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Fahrenfort, J.J.

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Chapter 4.

Tunnel vision in visual cortex: Suppression of cortical activity in the periphery of figure-ground segregation

Abstract

Although there is strong evidence that extra-classical receptive field effects play an important role in figure ground segregation, the exact mechanisms which underlie it remain incompletely understood. In order to characterize these mechanisms more clearly, we set out to determine the distribution of cortical responses to lightly masked figure-ground stimuli in early visual areas using fMRI. We found two effects in striate and extrastriate cortex, which together constitute what could be construed as cortical tunnel vision: enhanced cortical processing at the location of the figure surface and strong background suppression at increasingly peripheral locations around the figure surface, even though local physical stimulation is – on average – the same. These effects extend way beyond the classical receptive field of neurons in V1. Similar effects have previously been observed in the literature on endogenous top down attention, but not as a sensory-driven exogenous effect. When splitting up the data in seen and unseen figure trials, suppressive effects remained intact for both seen and unseen trials, whereas enhanced processing at the location of the figure surface was selectively abolished in unseen trials. From this we conclude two things: (1) Suppression of the (far) surround occurs in V1 and up, and is not exclusively a top down attentional phenomenon but may also result from sensory-driven processing within visual cortex due to the global organization of the stimulus. (2) Enhanced activity at retinotopic locations in V1 corresponding to the figure surface is only present for seen trials and not for unseen trials.

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Introduction

In top down spatial attention, a type of biasing seems to take place in retinotopic cortex with respect to location. Facilitation takes place for attended locations (Gandhi, Heeger, & Boynton, 1999; Martinez, et al., 1999) and suppression occurs for unattended locations (Slotnick, Schwarzbach, & Yantis, 2003; A. T. Smith, Singh, & Greenlee, 2000; Tootell, et al., 1998). The co-occurrence of these mechanisms can be likened to the neural equivalent of what is often termed “the spotlight of attention” (Brefczynski & DeYoe, 1999); a sort of cortical tunnel vision in which processing at attended locations is enhanced at the expense of locations that are not attended. Notably, these effects have been shown in the earliest human visual area, V1, which points to a role for feedback mechanisms. Such top down influences are commonly thought to originate from frontoparietal cortex (Desimone & Duncan, 1995; Kastner & Ungerleider, 2000), although it is difficult to ascertain causality and origin with certainty (Miller & D'Esposito, 2005; Sirotin & Das, 2009).

Many physiological studies have shown that neurons in V1 can also be influenced by context information due to physical stimulation outside their classical receptive field (cRF) (Cavanaugh, Bair, & Movshon, 2002; Knierim & Van Essen, 1992). In studies of figure ground segregation, enhancements caused by stimulation outside the cRF have been dubbed contextual modulation (CM). These are probably caused by top down feedback from higher areas within visual cortex (Lamme, Super, et al., 1998), and seem to play an important role in segregating a figure from its background (Lamme, 1995; Roelfsema, et al., 2002; Zipser, et al., 1996). CM in the context of figure ground segregation has also been shown in humans (Skiera, Petersen, Skalej, & Fahle, 2000), where it has been demonstrated to continue to operate even during complete inattention (Scholte, et al., 2006) and independently of attention (Heinrich, Andrés, & Bach, 2007).

Thus, unattended texture segregation seems to enhance cortical responses to the segregating surface in V1 and up (Scholte, et al., 2006), while voluntary attention in the absence of visual stimulation, has been shown to do the same thing; enhancing neural responses in early visual areas which retinotopically correspond to the

attended region (Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999). This suggests that even in cases where spatial attention and figure-ground segregation have been functionally dissociated, they both employ neural feedback mechanisms. Because they seem to employ similar mechanisms, some have hinted that they may recruit the same neural pathways (Roelfsema, 2006; Spratling & Johnson, 2004), although the fact that they can be dissociated shows that they are functionally different.

In this experiment, we explore whether “cortical tunnel vision” in early visual areas - as found in studies of endogenous spatial attention - may also play a role in a more stimulus driven context, such as texture segregation. We used fMRI to measure brain activity while showing lightly masked figure-ground stimuli. In order to exclude the possibility that observed effects are caused by the recruitment of endogenous top down attention, we separately analyzed seen and unseen trials, the latter of which should not draw endogenous attention. Cortical suppression of the surround was found in both seen and unseen trials. Enhancement of cortical responses to the figure surface was only present for seen trials, and strongest in V1.

Materials and Methods

Participants

Nineteen subjects were paid to participate in the experiment. All subjects (mean age 21.5, ± 3.6) had normal or corrected-to-normal vision. 79% were female. All subjects provided written informed consent and the study was approved by the ethical committee of the University of Amsterdam.

