIES

As in our previous study (Li et al. 2006), we found that V1 neurons encoded contour saliency: contours of longer lengths resulted in enhanced firing (Fig. 2.8a). The contour related facilitation in spiking activity emerged after 100 ms of stimulus presentation. Over the population, neuronal responses to the longest (most salient) embedded contour were more than double the response to a single bar in the RF, surrounded by the complex background (Fig. 2.8a, red curve). A degree of collinear facilitation in V1 activity was present even during the 'attend-away' task (Fig. 2.8c, broken curve) but the amount of facilitation was less than the facilitation observed when the animal was actively searching for a contour.

In V1, we observed contour facilitation in the frequency domain of LFPs. Figure 9b shows population averaged time course of LFP power in 10-120 Hz for contours of varying lengths: longer contours result in higher LFP power. The contour related facilitation emerged at a similar delay following stimulus onset as the spiking activity. The power in these frequencies was higher for longer and hence more salient contours (Fig. 2.8d, solid curve; ~30% facilitation for longest contour). Similar to spiking activity, contour saliency related facilitation of LFP power was higher during the detection task and the facilitation was reduced in the unattended case (Fig. 2.8d, broken curve).

Figure 2.8. V1 contour integrative properties. ***a,*** Population averaged spiking response profiles of V1 neurons for contours of varying lengths during the contour detection task (N=87). Longer, salient contours resulted in sustained higher spiking responses, starting ~100 ms following stimulus onset. ***b,*** Mean population V1 LFP power in the 10-120 Hz range for contours of varying length during the contour detection task. The LFP power was estimated using a 120 ms wide sliding window. The values on the x-axis indicate the center time-point of the moving window (e.g. 0 marks the time-window starting at 60 ms before stimulus onset and ending at 60 ms after stimulus onset, so that the power begins to rise when the forward end of the window reaches 50 ms after stimulus onset). LFP power increased with contour length, with a similar delay as that seen in spiking activity (N=54). ***c,*** Population averaged spiking activity in V1 neurons, for various contours, during the contour detection (solid curve) and unattended (broken curve) tasks. The mean neural response for each contour length, within a task condition, was normalized by the response to the 1-bar stimulus. The contour-related facilitation in neural responses was higher when the animal was actively looking for the contour (i.e., during the contour detection task) ***d,*** Population mean normalized LFP power in V1 as a function of contour length for the detection and unattended tasks (solid and broken curves respectively). The mean neural response for a contour length was normalized by the response to the 1-bar stimulus. The error bars represent ±s.e.m.


a
b
c
d
9 bar
7 bar
5 bar
3 bar
1 bar
Neuronal response (spikes/s)
Time after stimulus onset (ms)
Sum of LFP Power [10–120 Hz]
Time after stimulus onset (ms)
Detection Task
Control
Mean normalized neural response (a.u.)
Contour length (number of bars)
Mean normalized LFP Power (10 – 120 Hz, 150 – 500 ms after stim onset)
Contour length (number of bars)

2.2.7 V1 INTERACTIONS AND TOP-DOWN INFLUENCES DURING CONTOUR INTEGRATION

To understand how the V1 network was involved in perceptual integration of collinear lines into a contour, we analyzed both spiking and LFP-LFP interactions between V1 neurons that lay along the contour embedded within the complex background.

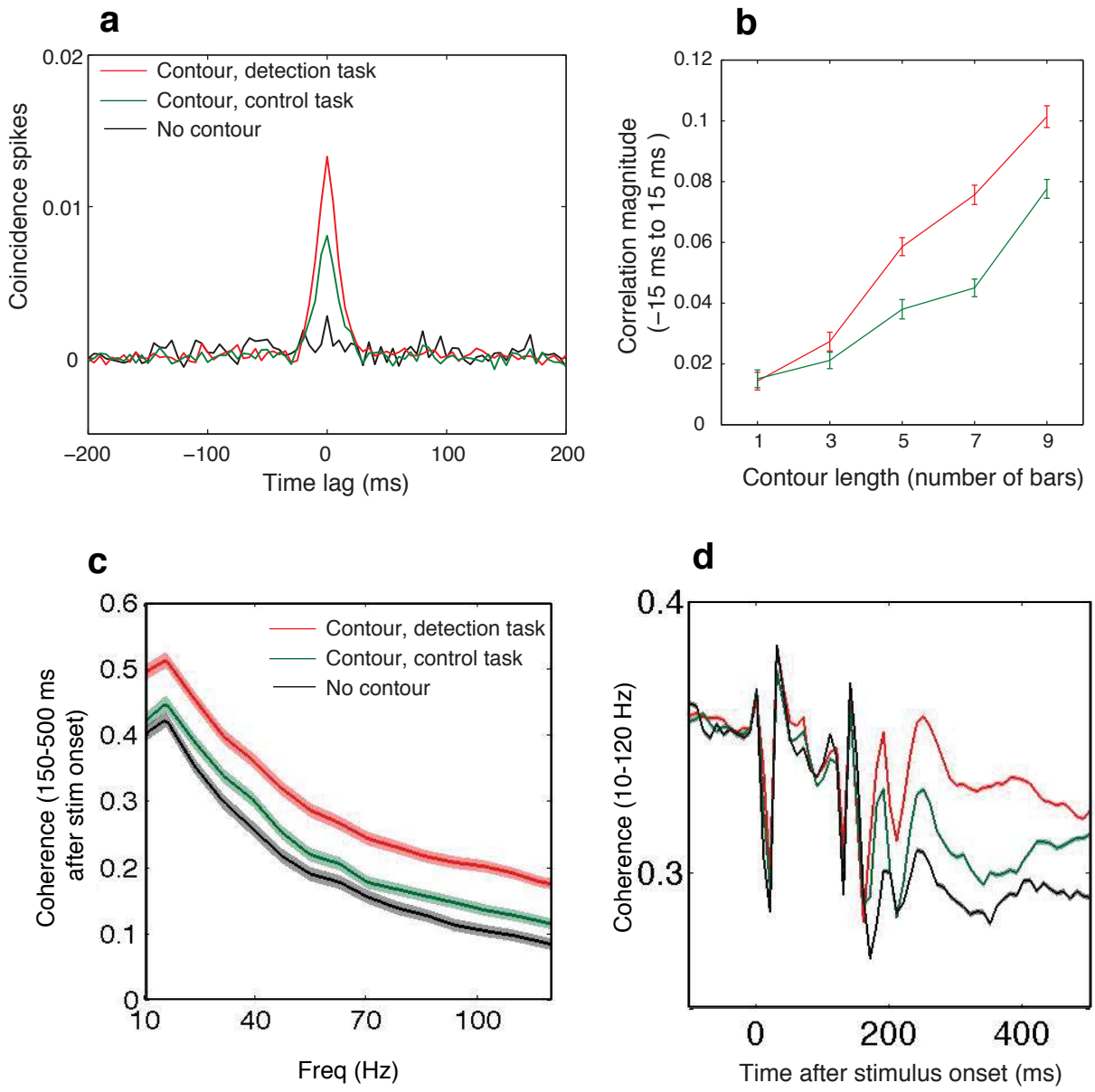
2.2.7.1 SPIKING CORRELATIONS

Figure 10a shows NCCGs for the population of recorded V1 cells whose RFs were on the contour and with similar orientation preference (< 10 degrees difference; N=354 pairs), during the contour detection task. When there was a contour present through the cells' RFs, the cells were correlated significantly (correlation magnitude: 0.058; red curve, Fig. 2.9a). However, when there was no contour present, there was little or no correlation between the V1 sites (Fig. 2.9a, black curve; correlation magnitude: 0.0019; $p < 0.001$ for the difference between contour and no contour conditions). The correlations between these V1 sites also captured the contour saliency information: longer contours produced stronger correlations (Fig. 2.9b, red curve).

We also observed task-related effects of contour facilitation in the spiking interactions between V1 contour sites. Although V1 neurons showed significant correlations when the contour elements were unrelated to the animal's behavior

(i.e., the attend-away task), the observed correlation (correlation magnitude, 0.0384) was significantly less than that observed during the contour detection task (Fig. 2.9a, green curve, attend-away task and red curve, contour detection task; $p < 0.001$ for the difference between contour detection and attend-away conditions). Thus, the top-down influences boosted the spiking interactions between V1 sites that encoded the contour when its saliency was behaviorally relevant.

Figure 2.9. Task-dependent modulation of contour related V1 interactions. ***a,*** Population spiking cross-correlations (normalized) between collinear V1 sites in the absence of a contour, in the presence of a contour during contour detection task and in the presence of a contour during the 'attend-away' task (black, red and green curves respectively; N=354). ***b,*** Correlation magnitude as a function of contour length and task conditions. The red curve gives the magnitude of correlations for different contour lengths when the animal performed the contour detection task, while the black curve gives the same information for the 'attend-away' task. ***c,*** LFP-LFP coherence over the population of collinear sites (N=452) as a function of frequency for no contour (black), contour during detection task (red) and contour during 'attend-away' task (green). Shift-corrected, mean LFP coherence from 150 to 500 ms after the stimulus onset is shown. ***d,*** Time course of mean population LFP coherence for different stimulus and task conditions (no contour, black; contour during detection task, red; contour during control task, green). Sustained differences in coherence were observed after 150 ms of stimulus presentation. The shaded area in ***c*** and ***d,*** and the error bars in ***b*** represent ±s.e.m.


a
Contour, detection task
Contour, control task
No contour
Coincidence spikes
0.02
0.01
0
−200
−100
0
100
200
Time lag (ms)
b
Correlation magnitude
(−15 ms to 15 ms)
0.12
0.1
0.08
0.06
0.04
0.02
0
1
3
5
7
9
Contour length (number of bars)
c
Contour, detection task
Contour, control task
No contour
Coherence (150-500 ms
after stim onset)
0.6
0.5
0.4
0.3
0.2
0.1
0
10
40
70
100
Freq (Hz)
d
Coherence (10-120 Hz)
0.4
0.3
0
200
400
Time after stimulus onset (ms)

2.2.7.2 LFP INTERACTIONS

Similar to spiking correlations, LFP coherence between V1 sites captured contour-related information. During the contour detection task, collinearly arranged sites increased their coherence when there was a contour present in the noise background compared to when there was no contour (Fig. 2.9c, red and black curve respectively). This contour-dependent increase in coherence was observed in both low and high frequencies, from 10-120 Hz and emerged at ~150 ms after stimulus onset and lasted the entire stimulus period (Fig. 2.9d).

