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Role of Feedforward and Feedback Projections in Figure-Ground Responses

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1. Introduction

In the visual brain incoming sensory information is first decomposed into elementary features in low-level areas and then transferred to high-level areas. There the features are grouped into coherent perceptual representations. Recent findings, however, have established that stimulus evoked responses in the primary visual cortex are modulated by surrounding stimuli. The modulated responses depend on proper recurrent interactions between different, separate visual regions. These extra-classical receptive field responses combine local visual signals with more global information from the visual scene and often reflect relatively high-level perceptual attributes of the stimuli. One of the fundamental problems to be solved by the visual system is the segregation of figure from ground (see Figure 1). A key factor in the figure-ground process is the combination of local with global information. Therefore, contextual influences on neuronal activity have been interpreted as the neural substrate of figure-ground perception.

2. Feedforward projections in the visual system

The visual brain is considered to be hierarchically structured. From the retina most information flows to the primary visual cortex (also referred to as striate cortex, V1, or E17) through the thalamic lateral geniculate nucleus (LGN). In V1 neurons extract simple, rather abstract features (e.g. orientation) within a small part of the visual scene. The feature information is further conveyed to surrounding extra-striate areas and from there to the higher level visual areas. In fact, the feedforward projection is dichotomized into two streams. Axons projecting towards areas in the temporal lobe define the ventral pathway (also called as the “what” or “perception” stream) and projections to the parietal areas form the dorsal pathway (also called the “where” or “action” stream). Information flowing to the

ventral pathway relates to objects and shapes whereas information conveyed to the dorsal pathway relates to attention and space (see Figure 2).



Figure 1. Figure-Ground: Classical psychophysical experiments highlighted that figures emerge from its parts, being perceived as single shapes. Many very well known cases of ambiguity (such as the Rubin vase) exemplify this fact. In these images at any given moment we can perceive as the figure only one of the alternative interpretations, the other becoming the background. The neurophysiological correlates of this phenomenon are discussed here.

The neurons in these latter areas have large receptive fields in order to integrate the elementary visual features. A classical receptive field is defined as the region of the visual scene from which a neuronal cell receives direct information by way of feedforward connections. Then, these cells responses to feedforward inputs are more closely related to our daily experience of the external visual world than are the responses in lower order areas since their selectivity is to more elaborated shapes of an object such as a face. That is, what Hubel and Wiesel advanced in 1968 is essentially true: receptive fields of cells at one level of the visual system are formed from inputs by cells at a lower level. In this way, small, simple receptive fields combine to form large, complex receptive fields.

Feedforward projections are therefore the anatomical substrate for the initial transient response of a neuron to a stimulus, and determine the size and tuning properties of the stimulus evoked response. For instance, the orientation tuning of V1 neurons is predominantly determined by feedforward inputs (Miller, 2003) and by the biophysical membrane properties of the cells (Cardin et al., 2007). The spatial arrangement of the receptive fields of cells in the primary visual cortex follows a retino-topical organization and provides a topographic map of the visual world. Simple cells have an elongated receptive field structure, with an excitatory central oval and an inhibitory surrounding region (Hubel & Wiesel, 1968). In order to excite these cells stimuli need to have a particular orientation or direction. In the case of V1 complex cells, the receptive fields have no clear separation of excitatory and inhibitory regions. To excite these cells an oriented stimulus may need to move in a particular direction and might also need to be of a particular length. Beside excitatory neurons, inhibitory cells are also tuned to orientation and spatial frequency (Cardin et al., 2007). Thus, V1 cells respond selectively to simple, rather abstract features that make up an object within a small part of the visual scene mainly by reason of their connections with striate projecting neurons.

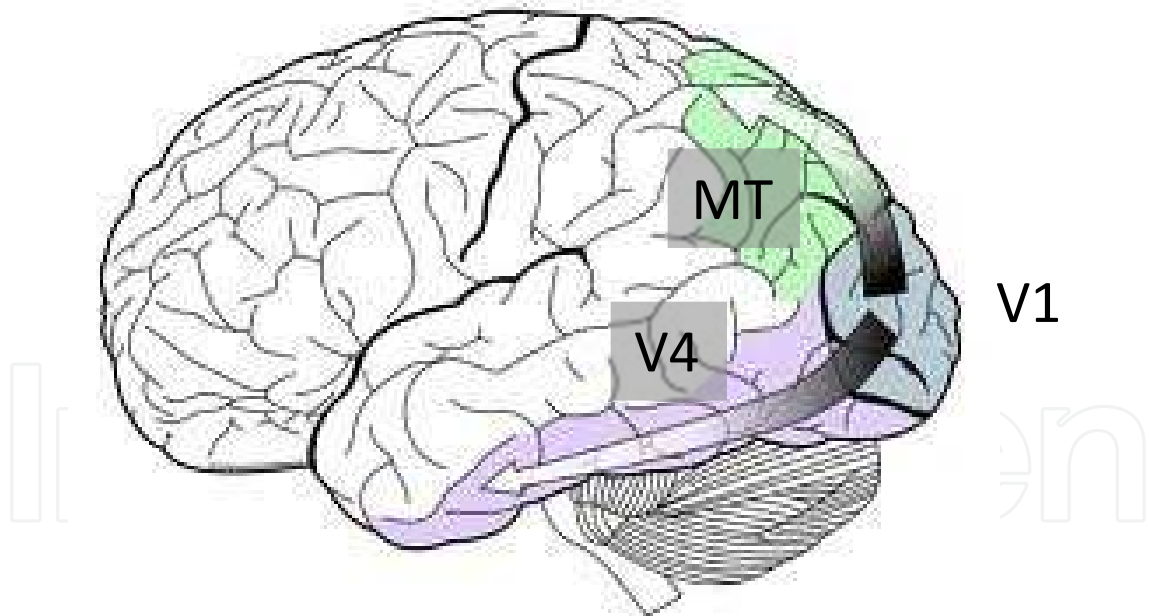
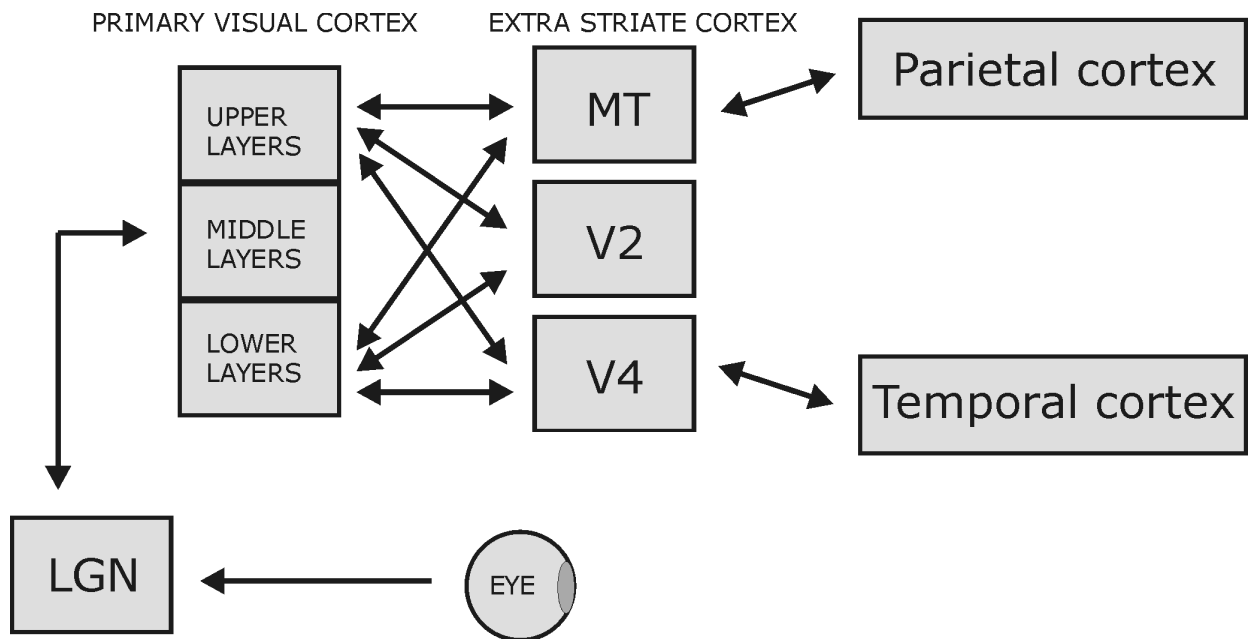