Stimulation

Stimuli were presented using a DLP beamer which projected onto a projector screen in the scanner room. Subjects viewed the projector screen via a mirror attached to the head coil. Projection size was 16.9° by 12.7° visual angle. The time course of stimulation during a typical

trial is shown in Figure 4.1. Example stimuli are shown in Figure 4.2. At the start of each trial, a fixation dot on a grey background would turn from dark into bright red, followed after 300 ms by texture target with a duration of 100 ms. In half of the trials this target contained an orientation defined square (Figure trials), in the other half the target was a homogenous texture (No Figure trials). All targets (both Figure and No Figure trials) were followed by a pattern mask containing an orientation defined square annulus (Figure 4.2) covering the same area as the target.

Figure 4.1 Example of a typical trial. The fixation dot lights up to bright red (shown here in black with white outline) 300 ms prior to target presentation. The target, which is either a Figure or a homogenous No Figure stimulus, is on screen for 100 ms, followed by a 16.7, 33.3 or 50 ms mask. The subject has 1000 ms to respond, after which the fixation turns back to dark red. The intertrial interval was 1800 ms.

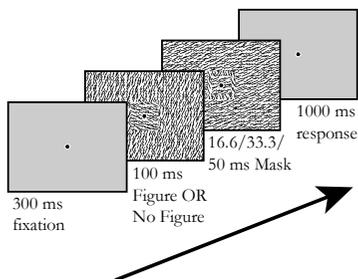
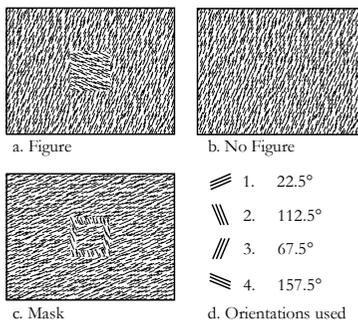


Figure 4.2 Example of stimuli. The target stimulus consisted of either a texture defined square (a. Figure) or a homogenous texture (b. No Figure). All targets were followed by a pattern mask (c). The texture mask contained an orientation defined annulus of which the outer borders coincided with the outer borders of the Figure target. Four orientations were used (d), which were balanced out over conditions so that on average, local physical stimulation for the Figure and No Figure trials was exactly equal.



Mask duration was varied between 16.7, 33.3 or 50 ms. for no other reason than to make the graded response scheme meaningful as a single mask duration would not have resulted in differential responses (see ‘Task and behavioral measure’ below). Subjects were given 1000 ms to respond, after which the fixation dot turned dark red until the start of the next trial. The intertrial interval was 1800 ms. All conditions were randomized and evenly distributed within each

run. Textures consisted of black (0.2 cd/m^2) on white (46.4 cd/m^2) line elements, spanning approximately 0.05° and 0.30° of visual angle, which were spaced apart by an average of 0.20° with a jitter of 0.13° visual angle. Line elements could have four possible orientations: 22.5° , 67.5° , 112.5° and 157.5° . A No Figure target contained a single orientation; a Figure target consisted of two orthogonal orientations. The square in the figure trial subtended 2.0° of visual angle in the center of the screen. Masks consisted of an orientation defined square annulus of the same size as, and in the same central location as the Figure target, and consisted of orientations not used in the preceding target. Border thickness of the mask annulus was 0.33° of visual angle. Stimuli were created using Matlab (The MathWorks, Inc., Natick, MA, USA) and were presented using Presentation (Neurobehavioral Systems, Inc., Albany, CA, USA).

All texture orientations used in a trial were counterbalanced over conditions in such a way that Figure and No Figure trials were equal with respect to local stimulation. This was done in order to be able to carry out the fMRI subtraction procedure detailed later on.

Task and behavioral measure

Approximately one week prior to the fMRI session, all subjects were given a 30 minute training session to become acquainted with the task. After training they took part in one or two fMRI sessions in which they carried out the same task. Subjects were instructed to distinguish between Figure and No Figure trials. A response was always required. With their right hand, they pressed a single button if they were absolutely sure they did not perceive a Figure target (Unseen response), or one of three buttons (3-point scale) if they perceived a Figure target - however faint - depending on perceptual strength. This graded response scheme ensured subjects based their responses on phenomenology and not on guessing, making sure that Unseen responses were truly not seen. It biases the response data towards a conservative measure for invisible trials, rather than diluting the Unseen category with visible trials. The 3-point 'Seen' scale was collapsed into a single response category (Seen response) and not used any further. Separate analyses were carried out on Seen and Unseen trials. To calculate overall visibility for each subject, a perfect observer

score was calculated based on Seen and Unseen responses, reflecting a subjects' ability to distinguish between Figure and No Figure trials. The perfect observer score is a linear and subject bias' free measure derived from d' (Wickens, 2002). It runs from 0 for chance performance to 1 for perfect performance.

fMRI measurements and pre-processing

Recordings were done on a Philips 3T Intera scanner. A total of 32 sessions were scanned using 19 subjects with an average of 5 runs per session. A run started and ended with 16 seconds rest and lasted approximately 10 minutes. The functional recordings were acquired using a T*-weighted sequence (TR 2261 ms, TE 28 ms, 35 slices, slice thickness 2.5 mm; slice gap 0.3 mm, FOV 200 mm). Each run consisted of 288 trials, of which 96 trials were dummy trials intended to improve deconvolution and counteract BOLD saturation in visual areas.