Collinear V1 sites along a contour also showed task-related effects in their LFP coherence. Similar to spiking correlations, the LFP coherence between the contour encoding sites was higher when the animal was actively looking for a contour compared to when the animal was doing an unrelated task (Fig. 2.9c, green curve). This difference in coherence between the two task conditions emerged after 150 ms of stimulus presentation (Fig. 2.9d) and was present in frequencies from 10-120 Hz.

The finding that the contour detection task, which requires grouping of collinear lines, increased LFP interactions supports the idea that perceptual strategy determines the direction of task-dependent modulation of LFP coherence. Both grouping tasks, 3-line bisection and contour detection, increased V1 interactions.

2.2.8 TOP-DOWN INFLUENCES OF V1 NOISE CORRELATIONS

The information carried by a neuronal ensemble is dependent on noise correlations – whether neurons exhibit similar trial-to-trial fluctuations in their responses (Lee et al. 1998, Bair et al. 2001, Shadlen et al. 1996, Abbott and Dayan 1999, Panzeri et al. 1999, Averback et al. 2006). Since noise correlations can affect the encoding accuracy of a cortical network, we investigated how behavioral context affected V1 noise correlations.

Our 5-bar discrimination experiments allowed us to study V1 noise correlation dynamics in three different conditions (Fig. 2.10a): When the animal: (1) performed a task involving the stimuli within the RFs of the cell pair under consideration (Fig. 2.10a, right panel); (2) attended to the same location, but performed a task that did not involve the flanking neuron's RF (Fig. 2.10a, middle panel); and (3) attended away from the location of the RFs of recorded cell pair (Fig. 2.10a, left panel). For example, for a pair of parallel V1 sites, these 3 different cases would be: (1) bisection task involving parallel bars, (2) vernier task involving collinear bars, and (3) 'attend-away' task involving the stimulus in the opposite hemi-field. These different task conditions could then be used to dissociate noise correlation changes due to spatial attention and due to the perceptual task. Since both parallel and collinear sites showed similar trends in the attention and task effect of noise correlations, we combined the data from both classes in our analysis.

We observed that V1 neurons decreased their noise correlations by ~60% when the animals shifted their attention from the opposite hemifield to the visual field of the recorded neurons (Fig. 2.10b). The mean noise correlation was 0.0381 for the 'attend-away' task and 0.0141 when the animals attended to the location of the receptive fields of the recorded neurons ($p<10^{-6}$ for difference). We saw a more substantial reduction in noise correlations when the animal performed a perceptual task at the receptive field locations of the recorded neurons (mean 0.0041; $p<10^{-6}$ for difference between the 'attend-away' task and the discrimination task at the RFs).

We further examined whether the top-down modulation of noise correlations depended on the tuning similarity between neurons. We studied the changes in noise correlations between V1 neurons as a function of their 'signal correlations' (i.e., the correlation between their tuning curves), for the 3 different task conditions (Fig. 2.10c). Across task conditions similarly tuned cells (positive signal correlation) showed higher noise correlations than cells with different tuning (negative signal correlation, all the curves in Fig. 2.10c). This result agrees with previous studies of noise correlations in various cortical areas and supports the idea that cells with similar tuning are subject to shared noise sources through their common inputs. Furthermore, task-driven reduction in noise correlations was observed for all cell pairs independent of their tuning similarity (signal correlation) of the cells. Both similarly and dissimilarly tuned cells reduced their correlations when the monkey shifted attention and performed a perceptual task using the stimulus encoded by the neurons. The biggest reduction in noise

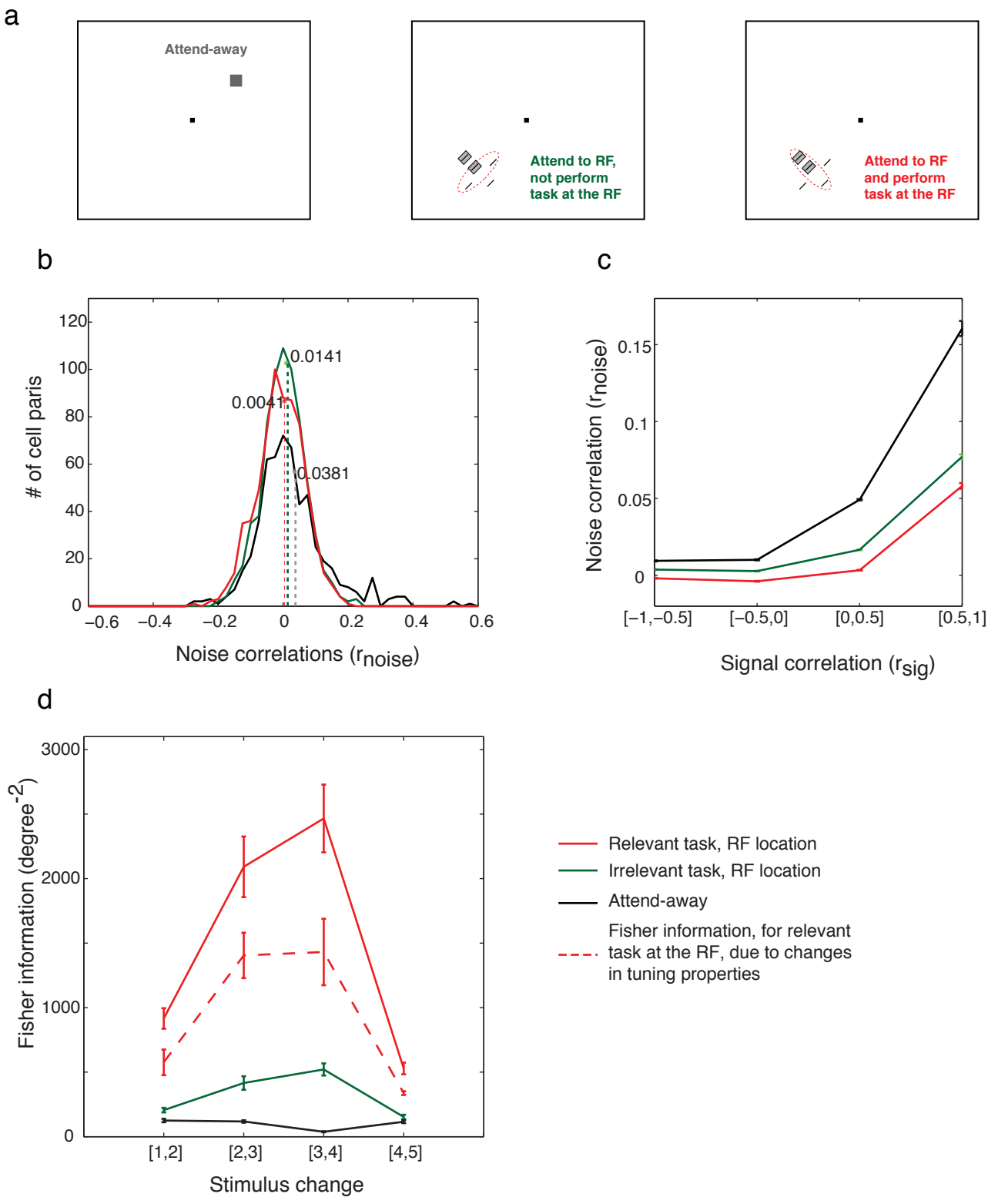
correlations, however, was seen for similarly tuned cells (Fig. 2.10c, compare the curves for positive signal correlations). Since positive noise correlations between similarly tuned cells limit information capacity more than positive correlations between neurons with dissimilar tuning, this is precisely the result we expect to maximize information capacity in V1 (Panzeri et al. 1999, Averback et al. 2006).

We consolidated these information theoretic observations into a quantitative measurement of the accuracy of the V1 population code. To do this, we calculated the Fisher information (I_F) present in our recorded neuronal ensembles, both when the stimulus was behaviorally relevant and when it was not. The inverse of the Fisher information is the minimum averaged squared error for an unbiased estimator of an encoded stimulus attribute and thus sets a limit on the population code accuracy (Abbott and Dayan, 1999). With attention directed toward the RFs of the recorded ensemble, but not specifically toward the encoded stimulus attribute (e.g., when the animal performed the bisection task but the encoded stimulus attribute was collinear offset), we observed a moderate increase in the Fisher information (Fig. 2.10d). The Fisher information increased much more considerably when the animal was engaged in a perceptual task involving the encoded stimulus attribute (Fig. 2.10d), and this increase was highest for the stimuli with the smallest lateral or collinear displacements and thus the highest discrimination difficulty (Fig. 2.10d, 2nd and 3rd point on the red curve). The results from our previous studies (Li et al. 2004, Li et al. 2006, McManus et al. 2011) and our current work show that changes in the tuning curves of individual neurons, as well as changes in the structure of noise

correlations in the network, can both improve the population code for a stimulus attribute. We therefore investigated how these two components of the behaviorally-driven change in network activity separately affect the population code. We found that the changes in the shape of the tuning curves of the neurons in the ensemble contributed 50-60% of the observed information enhancement (Fig. 2.10d, dashed red curve) and 40-50% of the information increase derived from changes in correlational structure.

Thus, various forms of top-down control result in different degrees of modulation of noise correlations. While changes in the locus of attention decreased correlations, performing a perceptual task involving the stimulus encoded by the neurons further reduced the noise correlations and substantially increased the information content of the V1 network.