Figure 2. Schematic representation of the main information pathways of the visual system and its anatomical location. Sensory information is conveyed from the retina to the primary visual cortex (V1) from where it is distributed across the higher visual areas via the extra-striate areas. The dorsal stream begins with V1, goes through visual area V2, then to the dorsomedial area and visual area MT (also known as V5) and to the posterior parietal cortex. The ventral stream begins with V1, goes through visual area V2, then through visual area V4, and to the inferior temporal cortex. Top-down information from high-level visual areas towards low-level areas is mediated by feedback connections.

3. Contextual modulation of classical receptive field responses

The feedforward established response property of visual neurons is not fixed. It can be modified by factors such as experience and learning, or, more importantly, by the spatial and temporal context in which a stimulus is presented. The latter strongly influences the stimulus evoked response of a cell. The prominence of contextual information processing is reflected by the fact that the majority of neurons in the primary visual cortex are sensitive to such contextual influences from surrounding regions. Surrounding stimuli outside the classical receptive field do not activate the cell but modulate the response to the stimulus that falls within it. This modulation by the extra classical receptive field signals contextual information to the cell which adds to the classical receptive field response. Such modulation effects are primarily seen for stimuli with high spatial frequencies (Meese & Holmes, 2007) and can be elicited by distal stimulus configurations at distances of up to 30mm within the primary visual cortex (Alexander & Wright, 2006).

The effects of surrounding stimuli on a centre stimulus are complex and signals from the surround have been reported both to be suppressive and facilitatory, as well as both selective and unselective. The way modulation interacts in V1 depends on the relative position and orientation of the centre and surrounding stimuli. For example, for static lines neuronal facilitation is observed when a near threshold stimulus inside the classical receptive field is flanked by high contrast collinear elements located in the surrounding regions of visual space when compared to a single presentation of the low threshold line (Polat et al., 1998). In contrast, when the flanked lines differ in their orientation or are not collinearly aligned suppression of neural activity to the target line is observed (Kapadia et al., 2000). For drifting gratings, surround influence is mainly suppressive and suppression tends to be stronger when the surround grating also moves in the neurons preferred direction. When the surround is 90 degrees from the preferred orientation (orthogonal), suppression becomes weaker and sometimes results in response facilitation (Jones et al., 2001). For an orthogonal surround grating suppression is strongest on the flanks (Cavanaugh et al., 2002). Similar accounts for surround suppression have been reported in optical imaging studies (Grinvald et al., 1994) and in the cat visual cortex (Walker et al., 1999). Context modulation is not only a robust feature of neurons in the primary visual cortex, it is also observed in high visual areas of the monkey, for instance for MT (middle temporal) neurons in the motion domain and for V4 neurons in the color domain (Allman et al., 1985).

Surround stimuli not only have an effect on cortical neurons but also on thalamic relay cells. For example, surround stimuli used for neurons in the primary visual cortex suppress the classical receptive field response of neurons in the lateral geniculate nucleus (LGN) suggesting that contextual interactions alter the transfer of thalamocortical information. Similar effects are also observed in the cat where surround suppression is not primarily attributable to intra-cortical inhibition but to a reduction of thalamocortical inputs (Ozeki et al., 2004). A modification in the feedforward signal by non-classical receptive field stimulation in the cat visual cortex is also seen to enhance orientation tuning selectivity (Chen et al., 2005). Context modulation seems thus to be a very general phenomenon

throughout the visual brain allowing the comparison of the sensory patterns inside and outside the receptive field.

4. Contextual modulation in figure-ground segmentation

Most of these contextual modulations are described for stimulations by a single bar with surrounding bars. Visual perception, however, requires the grouping of such individual features into coherent and meaningful objects. For example, for a figure-ground texture the orientated line segments are grouped in such a way that they generate the percept of a textured figure overlying a homogeneous background (see Figure 3). Thus, to form a neural representation of the figure the individual encoded line segments of the figure need to be grouped and to be segregated from line segments from the background. In the primary visual cortex, this grouping operation is likely implemented by the same mechanisms as for contextual modulation (Kapadia et al., 2000).