Analyses were done using BrainVoyager QX (Brain Innovation B.V., Maastricht, the Netherlands) and Matlab (The MathWorks, Inc., Natick, MA, USA). The functional images were motion corrected and slice time aligned. No spatial or temporal smoothing was applied. Images were then aligned to a structural image of the subject and transformed to Talairach space.

Regions of interest

For each subject, we extracted the activity of several visual areas. These areas were functionally defined using standard correlational mapping procedures (Wandell, 1999) using runs in which we presented an expanding/contracting wedge (eccentricity mapper) and a rotating wedge (polar mapper) which were obtained in a prior experiment. For each subject we used the averages of two eccentricity and two polar mappers. The following areas were mapped: V1, V2, V3, V3a, V3b, V4, V7 (Brewer, Liu, Wade, & Wandell, 2005; Wandell, Brewer, & Dougherty, 2005). Furthermore, we subdivided visual areas V1, V2 and V3 in three regions of differing eccentricity using the eccentricity mapper, in degrees of visual angle: 0° - 1.9° (center

region), $1.9^\circ - 5.9^\circ$ (near surround region) and $5.9^\circ - 12.7^\circ$ (far surround region), see Figure 4.3. The center region lies within the retinotopic region covered by the Figure stimulus; the near region is the region directly surrounding the Figure stimulus, while the far surround region represents the far surround. The other visual areas V3a, V3b, V4 and V7 were subdivided in just two eccentricities due to difficulties in accurately mapping three regions in these higher areas: $0^\circ - 1.9^\circ$ (center region) and $1.9^\circ - 12.7^\circ$ (surround region).

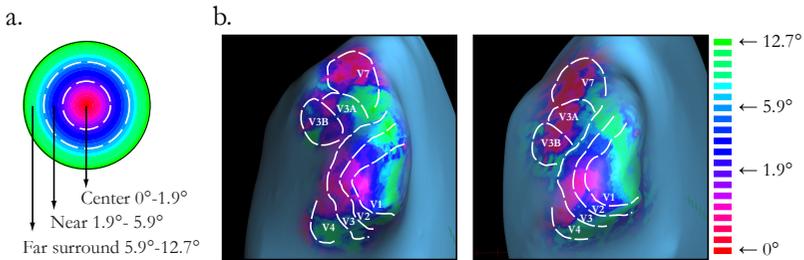


Figure 4.3 a) Color coding of eccentricity phase across the visual field as well as the spatiotopic subdivision in eccentricity bands of early visual areas V1, V2 and V3. The center region covered an area of approximately $0^\circ - 1.9^\circ$ visual angle, the near surround covered an area of $1.9^\circ - 5.9^\circ$ and the far surround an area of 5.9° to 12.7° . Note that the cortical magnification factor was applied to the physical stimulation in the eccentricity mapper so that degrees across the visual field are not linearly represented in this schematic. b) Left hemispheric eccentricity phase data of two arbitrarily chosen subjects projected on the occipital pole of their respective inflated brains. Retinotopic areas are demarcated by white dashed lines. Eccentricity is color coded, legend on the right. The $0^\circ - 1.9^\circ$ eccentricity band is coded in red, the $1.9^\circ - 5.9^\circ$ band in blue and the 5.9° to 12.7° band in green. For V3A, V3B, V4 and V7 the outer eccentricity band regions of interest were collapsed into a single surround band.

Analyses

The functional data was normalized towards percent signal change. Percent signal change over time was estimated for each session, region of interest and condition by running an event related Finite Impulse Response (FIR) deconvolution analysis (Glover, 1999). For each condition, eight predictors were used to code eight consecutive single delay responses from stimulus onset onwards. By fitting a GLM using these predictors, an eight-point haemodynamic response was deconvolved covering a time window of approximately

18 seconds. To give an unbiased depiction of deconvolved BOLD activity, no post-hoc baseline corrections were applied to the deconvolved data. The deconvolved data for each session, region of interest and condition were exported to Matlab for statistical testing and visualization. The No Figure condition was subtracted from the Figure condition; differences between the two conditions for were tested using paired t-tests separately for each time point. Subtracting No Figure from Figure trials has three major advantages:

1. The Figure minus No Figure subtraction isolates activity related to the processing of the figure. As Figure and No Figure targets are made up of the same sets of oriented textures (see Figure 4.2), the influence of local stimulation on cortical processing, such as caused by the line elements in the textures themselves, is subtracted out. The signal left is related to processing of differences in boundaries and figure-ground organization between Figure and No Figure trials. For other examples of this subtraction procedure using figure-ground stimuli see Caputo & Casco (1999), Fahrenfort, Scholte , & Lamme (2007) and Scholte et al. (2006).
2. By the same token, as the rest of the stimulus sequence is exactly equal between Figure and No Figure trials, any direct contribution of other stimuli in the sequence, such as fixation dots and masks, is subtracted out as well. Masks of different durations were balanced between Figure and No Figure trials, and were thus subtracted out.
3. Influences of top-down attention are subtracted out: subjects do not know in advance whether a Figure or a No Figure stimulus will be presented. Therefore the amount of (pre-stimulus) anticipatory top down attention for Figure and No Figure stimuli will – on average - be equal.

The Figure minus No Figure subtraction was also done separately for Seen and for Unseen responses. For this analysis, trials were selected in which subjects either indicated they saw a Figure (Seen), or positively did not see a Figure (Unseen). For both response types, post-hoc counterbalancing was done within each session, such that on average all local orientations and mask durations were equal for Figure and No Figure trials. Figure or No Figure trials that could not be used

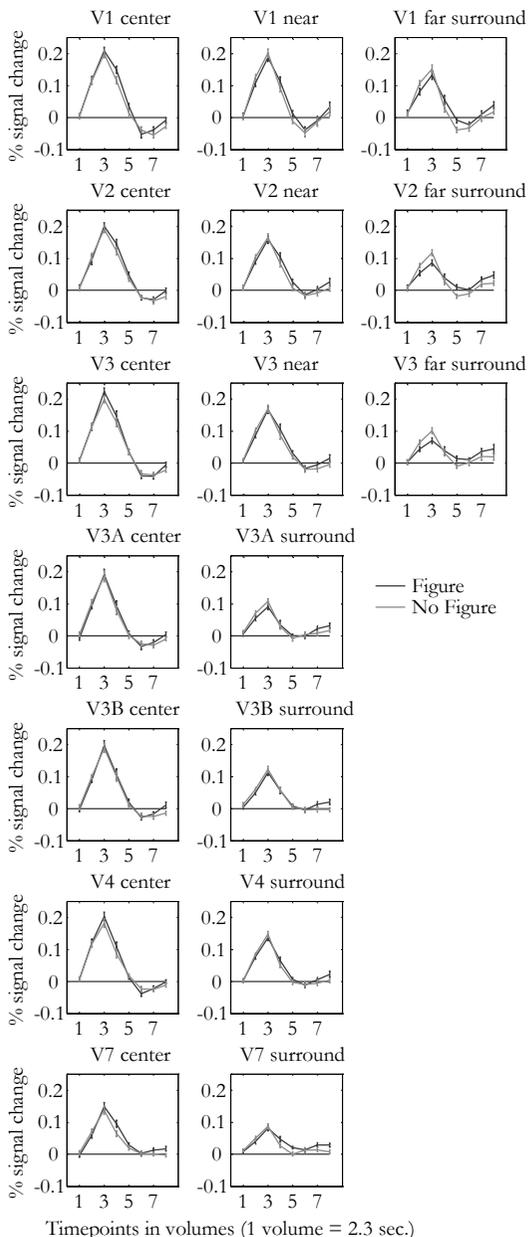
because they contained an orientation and/or mask duration that could not be matched to their counterpart within that response type were modeled separately and later on discarded. Consequently, local stimulation was balanced out between the Seen Figure and No Figure trials on the one hand, and between the Not Seen Figure vs. No Figure trials on the other hand. This ensured that the Figure minus No Figure subtraction procedure detailed above would retain its validity with respect to physical stimulation. If no balanced design for both response categories could be obtained for a particular session, that session would be discarded. 23 sessions were used for the Seen and Unseen analysis.

Results

The average perfect observer score for discriminating between Figure and No Figure trials for all three mask durations was 0.81 (± 0.11), indicating that masking had an effect but that many Figure trials were detected. Figure 4.4 shows the average deconvolved haemodynamic responses to cortical processing of Figure and No Figure trials in early visual areas, subdivided into two and three eccentricities (see Figure 4.3 and methods section), and collapsed over mask duration. Error bars indicate \pm one standard error of the mean. A typical haemodynamic response can be observed for all areas and conditions, with a peak around volume 3 and undershoot around volume 6. Naturally, all visual areas responded strongly to these texture stimuli. Because the relative contribution of the processing of high contrast textures is much larger than the contribution of global texture organization, the differences between Figure and No Figure stimuli is rather small. To highlight this difference, we subtracted Figure from No Figure trials (see Figure 4.5).