Figure 2.10. Top-down modulation of V1 neuronal variability. ***a,*** Depiction of the different task conditions used in the study. *Left panel*, 'attend-away' condition, when the animal performed a task in the hemifield opposite to the RF of the recorded neurons. *Middle panel*, when the animal attended to the recorded locations, but performed a task not involving the stimuli encoded by the cell pair *Right panel*, when the animal attended and performed a perceptual task at the recorded locations involving the stimuli encoded by the cell pair ***b,*** Comparison of noise correlations in V1 for the three task conditions given in ***a***. Black, 'attend-away'; green, attention at the recorded locations; red, attention and task at the recorded locations. The mean of each distribution is given by the numbers near the curves and the colored dotted lines. Noise correlations reduced considerably when the animal performed a task compared to just shift in attention. ***c,*** Comparison of relationship between signal and noise correlations in the three task conditions; same conventions as before. Similarly tuned neurons (neurons with positive signal correlations) showed the largest task-driven reduction in noise correlations. N=702 for all the cases. ***d,*** Fisher information for the recorded V1 population under the three task conditions (black, attend-away; green, attention at the recorded locations; red, task at the recorded locations), as a function of change in stimulus bar positions. V1 network carried substantially more information about the stimulus when the animal performed a task at the recorded locations (red curve) and the network was most informative for stimuli with greatest discrimination difficulty (condition 2 versus 3 and 3 versus 4). The dotted red curve provides a measure of task-dependent increase in information, when the animal performed a perceptual task at the recorded location, due to changes in neuronal tuning properties (see Methods). Error bars represent ±s.e.m.


a
Attend-away
Attend to RF, not perform task at the RF
Attend to RF and perform task at the RF
b
# of cell paris
0.0141
0.0041
0.0381
Noise correlations (rnoise)
c
Noise correlation (rnoise)
[−1,−0.5]
[−0.5,0]
[0,0.5]
[0.5,1]
Signal correlation (rsig)
d
Fisher information (degree-2)
Stimulus change
[1,2]
[2,3]
[3,4]
[4,5]
Relevant task, RF location
Irrelevant task, RF location
Attend-away
Fisher information, for relevant task at the RF, due to changes in tuning properties

2.3. DISCUSSION

Previously we have shown that the contextual responses of V1 neurons change to carry more information about behaviorally relevant stimulus features (Li et al. 2004). Using chronically implanted electrode arrays in awake animals, we investigated the mechanisms of such top-down control of contextual interactions. We proposed that the top-down control in V1 requires differential gating of inputs from stimulus components depending on their task relevance, for example the parallel lines involved in a bisection task versus the task irrelevant collinear lines. According to this idea, the gating requires an interaction between V1 horizontal connections, carrying information about stimulus context, and recurrent inputs to V1, providing information about behavioral context. To test this idea, we looked at the influence of perceptual task on two measures of lateral interactions: spiking correlations and LFP coherence. Furthermore, we measured the effect of perceptual task on V1 noise correlations and Fisher information for the recorded population, which provided a measure of the information carried by neuronal ensembles regarding the stimuli required for the task.

Both measures of neuronal activity, spikes and LFPs, showed top-down modulation of contextual interactions. Previous studies have shown that V1 spiking responses to local features are influenced by the global context of the scene (Kapadia et al. 1995, Kapadia, et al. 1999, Li et al. 2004, Li et al. 2006,

Blakemore and Tobin 1972, Knierim and VanEssen 1992, Nelson and Frost 1985, DeAngelis et al. 1995, Li et al. 2000, Hegde and Felleman 2003, Allman et al. 1985, Angelucci et al. 2002), and that such contextual influences are subject to cognitive control by attention, perceptual task and expectation (Li et al. 2004, Li et al. 2006, Ito and Gilbert 1999, Gilbert et al. 1996, Paradiso 2002, Zipser et al. 1996, Lamme 1995, Roelfsema et al. 1998, Roelfsema et al. 2004, Zhang and von der Heydt 2010, McManus et al. 2011). We observed that, similar to spiking activity, LFPs in frequencies from 10 to 120 Hz encoded stimulus context, such as parallel/collinear flank positions or contour lengths. This contextual tuning was modulated in a task-dependent fashion to extract behaviorally relevant stimulus information (parallel flank positions during bisection task, collinear flank positions during vernier task, number of contour elements during contour detection task). Our results agree with previous work showing that LFPs reflect the neuronal basis of feature selectivity, perception and attention (Henrie and Shapley 2005, Berens et al. 2008, Siegel and König 2003, Krieter and Singer 1996, Fries et al. 2001, Gail et al. 2000, Siegel et al. 2007, Womelsdorf et al. 2006).

Given that top-down control involves an interaction between sensory and behavioral context, the question arises as to the circuitry that mediates this interaction. The lack of task-dependent suppression of the activity of neurons which encode irrelevant stimulus components points instead towards a model involving changes in the interactions across the cortical network. We have proposed that such dynamic changes of V1 functional connectivity are one possible substrate for top-down modulation of encoded stimulus information.

The observed task-dependent changes in spike correlations and LFP coherence in V1 support this idea. We show that under identical stimulus conditions, but differing tasks, there can be large changes in the spike correlated activity. The observation that the task-dependent correlation strength increased between some cell pairs and decreased between others is perhaps not surprising, since the changes in effective connectivity required for the task-dependent changes in neuronal tuning may require strengthening between some sites and weakening between others. The task-driven alteration in LFP coherence, on the other hand, showed more consistent changes for a given task. This may be due to the fact that LFPs derive from a neuronal population spanning several hundred micrometers (Liu and Newsome 2006) and that they are likely to originate from currents generated by both sub-threshold inputs and spiking outputs.

Prior studies suggest that in most cases cortical interactions increase due to attention (Bichot et al. 2005, Fries et al. 2001, Gregoriou et al. 2009, Fries et al. 2008), though there are reports to the contrary (Chalk et al. 2010). In our experiments, we found changes in LFP coherence that depended not only on spatial attention per se but on the task being performed at the attended location. Interestingly, the direction of task-dependent changes in LFP coherence varied between tasks. The bisection task increased coherence between parallel sites and the vernier task decreased coherence between collinear sites. We suggest that this reflects the different perceptual strategies employed during the tasks, whereby the bisection task requires perceptually grouping the center bar with its nearest parallel flanking bar to judge if it's closer to the upper or lower bar.

Conversely, the strategy required in the vernier task to judge the relative position of three collinear bars is to break their perceptual continuity and to segregate the collinear flanks from the center bar. As a consequence, LFP interactions were enhanced between parallel sites in the bisection task and reduced between collinear sites in the vernier task. As further support of this idea, LFP coherence between collinear sites that mediated perceptual grouping, in the contour detection task, increased. Our results bear on the ongoing debate about the neural correlates of perceptual grouping and scene segmentation within visual cortex. One proposed theory suggests that neurons encoding features of the same object couple their activities to form synchronized assemblies (Gray et al. 1989, Fries et al. 2001, Engel et al. 1991, Castelo-Branco et al. 2000, Gail et al. 2000), though some studies have failed to support this idea (Lamme and Spekreijse 1998, Thiele and Stoner 2003, Palanca and DeAngelis, 2005; for review, see Gray 1999). Our observation—that perceptual grouping can increase V1 interactions, while perceptual segregation can reduce them—supports the idea that both coupled and decoupled activity in neuronal ensembles are important for executing perceptual tasks. The effect of such dynamic interactions between ensembles is to alter response rates along with effective connectivity, and ultimately to produce tuning characteristics that enable neurons to encode information useful for the task.

The task-driven effects in LFP coherence emerged earlier for the perceptual discrimination tasks (for the entire trial period) compared to the contour detection task (150 ms following the stimulus presentation). The stimuli

used in these two experiments differed in their foreground/background configuration: in discrimination tasks, 5-bar stimuli were used where the two irrelevant bars can be considered noise; in the contour detection experiments, the contour was embedded in a large complex background composed of randomly oriented line segments. The likely explanation for the delay, during the contour experiments, is the foreground/background interaction and the time required for a network to move from one stable state to another when exposed to such a stimulus (Piëch V, W.L., Reeke G, C.D.G. A network model of top-down influences on local gain and contextual interactions in visual cortex. Soc Neurosci Abstr 701.10, (2009)).

Interestingly, during the discrimination tasks, differences in LFP interactions were present even before the stimulus onset (though this was not true for the contour experiments). Since in our experiments task conditions were interleaved in blocks, the animal was primed to do the task before stimulus onset, enabling task expectation to preset the state of the cortical network and thereby to process the incoming stimulus from its onset. This idea is supported by previous attentional studies in visual cortex showing modulation of pre-stimulus cortical responses by behavioral cues (Kastner et al. 1999, Thut et al. 2006, Fries et al. 2001).

Given a pool of very similarly tuned neurons, it would be ideal, from a population coding perspective, if the noise in their responses were uncorrelated (Lee et al. 1998, Bair et al. 2001, Shadlen et al. 1996, Abbott and Dayan 1999, Panzeri et al. 1999, Averback et al. 2006). In this scenario, pooling responses

across progressively larger neuronal populations would correct for the variability present in individual neurons' responses, thereby allowing downstream neurons to reliably decode the information contained in the population response. However, it is well established that noise in the brain is correlated (for e.g. Gawne and Richmond 1993, Zohary et al. 1994, Gawne et al. 1996, Lee et al. 1998, Bair et al. 2001); moreover, these correlations can actually improve the population code when they occur between neurons with the appropriate tuning curve relationships (Abbott and Dayan 1999, Panzeri et al. 1999, Averback et al. 2006, Oram et al. 1998). Stochastic fluctuations in common neuronal inputs are thought to be the source of noise correlations (Bair et al. 2001, Thut et al. 2006, Kohn and Smith 2005), which can greatly influence the information encoded by neuronal ensembles. The mean noise correlations found in our study (attend-away: 0.0381; attended: 0.0141; attend and perform task: 0.0041) were lower than the previous values reported for noise correlations (0.1-0.3) in V1 (Gawne et al. 1996, Reich et al. 2001, Kohn and Smith 2005, Poort and Roelfsema 2006) and in other cortical areas (MT, Zohary et al. 1994; Motor and Parietal cortices: Lee et al. 1998). Conversely, they are comparable to the values reported by Ecker et al. (2010) in V1. This discrepancy between the values from our experiments and previous studies could be due to the different experimental conditions, including stimulus parameters, arousal state of subjects (awake, behaving or anesthetized), the time window over which spikes are counted and spike sorting conventions (Cohen and Kohn 2011). Similar to other studies (Zohary et al. 1994, Kohn and Smith 2005, Bair et al. 2001, Cohen and Maunsell

2009, Gu et al. 2011), noise correlations in our experiments were higher for cells with similar tuning properties across all task conditions and consistent with the idea that similarly tuned cells share common inputs and hence are subject to common noise sources.

Top-down modulation of noise correlations had been demonstrated in previous studies where attention and perceptual learning reduced noise correlations (Cohen and Maunsell 2009, Mitchell et al. 2009, Gu et al. 2011). Other studies (S1:Romo et al. 2003, V1:Poort and Roelfsema 2009) report mixed effects of noise correlations on encoded information: increased correlations between cells of one class (neurons encoding same object or vibro-tactile frequencies) were offset by decreased correlations in the other class of neurons (encoding different objects or vibro-tactile frequencies). In our experiments, attention and perceptual task improved information in V1 by decreasing noise correlations between cell pairs. Notably, our experimental design allowed us to study the changes in correlations due to shifting attention separately from the changes due to performing a task at the attended location. We found that top-down control improved V1 information content to a greater extent when the animal performed the discrimination task at the recorded location compared to when the animal simply shifted its locus of attention. Moreover, changes in both neuronal tuning and noise correlations equally affected this information enhancement. Notably, the V1 ensemble response was most informative for stimuli with the highest discrimination difficulty. Hence, while reorienting attention alone can improve the population code, actively engaging in a task using stimuli

encoded by these neurons can further improve its accuracy, thus allowing the downstream areas to reliably extract stimulus information critical to behavior.