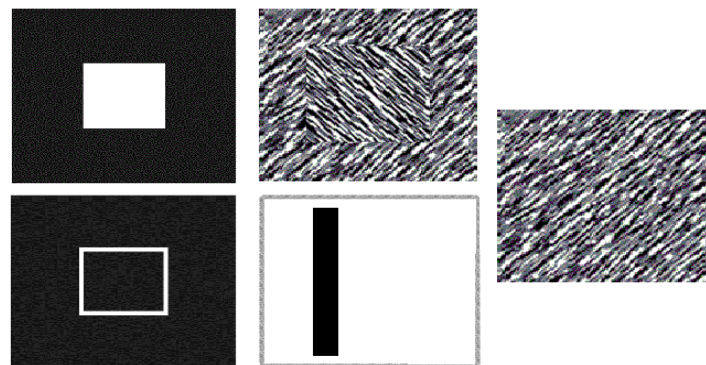


Figure 3. Four different types of figure-ground stimuli and a background in isolation. The figure is defined either by a difference in contrast, in the orientation of its texture lines or in the color of its borders.

While stimulating with such a figure-ground texture and recording neural spike activity in the primary visual cortex, two stages of neural processing after stimulus onset can be discerned. One dominated by the early (<100 msec) response transient, another occurring at relatively longer latencies (> 100 msec). The early stage is associated with feedforward processing and early feature extraction (e.g. stimulus orientation), the later stage has been related to recurrent processing and high level visual processes such as perceptual grouping and segmentation (Lamme & Roelfsema, 2000)(see Figure 4).

For example, at a latency of about 100 msec, (Lamme, 1995; Zipser et al., 1996), when a neuron has its receptive field on the figure location, the cell's activity is enhanced compared to the activity when its receptive field is located on the background. The neural segmentation signals the figure as a whole. Indeed, it is found to be present at the borders as well as at the centre of a textured defined figure (Lamme et al., 1999). This type of contextual modulation is referred to as figure-ground modulation. A study (Rossi et al., 2001) implied the absence of figure-ground based contextual modulation in macaque visual cortex, but it is possible that the authors underestimated the extent of modulation (Corthout & Supèr, 2004).

The delay in the onset of extra-classical receptive field modulation is independent of the time at which the receptive field itself was first stimulated and is not a side effect of the recent history of receptive field stimulation. Zisler et al. (Zipser et al., 1996) showed this by using a two-step procedure in which they first present a homogeneous texture display (thereby generating the initial burst of neural activity) and then subsequently modifying only the extra receptive field stimulus so that a textured-defined figure appeared. After the initial burst, the response strength settled into a steady state of activity. However, between 80 and 100 msec after the display changed to the figure configuration, the response rate rebounded to a more elevated level of activity.

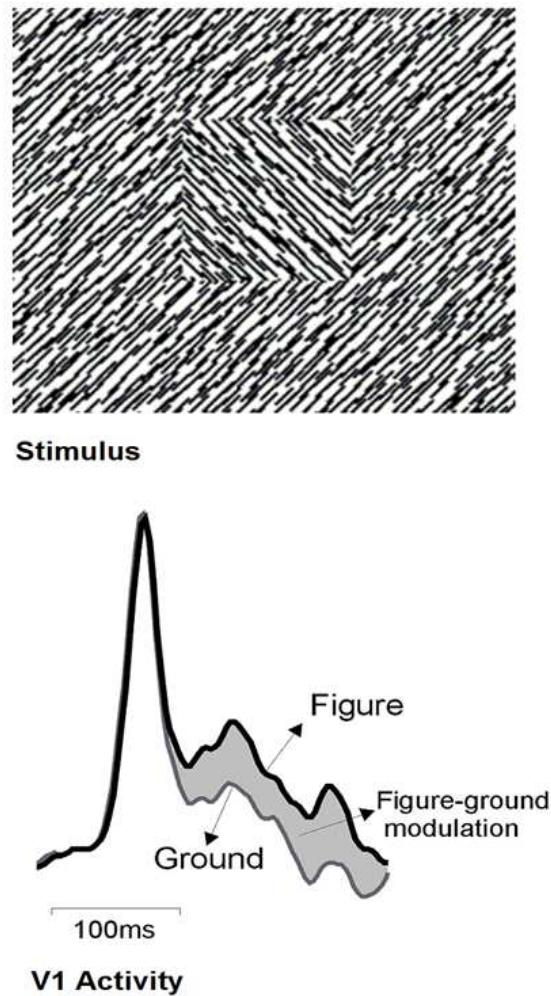


Figure 4. Late V1 responses signal figure-ground context (shaded area). Traces represent the strength of spiking activity over time. When a texture is presented to the eye neurons in the visual cortex respond robustly (= first peak of activity). After approximately 100 ms. responses differ according to the context of the classical receptive field stimulus. In the figure case responses are enhanced (black trace) compared to the homogeneous or ground condition (grey trace). This enhanced neural activity is referred to figure-ground modulation.

Neurophysiological observations show that figure-ground modulation occurs first at the border of the figure followed by modulation for the center region of the textured figure (Lamme et al., 1999; Marcus & Van Essen, 2002; Huang & Paradiso, 2008). These findings can be interpreted as a filling-in process or, alternatively, as two independent processes of border detection and a grouping operation where surface responses simply lag behind the responses to the border.

The finding that surface signals and not boundary signals are reduced by extra-striate lesions (Lamme et al., 1999) argues for two distinct mechanisms. Also, the finding that the onset of the modulated responses across the whole surface is the same (Lamme et al., 1999) argues against a gradual filling-in process of textured stimuli over time and favors independent mechanisms for boundary and surface detection. In Supèr et al. 2010, by means of computational modeling it was shown that the whole figure pops-out instantaneously and no filling-in process of the figural region takes place. Therefore, the model data also fit the idea of two independent mechanisms for local border and surface detection.

Lamme showed onset latencies for figure-ground modulation of 60-120 ms after stimulus onset, or 30-60 ms after response onset (Lamme et al., 1999). General, non-specific surround suppression, in contrast, is an earlier contextual effect which takes about 7 ms to develop after response onset (Knierim & Van Essen, 1992). This authors also found that the orientation specific modulation of responses to centre-surround stimuli occurs a bit later, around 15-20ms after the response onset (Knierim & Van Essen, 1992). In another study, early textured figure-ground segregation was seen to occur at 40-80 ms after stimulus onset (Marcus & Van Essen, 2002) and was not different between V1 and V2 neurons.