Subtracting Figure from No Figure trials has a number of advantages, more extensively highlighted in the Methods section under Analyses: (1) Activity related to the processing of the figure is isolated as influences of local contrast and orientation processing are subtracted out, (2) direct contributions of other stimuli in the sequence are subtracted out and (3) the amount of pre-stimulus top-

Figure 4.4 Shows the estimation of the haemodynamic response function for visual areas V1, V2, V3, V4, V3A, V3B and V7 for Figure and No Figure trials at different eccentricities (see Figure 4.3). Error bars indicate \pm one standard error of the mean. A peak can be observed at volume 3. In the center region the response is higher for the Figure than for the No Figure condition, whereas the surround shows the opposite pattern.



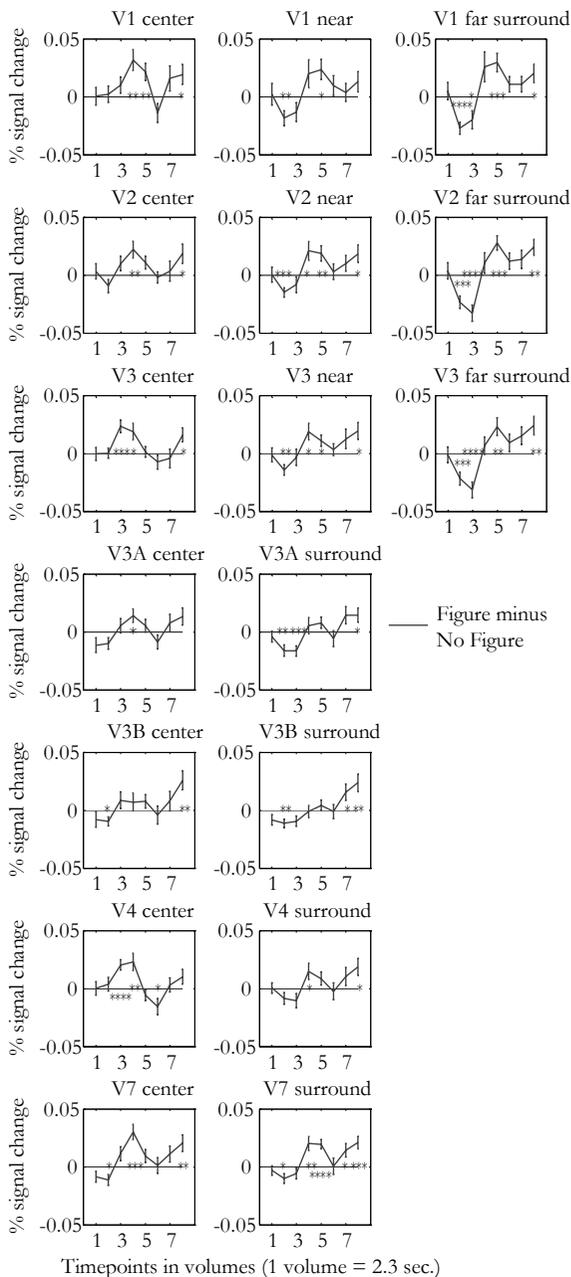
down attention is equal for both stimuli, and thus any influence of anticipatory attention is subtracted out.

Thus, the graphs in Figure 4.5 show the haemodynamic response to processing a figure, barring influence of textures, other stimuli in the stimulus sequence and pre-stimulus attentional effects. Paired t-tests were performed at each time point. Significant differences at a session population level are indicated by asterisks. Areas V1, V2 and V3 were subdivided in three regions of different eccentricities: center, near and far surround (see Figure 4.3a). Almost all areas, starting in V1, show a stronger response to the Figure than to the No Figure stimulus in the center region, as evidenced by the positivity around the time of volume 3 and 4. Similar CM effects have been found in single unit studies of figure ground segregation in macaques. These have shown that neurons in V1 with their receptive field on the figure surface start showing an enhanced response after about ~80-100 ms when compared to the response of these same neurons when they are stimulated by the background (e.g. Lamme, 1995; Zipser, et al., 1996).

The regions corresponding to the near and far surround of the Figure show a largely reversed pattern, with negativity around the time of volume 2 and 3. Thus, in the surround, there is a larger haemodynamic response to the presentation of a homogenous No Figure stimulus than to the presentation of a Figure. An analysis of variance (ANOVA) of these effects at volume 3 for V1, V2 and V3 shows a massive main effect of eccentricity $F(1,2) = 46.14$ ($p < 10^{-12}$) revealing enhancement in the center and increasingly strong suppression moving outwards to the surround. The suppression is strongest in the far surround.