Theoretical studies suggest that the impact of noise correlations on the information content of a neuron population depends on the tuning properties of the cells pooled. Increased noise correlations between neurons tuned to similar features reduce the reliability of the population code, since their shared variability can never fully be averaged out (Shadlen et al. 1998, Abbott and Dayan 1999). However, noise correlations can be beneficial if neurons are tuned to different features (Oram et al. 1998, Panzeri et al. 1999, Averbeck et al. 2006). In our studies, although task-dependent decreases in noise correlations were present for both similarly and dissimilarly tuned cells, the largest decrease was present for cells with similar tuning. Thus, in our experiments, top-down influences in V1 improved the coding accuracy of behaviorally relevant stimuli by reducing noise correlations between similarly tuned cells. This relationship, though not seen in other studies (Cohen and Maunsell, 2009), may depend on the cognitive demands of the task and the nature of the stimulus being discriminated. For example, decoding where a stimulus change occurred might be less sensitive to the tuning similarity of the cells, while discriminating the spatial configuration of a complex stimulus might be more dependent on similarity of tuning between the neurons participating in the task.

It has been suggested that in V1, top-down control could be mediated by interactions between feedback connections carrying the behavioral context and intrinsic horizontal connections providing the sensory context (Gilbert and

Sigman 2007). In our experiments, cognitive influences on V1 contextual interactions produced robust changes in functional connectivity (i.e, LFP interactions and spiking correlations) between cells encoding the stimulus. This suggests that even though the anatomical connectivity of the horizontal connections, which provides information about stimulus context, is stable over the short term, the functional efficacy of these connections can be controlled by task-driven influences, provided, for example, by recurrent projections to V1. Thus, behaviorally relevant sensory information can be extracted from V1 by creating ad-hoc, on-demand functional networks by selectively gating only appropriate horizontal connections between select sets of neurons. In this way, V1 can be viewed as an 'adaptive processor' that runs different computational programs as dictated by feedback from higher order areas. The knowledge and the 'switch-board' circuitry that is required to associate various behavioral needs with different brain states may be acquired through learning.

2.4. METHODS

2.4.1 ANIMAL PREPARATION AND ELECTROPHYSIOLOGY

Data were obtained from two adult rhesus monkeys (*Macaca mulatta*). The animals were implanted with head posts and trained in several tasks for 3-4 months (see Stimuli and Task design). Following training, two 6×8 multi-electrode arrays (Blackrock Microsystems, Utah) were implanted in the V1 opercular surface. The electrodes were 500-600μm long with 400μm inter-electrode spacing, and the two arrays were connected to a percutaneous connector that allowed electrophysiological recordings. Spike and local field potential (LFP) signals from orientation-selective cells in the V1 superficial layers were collected using a real-time multi-electrode data acquisition system (MAP system, Plexon Inc.). All procedures were conducted in compliance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals and under approval of the Institutional Animal Care and Use Committee at Rockefeller University.

2.4.2 STIMULI AND TASK DESIGN

Stimuli were generated by a visual stimulus generator (VSG2/5, Cambridge Research Systems) on a CRT monitor (NANAO FlexScan F2-21) at a

resolution of 1024 by 769 pixels and a refresh rate of 105 Hz. The viewing distance was 78 cm.

2.4.2.1 5-BAR DISCRIMINATION TASK

One of the two behavioral paradigms used in this study was a dual discrimination task on a 5-bar stimulus; the stimulus and behavioral protocol were as described in Li et al. 2004. The animals performed two discrimination tasks, bisection and vernier, on the same 5-bar stimulus: one fixed central bar, flanked by two parallel and two collinear bars (Fig. 2.1, top). The five oriented bars (0.4° × 0.08°) were displayed on a gray background (6.25 cd/m^2), with Michelson contrast ranging from 15% to 60%. For a given recording session, the central stimulus bar was fixed at the receptive field (RF) center of one chosen neuron, and all the bars in the stimulus array were oriented at the preferred orientation of this cell. An example arrangement of stimulus components in relation to the RF centers of neurons recorded from one of our arrays is shown in Figure 2.1 (bottom panel). In the bisection task, the animals discriminated the relative distance between the parallel bars. In different trials, either of the two parallel flanks was randomly displaced in varying steps of 0.1°-0.13°, and the animals reported which flank was nearer to the fixed central bar. The vernier task involved discriminating the offset of collinear bars. The two collinear flanks were displaced randomly to either side of the center bar, in steps of 0.1°-0.13°; the animals determined to which side of the central bar the flanks were offset. Each task (bisection or vernier) was performed in a continuous block of randomized

trials. Within a single experiment, we repeatedly switched the monkey's perceptual task by interleaving a block of trials on one task (e.g., the bisection task) with a block of trials on the other task (e.g., the vernier task). Each stimulus configuration, for a given task, was repeated for at least 20 times. Monkeys initiated a trial by pulling on a lever and fixating on a ~ 0.1° fixation point (FP) displayed at the monitor center. We used an infrared eye tracking system to ensure that monkeys maintained their fixation within 0.5º of the FP. At 196 ms following the fixation onset, the stimulus was presented for 496 ms, followed by two 0.15° saccade targets. The animals reported their choice by making a saccade to one of the two targets. We also collected data during control experiments designed to remove the influence of perceptual task on the recorded neural responses. In these experiments, we displayed the same 5-bar stimuli over the recorded RF locations, but had the monkeys perform a different task on a separate stimulus in the opposite hemifield. For one of the two monkeys, this consisted of a 3 line discrimination (bisection/vernier) task and in the second monkey this involved a brightness discrimination task.

2.4.2.2 CONTOUR DETECTION TASK

The second behavioral paradigm we examined was a contour detection task. For these experiments, the animals were trained to detect a contour, consisting of 3 to 9 collinear lines, embedded in one of two complex backgrounds (i.e., stimulus patches) of randomly oriented lines (Fig. 2.7, left). The stimulus parameters and experimental design have been described previously (Li et al.

2006). The stimulus patches consisted of 0.2° × 0.05° bars displayed on a gray background. Different stimulus conditions (1, 3, 5, 7 or 9 bar contours) were randomized and repeated 30 to 40 times in a recording session. Each trial began when the monkeys pulled a lever, followed by the display of a ~ 0.1° FP at the screen center. At 333 ms following fixation, two stimulus patches were displayed in opposite hemifields for 596 ms, followed by two corresponding saccade targets. The animal indicated which patch contained a contour by making a saccade to one of the targets. To study contour related effects in the absence of attention, we also collected data when the monkeys performed a visual task (3-line bisection or a brightness discrimination task) in the hemifield opposite to recorded neuronal RFs (Fig. 2.7, right).

2.4.3. DATA ANALYSIS

2.4.3.1. MUTUAL INFORMATION

For the 5-bar experiments, we used mutual information to quantify the amount of information neural responses conveyed about a stimulus attribute. This measure indicates to what extent an ideal observer could categorize stimulus information given the spike count of a cell during one trial. Given the probability of presenting a stimulus ($p(s_j)$), the probability of observing a spike count ($p(r_i)$) and the conditional probability of observing a spike count for a specific stimulus ($p(r_i \mid s_j)$), mutual information was calculated as:

$$I(R;S) = \sum_i \sum_j p(s_j) p(r_i|s_j) \log_2 \frac{p(r_i|s_j)}{p(r_i)}$$

The probabilities $p(r_i)$) and $p(r_i \mid s_j)$ were calculated by binning the spike counts at one standard deviation of the response to all stimulus conditions for a given task and cell, rounded to nearest integer. The mutual information present in the LFP responses was calculated similarly: instead of spike count, LFP power in frequencies 10-120 Hz from 100 - 500 ms following stimulus presentation was used. LFP power at a given frequency was estimated using the fast Fourier transform (Matlab, The Mathworks Inc.).

2.4.3.2 CONTOUR TUNING CURVES

The mean responses of cells with RFs lying along the contour stimuli were used to calculate contour-dependent facilitative responses in V1. Spike counts within 100 to 600 ms after stimulus presentation were used to calculate average firing rates, since the initial neuronal responses do not contain information about the embedded contour (Li et al. 2006). The mean response of a cell to varying contour lengths was normalized to the cell's average response to the background pattern (i.e., a 1-bar 'contour'), and then averaged over all the recorded cells to get the population responses. Similarly, LFP power within the 10-120 Hz frequency band, within 150 to 600 ms after stimulus presentation, were used to obtain contour related tuning curves.

2.4.3.3 SPIKING CROSS CORRELATIONS

We estimated the effective connectivity between spiking neurons using cross-correlation analysis, which provides a measure of synchronous activity between neurons. Raw cross-correlograms were obtained from the Joint Peri-Stimulus Histogram (JPSTH), with 5 ms resolution, of the spike trains of a cell pair (Aersten et al. 1989). We corrected for the stimulus induced synchronous activity by estimating a modified shift-predictor as follows:

1. For each neuron of a cell pair, for each trial, we simulated a spike train from an inhomogenous Poisson process (i.e., a Poisson process whose mean rate varies as a function of time, to match the PSTH of each neuron). The simulated spikes exactly matched both the observed spike count at each trial and the shape of the mean PSTH for each neuron. Only the *timing* of individual spikes *in individual trials* differed between the observed and simulated spike trains. Since the Poisson process used to simulate the spikes for one neuron was independent of the Poisson process used to simulate the spikes for the second neuron of the pair, these simulations yield the number of coincident spikes expected under the null hypothesis of no neuronal temporal correlation.
2. We then calculated cross-correlograms from the simulated spike trains. Even if the precise spike timing of two neurons is independent, the two cells will still exhibit a basal level of correlation in the correlogram, caused by the similarity of the neurons' PSTHs and any covariation in their firing rates. The cross-correlograms computed from the simulated spike trains

reflect exactly this basal component of the correlogram, expected from independent neurons whose individual firing statistics match those of the real neurons recorded.