5. Figure-ground activity as a neural correlate of visual perception

So far we have described how by modulating the classical receptive field activity extra-classical receptive field effects combine local signals with more global information from the visual scene. Such extra classical receptive field responses, therefore, will reflect in our brain relatively high-level perceptual attributes of the stimuli that fall within the neuron's small receptive field.

Several studies show that the influences of various contextual patterns on neuronal activity in the primary visual cortex of awake, behaving monkeys resemble in many respects with the influences of the same contextual stimuli on human perception (Li et al., 2000; Kapadia et al., 2000). For example, when an oriented line is embedded in similar lines within similar orientation, it will be less salient than when the surrounding lines have an orthogonal orientation. Correspondingly, contextual modulation is stronger in the latter case than in the first case. Furthermore, presence of surround features result in neuronal response suppression and also in perceptual masking (Li et al., 2000). This masking can be relieved by a difference in orientation between the target and surrounding features (Van der Smagt et al., 2005). Similarly, contextual modulation has been interpreted as the neural substrate of many perceptual phenomena, like pop-out (Knierim & Van Essen 1992), perceived

brightness (Rossi et al., 1996), figure-ground segmentation (Lamme, 1995; Zisper et al., 1996), detection of focal orientation discontinuity (Sillito et al., 1995), tilt illusion (Gilbert & Wiesel, 1990), and perceptual grouping (Kapadia et al., 2000).

In figure-ground perception, neurons in the primary visual cortex not only provide border information from illusory contours (Von der Heydt et al., 1984; Grosf et al., 1993; Lee & Nguyen, 2001), they also carry information about surface perception. As we stated before the figure seems to pop-out: when, for example, a surface area is perceived neurons in the primary visual cortex are activated throughout the region topographically corresponding to the perceived surface and not restricted to the region representing the border of the surface (Komatsu, 2007). Similarly, they correlate with perceived surface lightness (MacEvoy & Paradiso, 2001).

But a direct link between the figure-ground modulation and the animal's percept of the figure was not found before a study by Supèr et al. (Supèr et al., 2001a) showing that figure-ground responses are present when the animal perceives the figure and absent when the animal does not perceive the figure. It also proves that the early stimulus driven activity (0-100 ms) does not relate to whether the figure is seen or not seen but exclusively the late figure-ground modulation (see Figure 5).

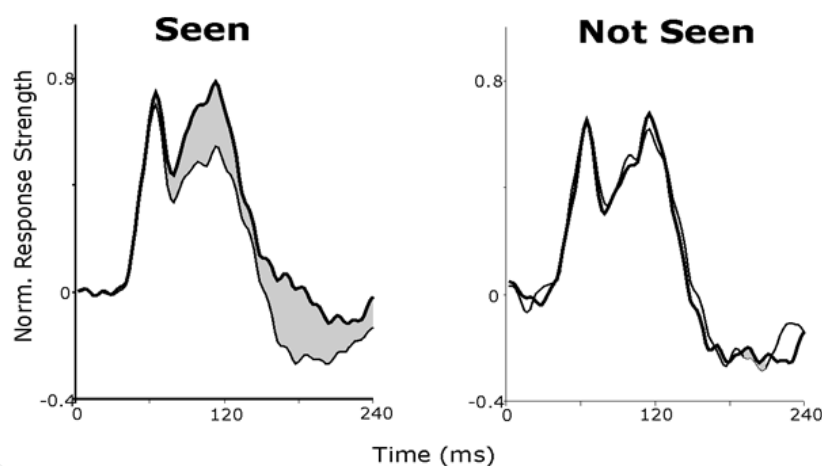


Figure 5. Figure-ground modulation (shaded areas) is present for perceived stimuli (left panel) and absent for not perceived (right panel) figures. Note that in both condition neurons are equally well activated by the feedforward projections, i.e. the first peak responses (adapted from Supèr et al 2001a).

Similarly, figure-ground modulation is selectively suppressed in anesthetized animals, while responses remain selective for low-level features such as orientation of texture bars (Lamme et al., 1998). Also backward masking of figure-ground textures rendering the figure invisible abolishes figure-ground modulation (Lamme et al., 2002), and figure-ground perception is severely impaired when feedback information from extra-striate areas is removed (Supèr & Lamme, 2007a). Finally, figure-ground modulation represents a neural correlate of working memory (Supèr et al., 2001b) and becomes part of the motor preparation (Supèr et al., 2003b, 2004; Supèr & Lamme, 2007b).

6. Feedback connections to primary visual cortex

Most, perhaps all, feedforward connections from V1 to higher visual areas are reciprocated by strong feedback projections. V1 connects with at least 12 subdivisions of the visual cortex. It receives projections from the following extra-striate visual areas: V2, V3, V3A, V4, V4t, MT (V5), parieto-occipital sulcus (PO) and posterior intraparietal area (PIP) (Felleman & Van Essen, 1991). Feedback pathways to V1 carry mainly excitatory input and project preferentially to pyramidal cells (see Figure 6).