After initial suppression in the surround around volume 3, an enhancement can be seen around the time of volume 5. These enhancements are most likely due to a larger undershoot for responses that have an initially larger primary response. As such, we think they should be interpreted as a reversal of the initial effect seen at volume 3, and meaningless when considered in isolation. Inspect Figure 4.4 for improved understanding of how the course of the raw haemodynamic responses influences the subtracted responses in Figure 4.5. Also note that it is tempting to draw conclusions regarding

Figure 4.5 Shows the Figure minus No Figure difference at different eccentricities (see Figure 4.3) for visual areas V1, V2, V3, V4, V3A, V3B and V7. Note that this is not a raw BOLD signal but a difference signal. For a better understanding of how the raw BOLD signal differs between Figure and No Figure trials please inspect Figure 4.4. Error bars indicate \pm one standard error of the mean. Differences were also tested using a paired *t*-test at each volume. Significant differences are indicated by asterisks: * $p < .05$, ** $p < .01$, *** $p < .001$, **** $p < .0001$.

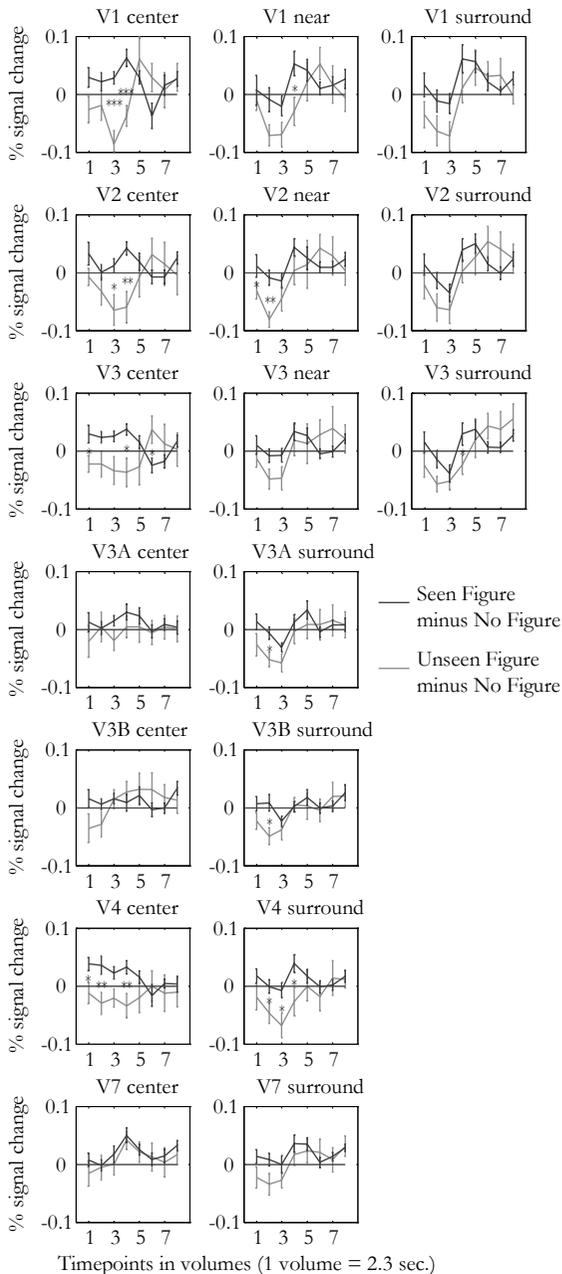


the temporal order of neural processing on the basis of the differences in the timing of peak activation between Figure and No Figure stimuli. For example, as the suppression observed in the far surround of V1, V2 and V3 precedes the timing of the peak response in the center V7 (see Figure 4.5) one may be tempted to conclude that the cortical activity associated with it precedes it as well. However, such putative temporal differences are caused by differences in the shape of the haemodynamic response (see Figure 4.4) and these shape differences are not only influenced by temporal differences in the sequence of neural processing but also by differences in neurovascular effects between cortical sites that are not related to neural activity *per se* (Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001). Moreover, abundant reactivation of cortical areas (e.g. Fahrenfort, Scholte, & Lamme, 2008) potentially causes smearing of the peak of the haemodynamic response function over time, further making between-site inferences regarding the temporal sequence of neuronal activation on the basis of the BOLD signal unwarranted.

Large surround suppressive effects in early visual areas as observed in Figure 4.5 have also been reported in the cortical surround of locations receiving voluntary top down attention (Müller & Kleinschmidt, 2004; Slotnick, et al., 2003; A. T. Smith, et al., 2000). Even though anticipatory attention should be the same for both Figure and No Figure stimuli, it is quite conceivable that the presentation of the Figure stimulus captured additional endogenous attentional resources, indirectly causing suppression of the surround through attention networks. In order to preclude this interpretation, we separately modeled Figure stimuli that were seen and Figure stimuli that were not seen. If suppression of the surround is also present in unseen trials (where the Figure does not attract top down attention), this would show that the suppressive effect is in fact stimulus driven and not caused by endogenous top-down attention.