3. We repeated steps 1 and 2 1000 times and averaged the resultant 1000 correlograms to obtain the *shift-predictor*.

After subtracting a shift-predictor from the raw cross-correlogram, we normalized the correlogram by the geometric mean of the auto-correlograms of the cells under study. All the correlograms presented in the paper are such normalized cross-correlograms (NCCGs). Because of the application of our shift predictor, the correlograms reflect only very precise spike timing correlations; they ignore spike timing coincidences that occur at large time lags and that constitute a component of neuronal noise correlations.

The effective connectivity between a neuron pair was measured by estimating the area under the normalized cross-correlogram peaks (±15 ms for all experiments and task conditions). To test for significance of an observed correlation, we used the 1000 correlograms obtained from the simulations mentioned above: the *p*-value was calculated as the proportion of simulated correlograms with correlation magnitude greater than or equal to the observed correlation. We used a permutation test to determine if observed correlations between a cell pair were significantly different under different task conditions. The permutation test was performed as follows: for the cell pair under consideration, the trials from the two tasks were pooled into one set and then were randomly

reassigned into two subsets; NCCGs were then computed from these two subsets and the difference in their correlation magnitudes were calculated. The random permutation and estimation of correlation magnitude difference was done 1000 times and the *p*-value was reported as the probability that the difference in the correlation magnitudes from the permuted dataset was as large as the one observed from the original dataset.

For contour detection experiments, we compared the spiking correlations at the population level. For each cell pair we estimated NCCGs (as mentioned above) under different stimulus (1, 3, 5, 7, 9 bar) and task (detection and attend-away) conditions. We averaged the NCCGs of all the cell pairs for 1 bar condition during the detection task to obtain the 'no contour' correlogram. The NCCGs for 3, 5, 7, 9 bar conditions were averaged to get the 'contour' correlograms for the detection and attend-away conditions separately. To test if the observed correlations at the population level differed significantly between two stimulus/ task conditions, we used paired the Wilcoxon signed rank test (α=0.05) on the correlation magnitudes (sum of coincidence spikes in ±15 ms) of the individual NCCGs (Matlab, The Mathworks Inc.).

2.4.3.4 LFP COHERENCE

We determined LFP interactions between recording sites by measuring the coherence of their LFP signals. Cross-spectra and auto-spectra of LFP signals for a pair of sites were calculated by the Fourier transform. Coherence was then calculated as

$$\frac{|S_{xy}|^2}{S_{xx}S_{yy}}$$

S_{xy} is the cross-spectra, S_{xx} and S_{yy} the auto-spectra of the LFP signals. LFP coherence, which varies between 0 and 1, measures the linear correlation between two signals as a function of frequency. For a given frequency, coherence between two LFP signals will be unity if their amplitudes covary and if they maintain a constant phase relationship. If the two signals are independent, coherence will be equal to 0. The cross-spectra and auto-spectra were averaged over trials for a task condition before calculating the coherence. The Fourier analysis was done in 120 ms sliding windows with 1 ms shifts, resulting in a coherogram giving the time-frequency relationship of the coherence. We corrected for stimulus-induced coherence changes by computing the coherence shift-predictor (i.e., the mean coherence computed from all possible permutations of trials) and subtracting it from the coherence to estimate corrected coherence. All the coherence results presented in this paper are such corrected coherence. To obtain the coherence as a function of frequency only, we averaged coherence over the entire trial period after the initial burst at stimulus onset. The time course of coherence dynamics was obtained by averaging the coherence in the frequencies 10-120 Hz.

2.4.3.5 NOISE CORRELATIONS

We studied two measures of correlation between the responses of a cell pair: signal correlation and noise correlation (Gawne and Richmond, 1993).

Signal correlation, r_{sig}, estimates the similarity in tuning to a stimulus set between a pair of neurons. In our case, it was simply the Pearson correlation coefficient of a cell-pair's tuning curves for parallel bar / collinear bar positions. Noise correlation, r_{noise} , estimates correlated trial-by-trial variability for a pair of cells. We calculated r_{noise} by first normalizing the spike counts by z-scores (Bair et al. 2001) and then taking the Pearson correlation coefficient of the normalized spike counts. Differences in noise correlations between task conditions were tested by paired the Wilcoxon signed rank test (α=0.05; Matlab, The Mathworks Inc.).

2.4.3.6 FISHER INFORMATION

The Fisher information (I_F) provides a limit on the accuracy with which an unbiased decoder can read out a population code. We estimated the information present in a neuronal ensemble as (Abbott and Dayan 1999)

$$I_F(x) = f'(x)^T Q^{-1}(x) f'(x) + \frac{1}{2} Tr[Q'(x) Q^{-1}(x) Q'(x) Q^{-1}(x)]$$

Here, f(x) is the vector of responses of the neurons in the population for the stimulus x; Q denotes the covariance matrix; superscript T denotes the matrix transpose, superscript -1 the matrix inverse and Tr represents the trace operation. To estimate the contribution of tuning curve changes to change in information content when the animal performed the perceptual task at the RFs, we recomputed Fisher information as before but using the tuning curves (f(x)) during the perceptual task at the RFs and covariance matrices (Q(x)) from the

task condition when the animal attended to the RFs, but did not perform a task at the RFs. We did a Box-Cox transform of the spiking rates before the calculation, to ensure that the neuronal responses for a given stimulus follows a normal distribution. Since the above transformation can result in non-zero spike responses, we adjusted the transformed data such that the spike response distribution is shifted away form zero. Qualitatively, the results were similar for the original, untransformed dataset.

3. REFERENCES

Abbott, L. F., and Dayan, P. (1999). The effect of correlated variability on the accuracy of a population code. Neural Comput, 11(1), 91-101.

Aertsen, A. M., Gerstein, G. L., Habib, M. K., and Palm, G. (1989). Dynamics of neuronal firing correlation: Modulation of "effective connectivity". J Neurophysiol, 61(5), 900-17.

Albright, T.D., and Stoner, G.R. (2002). Contextual influences on visual processing. Annual Review of Neuroscience 25, 339-379.

Allman, J., Miezin, F., and McGuinness, E. (1985). Stimulus specific responses from beyond the classical receptive field: Neurophysiological mechanisms for local-global comparisons in visual neurons. Annu Rev Neurosci, 8, 407-30.

Anderson, J., Lampl, I., Reichova, I., Carandini, M., and Ferster, D. (2000). Stimulus dependence of two-state fluctuations of membrane potential in cat visual cortex. Nat Neurosci, 3(6), 617-21.

Angelucci, A., Levitt, J. B., Walton, E. J., Hupe, J. M., Bullier, J., and Lund, J. S. (2002). Circuits for local and global signal integration in primary visual cortex. J Neurosci, 22(19), 8633-46.

Arieli, A., Sterkin, A., Grinvald, A., and Aertsen, A. (1996). Dynamics of ongoing activity: explanation of the large variability in evoked cortical responses. Science 273, 1868–1871.

Averbeck, B. B., Latham, P. E., and Pouget, A. (2006). Neural correlations, population coding and computation. Nat Rev Neurosci, 7(5), 358-66.

Bair, W., Zohary, E., and Newsome, W. T. (2001). Correlated firing in macaque visual area MT: Time scales and relationship to behavior. J. Neurosci, 21(5), 1676-97.

Bair, W., Cavanaugh, J.R., and Movshon, J.A. (2003). Time course and time-distance relationships for surround suppression in macaque V1 neurons. J. Neurosci, 23, 7690–7701.

Ball, K., and Sekuler, R. (1982). A specific and enduring improvement in visual motion discrimination. Science, 218(4573), 697-8.

Ball, K., and Sekuler, R. (1987). Direction-Specific improvement in motion discrimination. Vision Res, 27(6), 953-65.

Baumann, R., ver der Zwan, R., Peterhans, E. 1997. Figure-ground segregation at contours: a neural mechanism in the visual cortex of the alert monkey. Eur. J. Neurosci,9, 1290–303

Berens, P., Keliris, G. A., Ecker, A. S., Logothetis, N. K., and Tolias, A. S. (2008). Comparing the feature selectivity of the gamma-band of the local field potential and the underlying spiking activity in primate visual cortex. Front Syst Neurosci, 2, 2.

Bichot, N. P., Rossi, A. F., and Desimone, R. (2005). Parallel and serial neural mechanisms for visual search in macaque area V4. Science, 308(5721), 529-34.

Blakemore, C., and Tobin, E. A. (1972). Lateral inhibition between orientation detectors in the cat's visual cortex. Exp Brain Res, 15(4), 439-40.

Bland, B.H., and Oddie, S.D. (2001). Theta band oscillation and syn- chrony in the hippocampal formation and associated structures: the case for its role in sensorimotor integration. Behav. Brain Res. 127, 119–136.

Blaser, E., Pylyshyn, Z.W., and Holcombe, A.O. (2000). Tracking an object through feature space. Nature 408, 196-199.

Bosking, W. H., Zhang, Y., Schofield, B., and Fitzpatrick, D. (1997). Orientation selectivity and the arrangement of horizontal connections in tree shrew striate cortex. J Neurosci, 17(6), 2112-27.

Bulthoff, I., Bulthoff, H., and Sinha, P. (1998). Top-down influences on stereoscopic depth-perception. Nat Neurosci, 1, 254-257.

Castelo-Branco, M., Goebel, R., Neuenschwander, S., and Singer, W. (2000). Neural synchrony correlates with surface segregation rules. Nature, 405(6787), 685-9.

Chalk, M., Herrero, J. L., Gieselmann, M. A., Delicato, L. S., Gotthardt, S., and Thiele, A. (2010). Attention reduces stimulus-driven gamma frequency oscillations and spike field coherence in V1. Neuron, 66(1), 114-25.

Chelazzi, L., Duncan, J., Miller, E.K., and Desimone, R. (1998). Responses of neurons in inferior temporal cortex during memory-guided visual search. Journal of Neurophysiology 80, 2918-2940.

Chelazzi, L., Miller, E.K., Duncan, J., and Desimone, R. (1993). A Neural Basis for Visual-Search in Inferior Temporal Cortex. Nature 363, 345-347.

Chelazzi, L., Miller, E.K., Duncan, J., and Desimone, R. (2001). Responses of neurons in macaque area V4 during memory-guided visual search. Cerebral Cortex 11, 761-772.

Chisum, H.J., Mooser, F., and Fitzpatrick, D. (2003). Emergent properties of layer 2/3 neurons reflect the collinear arrangement of horizontal connections in tree shrew visual cortex. Journal of Neuroscience 23, 2947-2960.

Cohen, M. R., and Kohn, A. (2011). Measuring and interpreting neuronal correlations. Nat Neurosci, 14(7), 811-9.