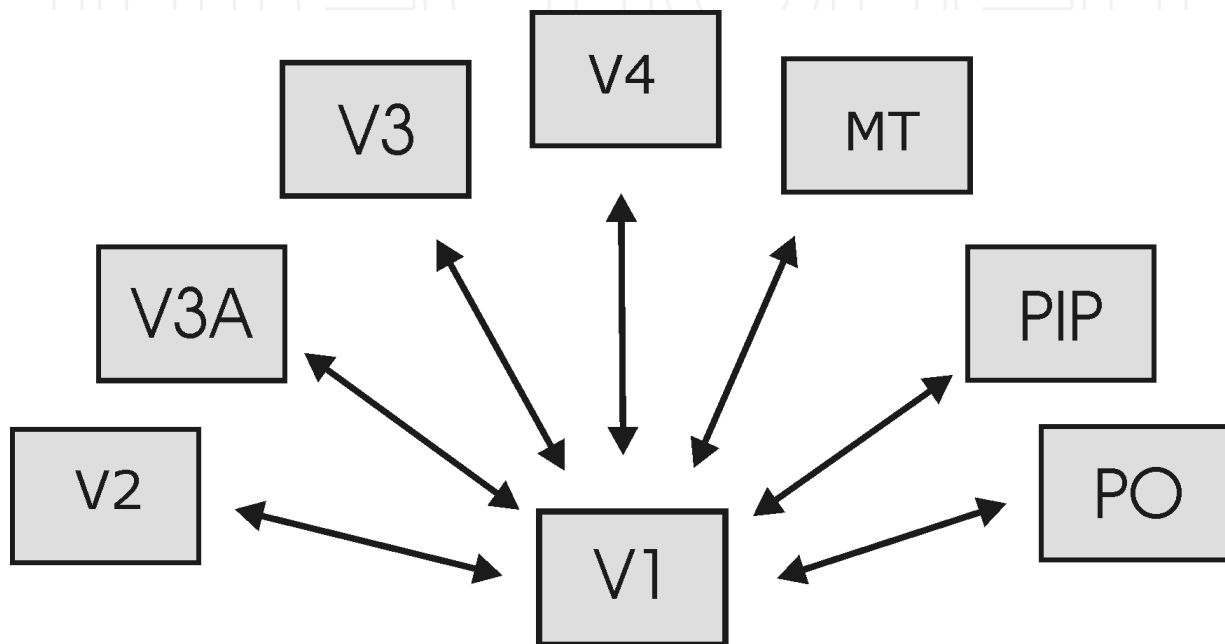


Figure 6. Main feedforward and feedback projections between V1 and extra-striate areas.

Being the number of feedback axons significant, the cortico-cortical connections generate a lower mean-amplitude excitatory post-synaptic potential (PSP) than either thalamo-cortical or feedforward cortico-cortical connections (Shao & Burkhalter, 1996). Conceivably these weak synaptic connections indicate a modulatory role for feedback to V1 neurons since it does not suffice to activate its otherwise silent cells.

In fact, feedback connections show an orderly topographic organization and terminate in discrete patches within V1. The patchy feedback terminations overlap with patches of V1 feedforward projecting neurons (Angelucci et al., 2002), tend to target alike tuned cells (Budd, 1998), and correlate with ocular dominance, iso-orientation columns, and the so called Cytochrome Oxidase-rich blobs (neurons assembled in cylindrical shapes) (Sincich & Horton, 2005).

What's more, the distribution patterns of feedback axons follow a laminar segregation (Felleman & Van Essen, 1991). Feedback axons terminate in upper layers 1, 2/3, 4B and lower layers 5/6, whereas the granular layer is excluded from feedback projections. Some layers appear to have reciprocal connections: projections from primary visual cortex to MT originate from layers 4B and 6. Feedback from MT is predominantly to layers 4B and 6.

Similarly, feedforward projection to V2 and V3 comes mainly from layers 2/3, which also receive most feedback from V2 and V3. Besides feedback to V1, the striate cortex also feeds back to the LGN. Feedback to the LGN is retinotopically organized, and the cells in layer 6 of the visual cortex that provide the feedback arise from differently distributed cell groups, which have functionally selective visual-response properties.

On the other hand, conduction velocities of feedback connections are just as fast as those of feedforward connections (~3-10 m/sec). Apparently, feedback acts on the early part of the stimulus evoked response (Hupé et al., 2001) which suggests that feedback signals are present in V1 all together with feedforward signals from the thalamus. The role of feedback in the early stage response can be seen specifically in the fact that inactivation of areas V2 and MT reduces the response of neurons in V1 to visual stimulation of their receptive field center. It also reduces the suppressive effect of surround motion stimulation. Moreover, feedback-enhanced centre-surround antagonism influences the stimulus driven synchronization. For instance, orientation tuning curves are much broader in the absence of feedback. Thus, retinal stimulation not solely determines the responses of V1 neurons but they are deeply influenced by extensive top-down information.

7. Horizontal connections

Intrinsic horizontal connections that link surrounding neurons convey information from beyond the classical receptive field representing an alternative to feedback for providing contextual information of the target stimulus (Angelucci et al., 2002; Cudeiro and Sillito, 2006). In V1 they are intra-laminar projections made by excitatory neurons in layers 1, 2/3, 4B, and 5/6. Horizontal connections are frequently reciprocal and project locally (short; limited to a few hundreds of microns) up to several millimeters (long) within the primary visual cortex. The distribution of horizontal axonal projections is not globular but tends to be co-aligned with the shape of the receptive fields where axons project collinearly (Angelucci et al., 2002). Moreover, the termination of horizontal axons appears to be patchy indicating that these axons specifically select neighboring cells to contact. For instance, horizontal connections preferentially interconnect columns of similar ocular dominance and cells with similar orientation preference. Interestingly, the excitatory inputs from lateral connections and also from feedback pathways can suppress activity of neurons in the column.

It has been proposed that short horizontal connections shape the spatial summation properties of V1 neurons at low contrast. One example of such “short-range” surround modulation is the enhancement of the receptive field center response to an optimally oriented low-contrast stimulus by flanking co-oriented and co-axial high-contrast stimuli; a phenomenon thought to underlie perceptual grouping of contour elements named co-linear facilitation. A further reason why short horizontal connections may be the underlying anatomical substrate of this phenomenon is that GABA inactivation of laterally displaced V1 sites reduces co-linear facilitation. Horizontal axons have slow velocity conductance (typically 0.1-0.2 m/sec), i.e. about 30-50 times slower than feedforward and feedback connections (Girard et al., 2001). Since it has been shown that contextual suppressive effects

come from large regions (4-7mm), the limited horizontal spread of axons (up to 3.5-4.5 mm radius in V1 monkey) together with the already mentioned slow conductance velocities of these fibers cast doubt on a role for horizontal connections in perceptual integration (See Supèr et al., 2010).

8. Role of feedback in figure-ground

Feedback projections from higher visual areas to lower areas are more suitable to provide the contextual information necessary for figure-ground segmentation since they have high conductance velocity (~3-10 m/sec), have large spread in V1 and influence surround mediated responses in it.

Figure-ground segregation may start with a boundary detection process followed by filling-in the surface between these boundaries. Psychophysical studies where detection is initiated at the boundaries between surfaces (Motoyoshi, 1999) lead to such an interpretation. Discriminating local discontinuities in texture elements suffices for border detection, which in principle can be accomplished by horizontal projections. Surface detection, however, is likely an expression of more global influences. Neurophysiological data show that surface signals, and not boundary signals, are abolished by extra-striate lesions (see Lamme et al., 1999) and support such a role for feedback.