Figure 4.6 shows the Seen/Unseen analysis. Here, the same Figure minus No Figure difference from Figure 4.5 is shown, but now separately for Seen and Unseen trials. Figure and No Figure trials were carefully balanced with respect to orientation and mask duration so that the subtraction procedure detailed above retains its validity.

Figure 4.6 Shows the Figure minus No Figure difference separately for Seen and Unseen Figure trials at different eccentricities (see Figure 4.3) for visual areas V1, V2, V3, V4, V3A, V3B and V7. Note that these are not raw BOLD but difference signals. For a better understanding of how the raw BOLD signal differs between Figure and No Figure trials please inspect Figure 4.4. Error bars indicate \pm one standard error of the mean. The pattern for Seen trials is the same as the overall pattern observed in Figure 4.5. Unseen trials, like Seen trials, show suppression in the surround, but the enhancement in the center representation which is present in Seen trials is abolished. Differences between Seen and Unseen trials were ascertained using a paired *t*-test at each volume. Significant differences are indicated by asterisks: * $p < .05$, ** $p < .01$, *** $p < .001$.



Differences between Seen and Unseen trials were determined using paired t-tests, significant differences are indicated with asterisks. Overall, the pattern for Seen trials is the same as in Figure 4.5. Baseline levels at volume 1 seem to be slightly higher for Seen than for Unseen trials, although paired t-tests show that these differences are by and large not significant. These may be due to incidental differences in overall vigilance throughout the experiment, leading to more Figures being detected when vigilance is higher.

The graphs representing the surround in Figure 4.6 (rightmost column) show that even when Figure stimuli were Unseen (classified as No Figure stimuli) they still evoked strong stimulus driven suppression in the surround. The shape of the stimulus induced trough in the surround is roughly the same for Unseen and for Seen Figures, strongly suggesting that the suppressive effect is not caused by endogenous top down attention. The pattern is quite different in the center representations of V1, V2 and V3. Here, the enhancement that is found for Seen Figures is abolished and in fact is reversed when Figures are Unseen. The difference between Seen and Unseen trials is most striking in the center region of V1, resulting in a highly significant difference at volume 3 and 4. As a result of this reversal in the center, Unseen Figure trials seem to cause suppression across the entire visual field in V1, V2 and V3.

Discussion

We observed a highly significant cortical tunnel effect, in which the retinotopic region corresponding to the figure is enhanced, while the surround is strongly suppressed in all early visual areas, including V1. Because cortical responses to masked Figure trials are contrasted with masked No Figure trials (both of which are created from the same set of oriented textures) the effect cannot be attributed to anticipation, to differences in local stimulation or to any effects originating from the presentation of the mask itself. This cortical tunnel effect is reminiscent of effects found in the spatial attention literature, where activity levels in areas on which attention is focused are enhanced, whereas activity levels at locations where attention is not directed are suppressed (Müller & Kleinschmidt, 2004; Slotnick, et al., 2003; A. T. Smith, et al., 2000).

It is therefore conceivable that these effects are partially caused by the allocation of top down endogenous attention to visible Figure stimuli. To rule out this possibility, we separately analyzed seen and unseen trials. The result of this analysis shows that suppressive effects in the surround also occur when a Figure stimulus is completely unseen due to masking. This effectively rules out the influence of endogenous attention as a cause for the extra-classical suppressive effects in the far surround. However, it does not imply that invisible figures are free from attentional influences altogether. Some experiments have shown that invisible stimuli may capture exogenous bottom up attention (McCormick, 1997; Mulckhuysen, Talsma, & Theeuwes, 2007). Nevertheless, such bottom up effects are different from endogenous top down attention in that they are automatic and stimulus driven, as supported by recent evidence in which top down and bottom up attention were dissociated (Buschman & Miller, 2007). Therefore the claim we make that to our knowledge has not been made prior, is that the massive extra-classical suppressive effects we find in the surround are caused by stimulus driven activity originating from sensory areas (which may include exogenous bottom up attention), as they can also be observed for unseen stimuli.