Cohen, M. R., and Maunsell, J. H. (2009). Attention improves performance primarily by reducing interneuronal correlations. Nat Neurosci, 12(12), 1594-600.

Cohen, M. R., and Newsome, W. T. (2008). Context-Dependent changes in functional circuitry in visual area MT. Neuron, 60(1), 162-73.

Cossart, R., Aronov, D., and Yuste, R. (2003). Attractor dynamics of network UP states in the neocortex. Nature, 423(6937), 283-8.

Crist, R. E., Kapadia, M. K., Westheimer, G., ans Gilbert, C. D. (1997). Perceptual learning of spatial localization: Specificity for orientation, position, and context. J Neurophysiol, 78(6), 2889-94.

Crist, R. E., Li, W., and Gilbert, C. D. (2001). Learning to see: Experience and attention in primary visual cortex. Nat Neurosci, 4(5), 519-25.

Das, A., and Gilbert, C. D. (1995). Long-Range horizontal connections and their role in cortical reorganization revealed by optical recording of cat primary visual cortex. Nature, 375(6534), 780-4.

De Weerd, P., Gattass, R., Desimone, R., Ungerleider, L. G. (1995). Responses of cells in monkey visual cortex during perceptual filling-in of an artificial scotoma. Nature,377, 731–34.

DeAngelis, G. C., Anzai, A., Ohzawa, I., and Freeman, R. D. (1995). Receptive field structure in the visual cortex: Does selective stimulation induce plasticity?. Proc Natl Acad Sci U S A, 92(21), 9682-6.

Desimone, R., and Duncan, J. (1995). Neural mechanisms of selective visual attention. Annual Reviews in Neuroscience, 18(1), 193-222.

Duncan, J. (1984). Selective attention and the organization of visual information. J Exp Psychol Gen, 113(4), 501-17.

Eagleman, D. M. (2001). Visual illusions and neurobiology. Nat Rev Neurosci, 2(12), 920-6.

Egly, R., Driver, J., and Rafal, R.D. (1994). Shifting visual attention between objects and locations: evidence from normal and parietal lesion subjects. J Exp Psychol Gen, 123, 161-177.

Ecker, A. S., Berens, P., Keliris, G. A., Bethge, M., Logothetis, N. K., and Tolias, A. S. (2010). Decorrelated neuronal firing in cortical microcircuits. Science, 327(5965), 584-7.

Eckhorn, R., Bauer, R., Jordan, W., Brosch, M., Kruse, W., Munk, M., and Reitboeck, H.J. (1988). Coherent oscillations: a mechanism of feature linking in the visual cortex? Multiple electrode and correlation analyses in the cat. Biol. Cybern. 60, 121–130.

Engel, A. K., Kreiter, A. K., König, P., and Singer, W. (1991). Synchronization of oscillatory neuronal responses between striate and extrastriate visual cortical areas of the cat. Proc Natl Acad Sci U S A, 88(14), 6048-52.

Fahle, M., Edelman, S., and Poggio, T. (1995). Fast perceptual learning in hyperacuity. Vision Research, 35, 3003-3013.

Fahle, M., and Morgan, M. (1996). No transfer of perceptual learning between similar stimuli in the same retinal position. Current Biology, 6, 292-297.

Fiorentini, A., and Berardi, N. (1980). Perceptual learning specific for orientation and spatial frequency. Nature, 287, 43-44.

Fiorani, J.M., Rosa, M.G., Gattass, R., Rocha- Miranda, C.E. (2001). Dynamic surrounds of receptive fields in primate striate cortex: a physiological basis for perceptual completion? Proc. Natl. Acad. Sci., 89, 8547–51.

Fox, M. D., Snyder, A. Z., Vincent, J. L., Corbetta, M., Van Essen, D. C., and Raichle, M. E. (2005). The human brain is intrinsically organized into dynamic, anticorrelated functional networks. Proc Natl Acad Sci U S A, 102(27), 9673-8.

Fox, M.D., Corbetta, M., Snyder, A.Z., Vincent, J.L., and Raichle, M.E. (2006). Spontaneous neuronal activity distinguishes human dorsal and ventral attention systems. Proc. Natl. Acad. Sci. USA 103, 10046– 10051.

Fries, W., Albus, K., and Creutzfeldt, O.D. (1977). Effects of Interacting Visual-Patterns on Single Cell Responses in Cats Striate Cortex. Vision Res., 17, 1001-1008.

Fries, P., Reynolds, J. H., Rorie, A. E., and Desimone, R. (2001). Modulation of oscillatory neuronal synchronization by selective visual attention. Science, 291(5508), 1560-3.

Fries, P., Womelsdorf, T., Oostenveld, R., and Desimone, R. (2008). The effects of visual stimulation and selective visual attention on rhythmic neuronal synchronization in macaque area V4. J Neurosci, 28(18), 4823-35.

Gail, A., Brinksmeyer, H. J., and Eckhorn, R. (2000). Contour decouples gamma activity across texture representation in monkey striate cortex. Cereb Cortex, 10(9), 840-50.

Gawne, T. J., and Richmond, B. J. (1993). How independent are the messages carried by adjacent inferior temporal cortical neurons?. J Neurosci, 13(7), 2758-71.

Gawne, T. J., Kjaer, T. W., Hertz, J. A., and Richmond, B. J. (1996). Adjacent visual cortical complex cells share about 20% of their stimulus-related information. Cereb Cortex, 6(3), 482-9.

Ghose, G.M., and Maunsell, J. (1999). Specialized representations in visual cortex: a role for binding? Neuron 24, 79–85, 111–125.

Gibson, J. J., and Radner, M. (1937). Adaptation, after-effects and contrast in the perception of tilted lines. J. Exp. Psychol., 20, 453–467.

Giesbrecht, B., Woldorff, M.G., Song, A.W., and Mangun, G.R. (2003). Neural mechanisms of top-down control during spatial and feature attention. Neuroimage 19:496-512.

Gilbert, C. D. (1992). Horizontal integration and cortical dynamics. Neuron, 9(1), 1-13.

Gilbert, C. D. (1993). Circuitry, architecture, and functional dynamics of visual cortex. Cereb Cortex, 3(5), 373-86.

Gilbert, C. D., Das, A., Ito, M., Kapadia, M., and Westheimer, G. (1996). Proceedings of the national academy of sciences. National Acad Sciences.

Gilbert, C., Ito, M., Kapadia, M., and Westheimer, G. (2000). Interactions between attention, context and learning in primary visual cortex. Vision Res, 40(10-12), 1217-26.

Gilbert, C. D., and Kelly, J. P. (1975). The projections of cells in drfferent layers of the cat's visual cortex. J. Comp. Neural., 763, 81-106.

Gilbert, C. D., and Sigman, M. (2007). Brain states: Top-Down influences in sensory processing. Neuron, 54(5), 677-96.

Gilbert, C. D., Sigman, M., and Crist, R. E. (2001). The neural basis of perceptual learning. Neuron, 31(5), 681-697.

Gilbert, C. D., and Wiesel, T. N. (1979). Morphology and intracortical projections of functionally characterised neurones in the cat visual cortex. Nature, 280(5718), 120-5.

Gilbert, C. D., and Wiesel, T. N. (1983). Clustered intrinsic connections in cat visual cortex. Journal of Neuroscience, 3(5), 1116-1133.

Gilbert, C. D., and Wiesel, T. N. (1989). Columnar specificity of intrinsic horizontal and corticocortical connections in cat visual cortex. J Neurosci, 9(7), 2432-42.

Gilbert, C. D., and Wiesel, T. N. (1990). The influence of contextual stimuli on the orientation selectivity of cells in primary visual cortex of the cat. Vision Res, 30(11), 1689-701.

Gilbert, C. D., and Wiesel, T. N. (1992). Receptive field dynamics in adult primary visual cortex. Nature, 356(6365), 150-152.

Goldberg, M.E., and Wurtz, R.H. (1972). Activity of superior colliculus in behaving monkey. II. Effect of attention on neuronal responses. J Neurophysiol, 35, 560-574.

Goldman, P. S.,and Nauta, W. J. H. (1977). Columnar distributron of cortico-cortical fibers in the frontal association, limbic and motor cortex of the developing rhesus monkey. Brain Res., 722, 393-413.

Golledge, H.D., Hilgetag, C.C., and Tovee, M.J. (1996). A solution to the binding problem? Information processing. Curr. Biol. 6, 1092–1095.

Gray, C. M. (1999). The temporal correlation hypothesis of visual feature integration: Still alive and well. Neuron, 24(1), 31-47, 111-25.

Gray, C. M., König, P., Engel, A. K., and Singer, W. (1989). Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties. Nature, 338(6213), 334-7.

Gregoriou, G. G., Gotts, S. J., Zhou, H., and Desimone, R. (2009). High-Frequency, long-range coupling between prefrontal and visual cortex during attention. Science, 324(5931), 1207-10.

Grosof, D. H., Shapley, R. M., and Hawken, M. J. (1993). Macaque V1 neurons can signal 'illusory' contours. Nature, 365(6446), 550-2.

Gu, Y., Liu, S., Fetsch, C. R., Yang, Y., Fok, S., Sunkara, A., et al. (2011). Perceptual learning reduces interneuronal correlations in macaque visual cortex. Neuron, 71(4), 750-61.

Gutnisky, D. A., and Dragoi, V. (2008). Adaptive coding of visual information in neural populations. Nature, 452(7184), 220-4.

Haenny, P. E., Maunsell, J. H., and Schiller, P. H. (1988). State dependent activity in monkey visual cortex. II. Retinal and extraretinal factors in V4. Exp Brain Res, 69(2), 245-59.

Haider, B., Duque, A., Hasenstaub, A.R., and McCormick, D.A. (2006). Neocortical network activity in vivo is generated through a dynamic balance of excitation and inhibition. J. Neurosci. 26, 4535–4545.

Hegdé, J., and Felleman, D. J. (2003). How selective are V1 cells for pop-out stimuli?. J Neurosci, 23(31), 9968-80.

Henrie, J. A., and Shapley, R. (2005). LFP power spectra in V1 cortex: The graded effect of stimulus contrast. J Neurophysiol, 94(1), 479-90.

Hubel, D. H., and Wiesel, T.N. (1974). Uniformity of monkey striate cortex: a parallel relationship between field size, scatter and magnification factor. J.Comp.Neurol, 158, 295 – 306.