Not all feedback may contribute to figure-ground segmentation; although inactivation of V2 does decrease the neuronal response to the single bar, it has no effect on centre-surround interactions of neurons in the primary visual cortex (Hupé et al., 2001). This may mean that figure-ground segmentation occurs in parts of the cortex that do not receive feedback, at least from V2. Indeed, the exact role of feedback in figure-ground segregation is not clear. For instance, does feedback have a decisive role in the occurrence of figure-ground activity or a more modulatory role in controlling the strength of the figure-ground signal? Many arguments are inconsistent with a leading role of feedback projections in producing either contextual effects or directly figure-ground segmentation. A lesion study provides further evidence showing that after removing most of the feedback (including V3, V4, MT, MST, but not V2) to V1 detection of textured figure-ground stimuli presented in the lesioned field was not affected (Supèr & Lamme, 2007a).

However, consistent with the modulatory role, visual context presumably transmitted by feedback may activate non-stimulated regions of V1 (Smith & Muckli, 2010), and in agreement with TMS experiments (Pascual-Leone & Walsh, 2001; Silvanto et al., 2005; Corthout, 1999), patient studies demonstrate that V1 alone is not sufficient for simple figure-ground segregation (Allen et al., 2009) suggesting that feedback is required. Yet, as stated before, inactivation of V2, which is the main contributor of feedback to the primary visual cortex, has no effect on centre-surround interactions of V1 neurons (Hupé et al., 2001).

Alternatively, feedback may enhance the response modulation of the figure as a whole. Feedback has been shown to have a push-pull effect where the responses to centre stimulus are enhanced and the responses to surrounding stimuli suppressed (Cudeiro & Sillito, 2006).

A sort of push-pull operation also takes place during figure-ground segregation. Compared to responses to homogeneous textures, responses to figure elements are enhanced and responses to ground elements, where a figure is presented outside the receptive field, are weakened. In this case, feedback acts as a kind of attention mechanism by pulling the figure signal and pushing the ground responses and so enhancing stimulus contrast (De Weerd et al., 1999; Hayes & Merigan 2007). Note that this does not mean that figure-ground activity represents a neural correlate of attention. Figure enhancement is observed when attention is divided or directed away from the figure (Landman et al., 2003b). Shifting attention away from the figure location by presenting a pop-out stimulus outside the receptive field produces a suppressive effect for both 'figure' and 'ground' responses, but not necessarily abolish the figure-ground signal (Supèr et al., 2001b).

9. Arguments against a prominent role of feedback in figure-ground

Several more arguments are inconsistent with a leading role of feedback projections in producing contextual effects and figure-ground segmentation. Surround effects are primarily suppressive but blockade of intra-cortical inhibition does not reduce significantly surround suppression (Ozeki et al., 2004). Surround suppression is fast and may arrive even earlier than the feedforward triggered excitatory classical receptive fields response (Bair et al., 2003; Webb et al. 2005). This timing is inconsistent with contextual modulation by late feedback. Also surround suppression in the monkey LGN emerges too fast for an involvement from cortical feedback (Alitto & Usrey, 2008).

Moreover, Supèr and Lamme results in 2007(a), where by removing feedback (but not V2) to V1 figure-ground perception was impaired though visual detection of textured figure-ground stimuli was not affected, imply that figure-ground segmentation occurs without feedback from these extra-striate areas and without producing visual awareness. This agrees with the belief that figure-ground organization is an automatic process (Qiu et al., 2007). For example, preserved figure-ground segregation is observed in neglect patients (Driver et al., 1992) and surface segregation signals evolve independent of attention (Landman et al., 2003b). Similarly, the assignment of border-ownership precedes object recognition and the deployment of attention (Qiu et al., 2007; Von der Heydt et al., 2004). Furthermore, the short onset latencies and sometimes incomplete cue invariance suggest that border-ownership assignment is not generated in higher level visual areas but within the lower visual areas (Zhou et al., 2000).

In addition, figure-ground segmentation depends on the size of the figure region and drops with increasing figure sizes ($>8^{\circ}$ - 12°). This size dependency argues against segregation by feedback since termination fields of feedback projections cover large regions of visual space in V1. Finally, an intriguing finding is that contextual neural interactions corresponding to perception are observed at sub-cortical levels in the LGN and even in the retina (Rossi & Paradiso, 1999) and that competition for object awareness is fully resolved in monocular visual cortex (Tong & Engel, 2001). So, there is considerable evidence against a major role of feedback in figure-ground segregation.

10. Feedforward segregation of figure-ground

Recently it has been demonstrated that figure-ground segregation can be achieved in a purely feedforward manner (Supèr et al., 2010). By means of a computational model (see Figure 7) and using biological plausible spiking neurons surround inhibition was the key factor. The feedforward segregation of figure from ground was robust. A decrease of the input contrast by 80% still yielded figure-ground segregation. Figure-ground segregation occurred for very small figures (even for the size of 1x1 pixel) and for large figures. Since the surround inhibition depended on stimulus size, figure-ground segregation failed when the figure size approximated the background size. This agrees with human figure-ground perception, where small stimuli are interpreted as figures and larger ones as background. When figure and background have the same size the assignment of figure and ground became ambiguous (Barenholtz & Feldman, 2006).

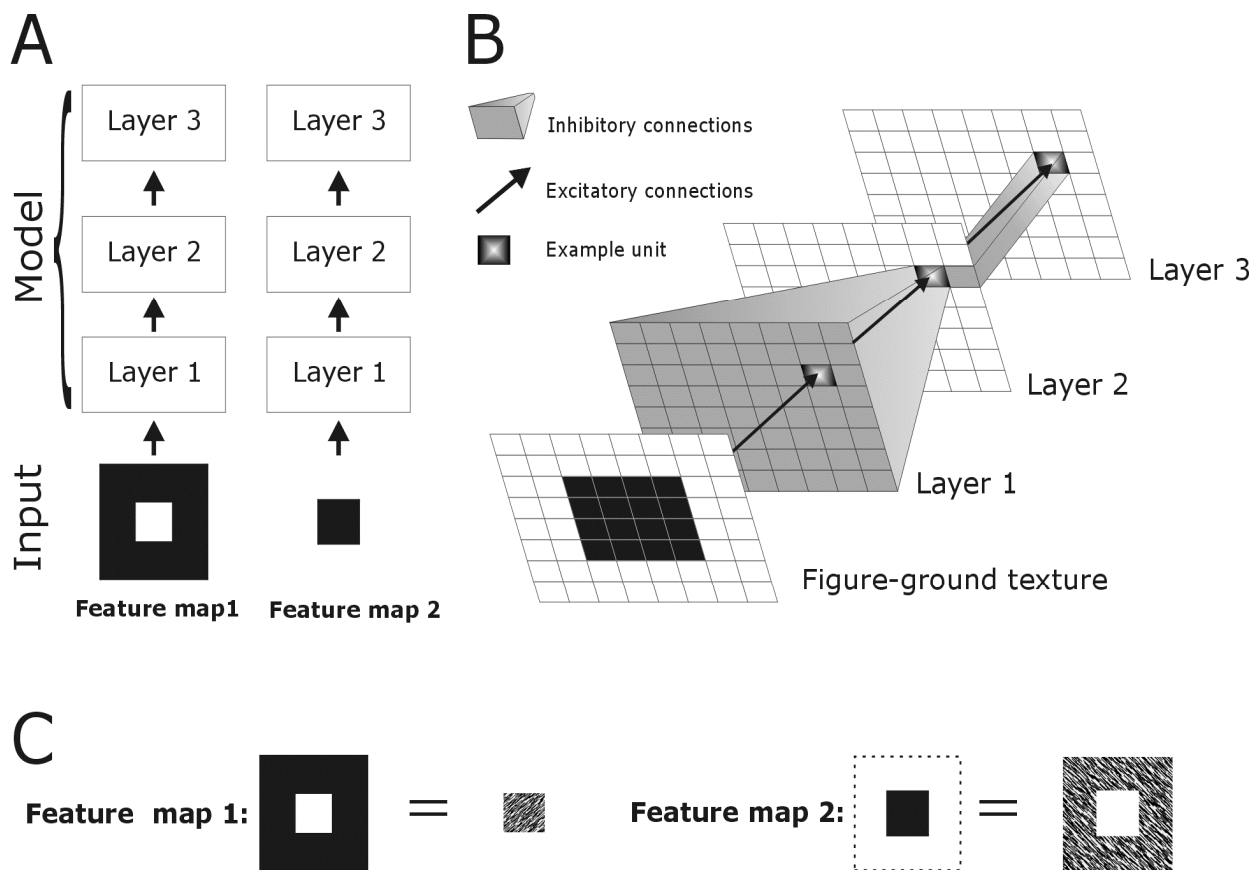


Figure 7. A) Model architecture. It was a three layered model of spiking neurons. B) Connectivity. Local excitation was combined with global inhibition. C) Equivalence between the used feature maps and the original figure-ground textured stimuli.

Feedback has a direct consequence on the activity of the ascending neurons where it lowers the responses to figure elements in layer 1. Despite the inhibitory nature, feedback enhances the figure-ground signal in layer 2. Feedback accomplishes this by a differential effect on neural activity; it enhances figure responses and lowers background responses (Supèr & Romeo, 2011). Such push-pull effect is also observed in neurons of the visual cortex

responding to figure-ground textures (Supèr et al., 2001a; Landman et al., 2003a; Scholte et al., 2008). Moreover, the model shows that feedback especially enhances figure-ground signal when the feedforward input is relatively weak. So feedback acts as a kind of attention mechanism enhancing stimulus contrast (De Weerd et al., 1999; Hayes & Merigan, 2007). In accordance, feedback improves stimulus response precision (Andolina et al., 2007) and feature contrast (Huang et al., 2007), and enhances figure-ground discrimination (Hupé et al., 1998) and top-down attention may enhance both feedforward responses in the LGN (McAlonan et al., 2008) and figure-ground modulatory responses in early cortex (Scholte et al., 2006; Roelfsema et al., 2007; Qiu et al., 2007). Therefore, instead of generating the contextual effects needed for figure-ground segmentation, it is speculated that inhibitory feedback boosts the feedforward generated figure-ground activity. Markedly, feedforward inhibition decreases the figure-ground signal (Supèr et al., 2010) whereas inhibition through feedback increases the figure-ground signal (Supèr & Romeo, 2011). Further studies are needed to understand the dynamics that lead to such a difference.

11. Cortical state, attention, and figure-ground segmentation

The strength of figure-ground modulation depends on the momentary state of the visual cortex (Supèr et al., 2003a, 2003b; Van der Togt et al., 2006. See Figure 8). A proper state is characterized by low-frequency correlated neural firing. Absence or deficiency in such synchronous firing prohibits figure-ground segregation resulting in the occasional failure to detect a stimulus (Supèr et al., 2003a). Supèr & Romeo (2011) showed that feedback affects the strength of figure-ground activity by changing the cortical state, i.e. changing the firing from low-frequency bursting mode (9Hz) to a tonic firing pattern, which is consistent with the observations that feedback shifts neural responses in the thalamus from a bursting mode into a tonic mode (Sherman, 2001).

Low frequency or bursting activity is generally associated with less attentive states. For example, in the thalamic LGN of the awake animal, bursting is more common during periods of drowsiness and is largely restricted to episodes lasting a few seconds with most of the episodes showing rhythmic bursting activity in the delta (0.5-4Hz) frequency (Weyland et al., 2001). In accordance, other studies report that the state of vigilance is associated with single or tonic firing patterns whereas rhythmic bursting at alpha frequencies (8-12Hz) relates to periods of low vigilance (Steriade et al., 1999; Llinás & Steriade, 2006). Furthermore, tonic firing increases the signal-to-noise ratio (Sherman, 2001). Similarly to the dynamical changes in cortical state, fast temporal changes in EEG activity have also been associated with changes in attention and discrimination (Vogel & Luck, 2000; Arnott et al., 2001; Bastiaansen & Brunia, 2001). Putting these findings together it is reasonable to assume that moments of high vs. low vigilance, so to say, have different strength of figure-ground modulation because of the different firing pattern of the ascending neurons (see also Supèr et al., 2003a).

Such an explanation may also be relevant for the observed discrepancy on attentional effects in V1. Whereas single-unit studies of attention in monkeys have repeatedly revealed

relatively modest attentional modulations in V1, human functional magnetic resonance imaging studies demonstrate a large attentional enhancement of the blood oxygen level-dependent (BOLD) signal in V1. A recent report shows that the neuronal metabolic rate differs between low frequency oscillatory bursting and more random or aperiodic (tonic) neural firing where the former gives smaller BOLD responses (Parkes et al., 2004). If one considers that attention, carried by top-down feedback, affects besides spike rate also the firing pattern (bursting versus tonic) fMRI recordings will measure a stronger attentional signals than single cell recordings. Finally, it has been shown that cognitive processing of sensory stimuli, like attention is represented by spike rate as well as by spike timing (synchrony). The finding that feedback changes spike rate by changing spike timing may shed some new light on the debate about the neural correlates of cognitive processing.