Hupe, J.M., James, A.C., Girard, P., Lomber, S.G., Payne, B.R., and Bullier, J. (2001). Feedback connections act on the early part of the responses in monkey visual cortex. J.Neurophysiol., 85, 134-145.

lmig, T. J., and Brugge, J. F. (1978). Sources and terminations of callosal axons related to binaural and frequency maps in primary auditory cortex of the cat. J. Comp. Neurol. ,782, 637-660.

Ito, M., and Gilbert, C. D. (1999). Attention modulates contextual influences in the primary visual cortex of alert monkeys. Neuron, 22(3), 593-604.

Ito, M., Westheimer, G., & Gilbert, C. D. (1998). Attention and perceptual learning modulate contextual influences on visual perception. Neuron, 20(6), 1191-7.

Jones, E. G., Coulter, J. D., and Hendry, S. H. C. (1978). Intracortical connectivity of architectonic fields in the somatic sensory, motor and parietal cortex of monkeys. J.Comp. Neurol., 787.291- 348.

Julesz, B. (1981). Textons, the Elements of Texture-Perception, and Their Interactions. Nature, 290, 91-97.

Kanizsa, G. (1976). Subjective contours. Sci Am, 234(4), 48-52.

Kapadia, M. K., Ito, M., Gilbert, C. D., and Westheimer, G. (1995). Improvement in visual sensitivity by changes in local context: Parallel studies in human observers and in V1 of alert monkeys. Neuron, 15(4), 843-56.

Kapadia, M. K., Westheimer, G., and Gilbert, C. D. (1999). Dynamics of spatial summation in primary visual cortex of alert monkeys. Proc Natl Acad Sci U S A, 96(21), 12073-8.

Kapadia, M. K., Westheimer, G., and Gilbert, C. D. (2000). Spatial distribution of contextual interactions in primary visual cortex and in visual perception. J Neurophysiol, 84(4), 2048-62.

Karni, A., and Sagi, D. (1991). Where practice makes perfect in texture discrimination: Evidence for primary visual cortex plasticity. Proc Natl Acad Sci U S A, 88(11), 4966-70.

Kastner, S., Pinsk, M. A., De Weerd, P., Desimone, R., and Ungerleider, L. G. (1999). Increased activity in human visual cortex during directed attention in the absence of visual stimulation. Neuron, 22(4), 751-61.

Knierim, J. J., and van Essen, D. C. (1992). Neuronal responses to static texture patterns in area V1 of the alert macaque monkey. J Neurophysiol, 67(4), 961-980.

Kohn, A., and Smith, M. A. (2005). Stimulus dependence of neuronal correlation in primary visual cortex of the macaque. J Neurosci, 25(14), 3661-73.

Komatsu, H., Kinoshita, M., Murakami, I. (2000). Neural responses in the retinotopic representation of the blind spot in the macaque V1 to stimuli for perceptual filling-in. J. Neurosci., 20, 9310–19.

Kreiter, A. K., and Singer, W. (1996). Stimulus-Dependent synchronization of neuronal responses in the visual cortex of the awake macaque monkey. J Neurosci, 16(7), 2381-96.

Lamme, V. A. (1995). The neurophysiology of figure-ground segregation in primary visual cortex. J Neurosci, 15(2), 1605-15.

Lamme, V. A., and Spekreijse, H. (1998). Neuronal synchrony does not represent texture segregation. Nature, 396(6709), 362-6.

Lampl, I., Anderson, J.S., Gillespie, D.C., and Ferster, D. (2001). Prediction of orientation selectivity from receptive field architecture in simple cells of cat visual cortex. Neuron 30, 263-274.

Lee, T.S., and Nguyen, M. (2001). Dynamics of subjective contour formation in the early visual cortex. Proc Natl Acad Sci U S A, 98, 1907-1911.

Lee, D., Port, N. L., Kruse, W., and Georgopoulos, A. P. (1998). Variability and correlated noise in the discharge of neurons in motor and parietal areas of the primate cortex. J Neurosci, 18(3), 1161-70.

Li, W., and Gilbert, C.D. (2002). Global contour saliency and local colinear interactions. J.Neurophysiol., 88, 2846-2856.

Li, W., Piëch, V., and Gilbert, C. D. (2004). Perceptual learning and top-down influences in primary visual cortex. Nat Neurosci, 7(6), 651-7.

Li, W., Piëch, V., and Gilbert, C. D. (2006). Contour saliency in primary visual cortex. Neuron, 50(6), 951-62.

Li, W., Thier, P., and Wehrhahn, C. (2000). Contextual influence on orientation discrimination of humans and responses of neurons in V1 of alert monkeys. J Neurophysiol, 83(2), 941-54.

Li, W., Thier, P., and Wehrhahn, C. (2001). Neuronal responses from beyond the classic receptive field in VI of alert monkeys. Exp. Brain Res., 139, 359-371.

Liu, J. and Newsome, W. T. (2006). Local field potential in cortical area MT: stimulus tuning and behavioral correlations. J. Neurosci 26, 7779-7790.

MacEvoy, S.P., Paradiso, M.A. (2001). Lightness constancy in primary visual cortex. Proc. Natl. Acad. Sci. USA, 98, 8827–31.

Maffei, L., Fiorentini, A., (1976). The unresponsive regions of visual cortical receptive fields. Vis. Res., 16, 1131–39.

Martin, K.A., Whitteridge, D. (1984). The relation-ship of receptive field properties to the dendritic shape of neurons in the cat striate cortex. J. Physiol., 356, 291–302.

Maunsell, J.H.R., Sclar, G., Nealey, T.A., and Depriest, D.D. (1991). Extraretinal Representations in Area-V4 in the Macaque Monkey. Vis Neuroscience 7, 561-573.

McAdams, C.J., and Maunsell, J.H.R. (1999a). Effects of attention on orientation-tuning functions of single neurons in macaque cortical area V4. J. Neurosci., 19, 431-441.

McAdams, C.J., and Maunsell, J.H.R. (1999b). Effects of attention on the reliability of individual neurons in monkey visual cortex. Neuron 23, 765- 773.

McIlwain, J.T. (1964). Receptive fields of optic tract axons and lateral geniculate cells: peripheral extent and barbiturate sensitivity. J. Neurophysiol., 27,1154–73

McManus, J. N., Li, W., and Gilbert, C. D. (2011). Adaptive shape processing in primary visual cortex. Proc Natl Acad Sci U S A, 108(24), 9739-46.

Mitchell, J. F., Sundberg, K. A., and Reynolds, J. H. (2009). Spatial attention decorrelates intrinsic activity fluctuations in macaque area V4. Neuron, 63(6), 879-88.

Moran, J., and Desimone, R. (1985). Selective Attention Gates Visual Processing in the Extrastriate Cortex. Science, 229, 782-784

Motter, B. C. (1993). Focal attention produces spatially selective processing in visual cortical areas V1, V2, and V4 in the presence of competing stimuli. J Neurophysiol, 70(3), 909-919.

Motter, B.C. (1994). Neural Correlates of Attentive Selection for Color or Luminance in Extrastriate Area V4. J.Neurosci., 14, 2178-2189.

Mountcastle, V.B., Motter, B.C., Steinmetz, M.A., and Sestokas, A.K. (1987). Common and Differential-Effects of Attentive Fixation on the Excitability of Parietal and Prestriate (V4) Cortical Visual Neurons in the Macaque Monkey. J.Neurosci., 7, 2239-2255.

Nelson, J. I., and Frost, B. J. (1985). Intracortical facilitation among co-oriented, co-axially aligned simple cells in cat striate cortex. Exp Brain Res, 61(1), 54-61.

O'Craven, K.M., Downing, P.E., and Kanwisher, N. (1999). fMRI evidence for objects as the units of attentional selection. Nature 401, 584-587.

Olson C.R. (2001). Object-based vision and attention in primates. Curr Opin Neurobiol 11:171-9.

Oram, M. W., Földiák, P., Perrett, D. I., and Sengpiel, F. (1998). The 'ideal homunculus': Decoding neural population signals. Trends Neurosci, 21(6), 259-65.

Palanca, B. J., and DeAngelis, G. C. (2005). Does neuronal synchrony underlie visual feature grouping?. Neuron, 46(2), 333-46.

Panzeri, S., Schultz, S. R., Treves, A., and Rolls, E. T. (1999). Correlations and the encoding of information in the nervous system. Proc Biol Sci, 266(1423), 1001-12.

Paradiso, M. A. (2002). Perceptual and neuronal correspondence in primary visual cortex. Curr Opin Neurobiol, 12(2), 155-61.

Pascual-Leone, A., and Walsh, V. (2001). Fast backprojections from the motion to the primary visual area necessary for visual awareness. Science 292, 510–512.

Petersen, C.C., Hahn, T.T., Mehta, M., Grinvald, A., and Sakmann, B. (2003). Interaction of sensory responses with spontaneous depolarization in layer 2/3 barrel cortex. Proc. Natl. Acad. Sci. USA 100, 13638– 13643.

Pettet M. W., and Gilbert, C.D. (1992). Dynamic changes in receptive field size in cat primary visual cortex. Proc. Natl. Acad. Sci. USA, 89, 8366 – 8370.

Poort, J., and Roelfsema, P. R. (2009). Noise correlations have little influence on the coding of selective attention in area V1. Cereb Cortex, 19(3), 543-53.

Posner, M. I., & Gilbert, C. D. (1999). Attention and primary visual cortex. Proc Natl Acad Sci U S A, 96(6), 2585-7.

Ramachandran, V.S., and Braddick, O. (1973). Orientation-specific learning in stereopsis. Perception, 2, 371-6

Ramachandran V. S., and Gregory T. L. (1991). Perceptual filling in of artificially induced scotomas in human vision. Nature 350: 699–702.

Recanzone, G.H., Merzenich, M.M., Jenkins, W.M., and Grajskim, K.A., and Dinse, H.R. (1992). Topographic reorganization of the hand representation in cortical area 3b owl monkeys trained in a frequency-discrimination task. J Neurophysiol., 67, 1031-1056

Recanzone, G., Schreiner, C., and Merzenich, M. (1993). Plasticity in the frequency representation of primary auditory cortex following discrimination training in adult owl monkeys. J. Neurosci., 13, 87-103.

Reynolds, J.H., Alborzian, S., Stoner, G.R. (2003). Exogenously cued attention triggers com- petitive selection of surfaces. Vision Res., 43(1), 59–66.

Reynolds, J.H., Chelazzi, L., and Desimone, R. (1999). Competitive mechanisms subserve attention in macaque areas V2 and V4. J.Neurosci., 19, 1736-1753.

Reynolds, J.H., and Desimone, R. (2003). Interacting roles of attention and visual salience in V4. Neuron 37, 853-863.