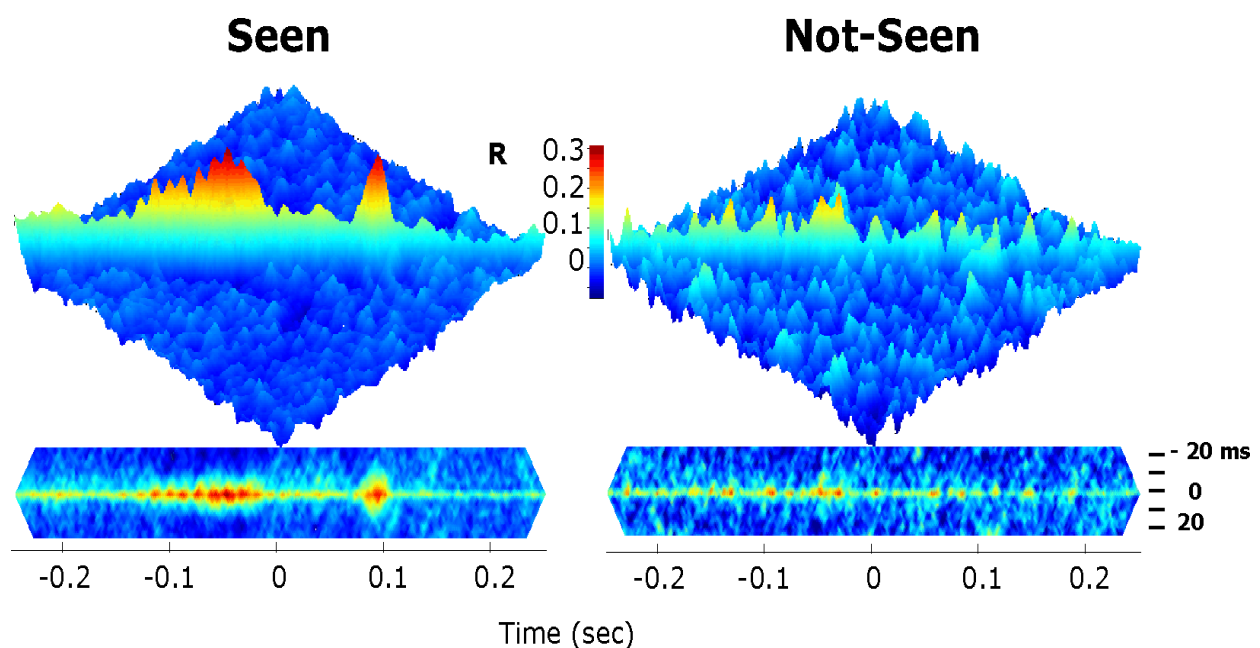


Figure 8. Synchronized V1 activity over time during a figure-ground perception task. Seen condition corresponds to those trials where the animal correctly detected the stimulus and Not-Seen condition corresponds to the trials where the animal failed to perceive the stimulus. A side and a top view are shown of these correlations. Color indicate correlation strength. Time is from onset of figure-ground texture (adapted from Van der Togt et al., 2006).

The states of arousal and attention are strongly linked with the natural release of neuromodulators, in particular acetylcholine, which influence recurrent processing. The neuromodulator acetylcholine reduces the efficacy of feedback and intra-cortical connections via the activation of muscarinic receptors (Kimura & Baughman, 1997). It also increases the efficacy of feedforward connections via the activation of nicotinic receptors (Disney et al., 2007). Application of acetylcholine in the primary visual cortex reduces the extent of spatial integration and enhances the neuronal responses especially in the later (sustained) part of the response (Roberts et al., 2005). Neuromodulators may also modify orientation tuning and improve signal-to-noise ratio of neural responses in the primary visual cortex (Zinke et al., 2006).

The finding that for a perceived figure the strength of neural activity and the functional connectivity (synchrony) between neurons in the primary visual cortex *prior* the textured figure-ground presentation is stronger than for a not perceived figure (Supèr et al., 2003a), exemplifies a role of cortical state in stimulus perception. In other words, activity immediately (~100 msec and not earlier) preceding the onset of the figure-ground stimulus relates to the animal's perception of the figure. Apparently, the visual cortex has to quickly attain an appropriate state before the sensory information enters the cortex. It appears that the different states of the brain preceding stimulus onset (receptive vs. unreceptive, so to say) have little or no effect on the early activity that is evoked by the stimulus, but are specifically associated with the occurrence of later recurrent interactions between areas (Supèr et al., 2003a).

During the later stages when figure-ground modulation develops the characteristics of synchronous activity changes. Still, it does not show an increase or a difference in high frequency components for figure and ground responses. This means that synchrony does not represent a neural correlate of figure-ground segregation, which is consistent with psychophysical (Kiper et al., 1996; Farid & Adelson, 2001), and other neurophysiological studies (Lamme & Spekreijse, 1998; Shadlen & Movshon, 1999; Bair et al., 2001; Thiele & Stoner, 2003). It is inconsistent, however, with a substantial amount of literature suggesting that synchronous activity has a role in high level processes such as perceptual organization, attention, sensory-motor binding, and consciousness (see Engel & Singer, 2001). The modulations in high frequency synchrony relate to perceptual grouping of local feature combinations, which in a figure-ground stimulus are similar for figure and ground textures. In other words the receptive fields of the recorded cells that are located in the centre of the figure are covered on average by identical local features as when they are located on the background. Thus no differences are expected in high frequency synchrony which may provide a plausible explanation for the absence of synchrony modulation in figure-ground task.

12. Conclusion

To sum up, the visual system uses feedforward suppression for figure-ground segmentation. It turns out that global inhibition is an important ingredient for figure-ground organization although it includes also a feedback component. The latter controls figure-ground segregation by influencing the neural firing patterns of feedforward projecting neurons, enhancing figure responses and further suppressing background responses which results in a stronger figure-ground signal.

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