Reynolds J. H., Pasternak T, and Desimone R. (2000). Attention increases sensitivity of V4 neurons. Neuron 26:703-14.

Reich, D. S., Mechler, F., and Victor, J. D. (2001). Independent and redundant information in nearby cortical neurons. Science, 294(5551), 2566-8.

Ress, D., Backus, B.T., and Heeger, D.J. (2000). Activity in primary visual cortex predicts performance in a visual detection task. Nat. Neurosci. 3, 940–945.

Riehle, A., Grun, S., Diesmann, M., and Aertsen, A. (1997). Spike synchronization and rate modulation differentially involved in motor cortical function. Science 278, 1950–1953.

Rockland, K. S., and Lund, J.S. (1982). Widespread periodic intrinsic connections in the tree shrew visual cortex. Brain Res., 169, 19– 40.

Rockland, K. S., and Lund., J. S. (1983). Intrinsic laminar lattice connections in primate visual cortex. J. Comp.Neurol., 216, 303 – 318.

Roelfsema, P.R., Engel, A.K., Konig, P., and Singer, W. (1997). Visuo- motor integration is associated with zero time-lag synchronization among cortical areas. Nature 385, 157–161.

Roelfsema, P. R., Lamme, V. A., and Spekreijse, H. (1998). Object-Based attention in the primary visual cortex of the macaque monkey. Nature, 395(6700), 376-81.

Roelfsema, P. R., Lamme, V. A., and Spekreijse, H. (2004). Synchrony and covariation of firing rates in the primary visual cortex during contour grouping. Nat Neurosci, 7(9), 982-91.

Romo, R., Hernández, A., Zainos, A., and Salinas, E. (2003). Correlated neuronal discharges that increase coding efficiency during perceptual discrimination. Neuron, 38(4), 649-57

Rossi, A.F., and Paradiso, M.A. (1999). Neural correlates of perceived brightness in the retina, lateral geniculate nucleus, and striate cortex. J.Neurosci., 19, 6145-6156.

Rossi, A.F., Rittenhouse, C.D., and Paradiso, M.A. (1996). The representation of brightness in primary visual cortex. Science 273, 1104- 1107.

Schein, S.J., and Desimone, R. (1990). Spectral Properties of V4 Neurons in the Macaque. J.Neurosci., 10, 3369-3389.

Schmidt, K.E., Goebel, R., Lowel, S., and Singer, W. (1997). The perceptual grouping criterion of colinearity is reflected by anisotropies of connections in the primary visual cortex. Euro. J.Neurosci., 9, 1083- 1089.

Schoups, A., Vogels, R., Qian, N., and Orban, G. (2001). Practising orientation identification improves orientation coding in V1 neurons. Nature 412, 549–553.

Shadlen, M. N., Britten, K. H., Newsome, W. T., and Movshon, J. A. (1996). A computational analysis of the relationship between neuronal and behavioral responses to visual motion. J Neurosci, 16(4), 1486-510.

Shadlen, M.N., and Movshon, J.A. (1999). Synchrony unbound: a critical evaluation of the temporal binding hypothesis. Neuron 24, 67–77, 111–125.

Shadlen, M. N., and Newsome, W. T. (1998). The variable discharge of cortical neurons: Implications for connectivity, computation, and information coding. J Neurosci, 18(10), 3870-96.

Shmuel, A., Korman, M., Sterkin, A., Harel, M., Ullman, S., Malach, R., and Grinvald, A. (2005). Retinotopic axis specificity and selective clustering of feedback projections from V2 to V1 in the owl monkey. J. Neurosci. 25, 2117–2131.

Siegel, M., and König, P. (2003). A functional gamma-band defined by stimulus-dependent synchronization in area 18 of awake behaving cats. J Neurosci, 23(10), 4251-60.

Siegel, M., Donner, T. H., Oostenveld, R., Fries, P., and Engel, A. K. (2007). High-Frequency activity in human visual cortex is modulated by visual motion strength. Cereb Cortex, 17(3), 732-41.

Sigman, M., and Gilbert, C. D. (2000). Learning to find a shape. Nat Neurosci, 3(3), 264-9.

Sigman, M., Pan, H., Yang, Y., Stern, E., Silbersweig, D., & Gilbert, C. D. (2005). Top-Down reorganization of activity in the visual pathway after learning a shape identification task. Neuron, 46(5), 823-35.

Sillito, A.M., Grieve, K.L., Jones, H.E., Cudeiro, J., and Davis, J. (1995). Visual cortical mechanisms detecting focal orientation discontinuities. Nature 378, 492-496.

Sincich, L. C., and Blasdel, G. G. (2001). Oriented axon projections in primary visual cortex of the monkey. J Neurosci, 21(12), 4416-26.

Singer, W. (1999). Neuronal synchrony: a versatile code for the defi- nition of relations? Neuron 24, 49–65, 111–125.

Singer, W., and Gray, C.M. (1995). Visual feature integration and the temporal correlation hypothesis. Annu. Rev. Neurosci. 18, 555–586.

Spitzer, H., Desimone, R., and Moran, J. (1988). Increased attention enhances both behavioral and neuronal performance. Science 240, 338- 340.

Steinmetz, P.N., Roy, A., Fitzgerald, P.J., Hsiao, S.S., Johnson, K.O., and Niebur, E. (2000). Attention modulates synchronized neuronal firing in primate somatosensory cortex. Nature 404, 187–190.

Stern, E. A., Kincaid, A. E., and Wilson, C. J. (1997). Spontaneous subthreshold membrane potential fluctuations and action potential variability of rat corticostriatal and striatal neurons in vivo. J Neurophysiol, 77(4), 1697-715.

Stettler, D. D., Das, A., Bennett, J., and Gilbert, C. D. (2002). Lateral connectivity and contextual interactions in macaque primary visual cortex. Neuron, 36(4), 739-50.

Tanigawa, H., Wang, Q., and Fujita, I. (2005). Organization of horizontal axons in the inferior temporal cortex and primary visual cortex of the macaque monkey. Cereb Cortex, 15(12), 1887-99.

Thiele, A., and Stoner, G. (2003). Neuronal synchrony does not correlate with motion coherence in cortical area MT. Nature, 421(6921), 366-70.

Thut, G., Nietzel, A., Brandt, S. A., and Pascual-Leone, A. (2006). Alpha-Band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. J Neurosci, 26(37), 9494-502.

Treisman, A., and Gormican, S. (1988). Feature Analysis in Early Vision - Evidence from Search Asymmetries. Psych. Rev, 95, 15-48.

Treisman, A.M., and Gelade, G.. (1980). A feature-integration theory of attention. Cog. Psych., 12, 97-136.

Treue, S. (2001). Neural correlates of attention in primate visual cortex. Trends Neurosci, 24(5), 295-300.

Treue, S., and Maunsell, J.H.R. (1996). Attentional modulation of visual motion processing in cortical areas MT and MST. Nature 382, 539-541.

Treue, S., and Trujillo, J.C.M. (1999). Feature-based attention influences motion processing gain in macaque visual cortex. Nature 399, 575-579.

Ts'o, D., Gilbert, C.D., and Wiesel, T.N. (1986). Relationships between horizontal connections and functional architecture in cat striate cortex as revealed by cross-correlation analysis. J. Neurosci.,6, 1160–1170.

Vaadia, E., Haalman, I., Abeles, M., Bergman, H., Prut, Y., Slovin, H., et al. (1995). Dynamics of neuronal interactions in monkey cortex in relation to behavioural events. Nature, 373(6514), 515-8.

von der Heydt, R., Peterhans, E., and Baumgartner, G. (1984). Illusory contours and cortical neuron responses. Science 224, 1260-1262.

von der Malsburg, C., and Schneider, W. (1986). A neural cocktail- party processor. Biol. Cybern. 54, 29–40.

Wachtler, T., Sejnowski, T.J., and Albright, T.D. (2003). Representation of color stimuli in awake macaque primary visual cortex. Neuron 37, 681-691.

Walker, G.A., Ohzawa, I., and Freeman, R.D. (1999). Asymmetric suppression outside the classical receptive field of the visual cortex. J.Neurosci., 19, 10536-10553.

Weller, R. E., Wall, J. T., and Kaas, J. H. (1984). Cortical connections of the middle temporal visual area (MT) and the superior temporal cortex in owl monkeys. J. Comp. Neurol. 228,81-104.

Wertheimer, M. (1923). Untersuchungen zur Lehre von der Gestalt II, Psychologische Forshung, 4, 301–350 [translated as Laws of organization in perceptual forms]. In W. D. Ellis, A Source Book of Gestalt Psychology (pp. 71–88). London, Harcourt, Brace and Javanovich.

Westheimer, C. (1990). Simultaneous orientation contrast for lines in the human fovea. Vision Res. 30, 1913-1921.

Williford T and Maunsell JHR (2006) Effects of Spatial Attention on Contrast Response Functions in Macaque Area V4. J Neurophysiol 96:40-54

Womelsdorf, T., Fries, P., Mitra, P. P., and Desimone, R. (2006). Gamma-Band synchronization in visual cortex predicts speed of change detection. Nature, 439(7077), 733-6.

Xiao, D.K., Marcar, V.L., Raiguel, S.E., and Orban, G.A. (1997). Selectivity of macaque MT/V5 neurons for surface orientation in depth specified by motion. Eur. J. Neurosci., 9, 956-964.

Yantis, S., and Serences, J.T. (2003). Cortical mechanisms of space-based and object-based attentional control. Curr Opin Neurobiol, 13,187-93.

Zeki, S. M. (1976). The projections to the superiortemporal sulcus from areas 17and 18 in the rhesus monkey. Proc. Roy. Soc. Lond. (6) 793, 199-207.

Zeki, S. (1983). Color coding in the cerebral cortex: the reaction of cells in monkey visual cortex to wavelengths and colors. Neuroscience 9,741–65.

Zhang N. R., and von der Heydt R. (2010). Analysis of the context integration mechanisms underlying figure-ground organization in the visual cortex. J Neurosci, 30(19), 6482-96.

Zhou, H., Friedman, H.S., and von der Heydt, R. (2000). Coding of border ownership in monkey visual cortex. J.Neurosci., 20, 6594-6611.

Zipser K., Lamme V. A. F., and Schiller, P. H. (1996). Contextual modulation in primary visual cortex. Journal of Neuroscience, 16(22), 7376-7389.

Zohary, E., Shadlen, M. N., and Newsome, W. T. (1994). Correlated neuronal discharge rate and its implications for psychophysical performance.