Regardless of whether the term bottom up attention is applicable in this context, it is clear that these extra-classical field suppressive effects are not caused by endogenous top down attention but driven by mechanisms originating from sensory cortex, and it is therefore worthwhile to examine what neurophysiological mechanisms may underpin it. If top down attention is not driving the effects, what is? In directed attention, enhancement has been observed for retinotopic locations that are attended at the expense of non-attended locations in V1 and up, plausibly due to feedback initiated from frontoparietal areas (Müller & Kleinschmidt, 2004; Slotnick, et al., 2003; A. T. Smith, et al., 2000). In automatic texture segregation on the other hand, instead of being triggered 'at will', feedback processing is thought to be triggered from within visual cortex, as a consequence of stimulus classification in the feedforward sweep. How this process might lead to figure ground segregation and grouping is worked out in some detail in the incremental grouping theory (Roelfsema, 2006). In this theory, base groupings with

increasing complexity are established in the feedforward sweep as a result of lateral interactions between neurons with increasingly large receptive field sizes. This feedforward cascade eventually leads to initial stimulus classification, after which feedback processing serves to incrementally group image regions corresponding to particular perceptual surfaces or objects in retinotopic cortex. In this way, retinotopic space in striate and extrastriate cortex is labeled through feedback as belonging to objects, thereby binding their constituting elements together. Recently it was shown that such feedback mechanisms may serve different roles during different feedback iterations, initially enabling figure-ground segregation, later on serving as a mechanism by which attentional selection operates (Roelfsema, et al., 2007)

Aside from providing a conceptual framework for how figure ground segregation, binding and attentional selection may be implemented in visual cortex, incremental grouping theory accounts for a number of neurophysiological findings, amongst which that of extra-classical receptive field effects, such as contextual modulation in V1 (Lamme, 1995; Zipser, et al., 1996). We suggest here that feedback processes that enable incremental grouping not only serve to bind the figure surface together, but that areas that do not correspond to an object or surface, may be actively suppressed to improve figural assignment and discriminability, in effect binding the background together. The combined role of enhancement and suppression could be akin to the process of contrast enhancement for objects in retinotopic cortex. A biologically inspired neural network model of texture segregation by Roelfsema (2002), explicitly models inhibitory feedback connections in order to reliably counter faulty assignment of background elements to figural regions in early visual areas. As a result, in this network, regions corresponding to the background of an image containing a figure are suppressed due to feedback after about 200 ms. Although speculative, our data nicely fits with such a model.

This suppression is different from endogenous attentional suppression in that it is an automatic, and not a cognitively driven process, as evidenced by the fact that it occurs for unseen stimuli. Rather, it may be driven by feedback following automatic stimulus classification in the feedforward sweep. The fact that unseen trials in this experiment seem to show suppression for *all* retinotopic locations

in early visual areas ties in with this idea. There is strong evidence that figure-ground detection in visual cortex as a result of initial feedforward processing can occur completely unimpaired, even when texture stimuli are strongly masked and figure presence is unreportable by the subject (Fahrenfort, et al., 2007). We conjecture that even though unseen figures may be detected by high visual areas in the feedforward sweep (e.g. V7 center in Figure 4.6), binding this figure representation to the corresponding retinotopic surface in low visual areas is unsuccessful in the case of unseen trials due to masking. This then results in effective suppression of the entire visual field as not belonging to the figure, which would explain why the entire early visual cortex seems to be suppressed as a result of unseen figures. In contrast, seen trials are marked by strong enhancement in the center of early visual areas, which is compatible with the notion of figural regions being successfully labeled as such through feedback, eventually leading to stimulus detection by the subject.

Aside from theoretical considerations when inferring neurophysiological mechanisms that may underpin these effects, the distribution of responses across retinotopic space in V1 found in this study is also informative. We show large scale differences between V1 processing of Figure and No Figure trials, the distribution of which extends far beyond the V1 cRF, while local physical stimulation and anticipatory attentional levels are roughly the same. Estimates of V1 cRF size in macaques are less than 1° even at sizeable eccentricities (A. T. Smith, Singh, Williams, & Greenlee, 2001), and estimates of early visual cRF size in humans using subdural electrodes also point to (much) smaller than 1° sizes (Yoshor, Bosking, Ghose, & Maunsell, 2007). The effects observed in this study take place at considerably larger distances, suggesting the involvement of feedback mechanisms originating from higher visual areas with larger receptive fields. Studies explicitly investigating the role of feedback connections in the integration of global organization to local responses have also shown the importance of feedback in this respect (Angelucci, et al., 2002; Hupe, et al., 1998; Lamme, Super, et al., 1998).

Nevertheless, one should be cautious when inferring feedback mechanisms from fMRI data. For example, some have noted that suppressive effects as observed in this study might be explained in terms of “blood stealing”, haemodynamic changes that

have no neural correlate (A. T. Smith, Williams, & Singh, 2004). However, in the present study, suppression of the BOLD signal for Unseen trials happens across the visual field for early retinotopic areas, so that it is unclear how blood stealing could have caused it. Recently, V1 BOLD has also been implicated in anticipatory arterial pumping (Sirotin & Das, 2009), but as the amount of anticipation was closely matched between conditions in this study, such mechanisms cannot account for our findings.

Conclusions:

1. Suppression of the surround occurs in V1 and up, and is not exclusively a top down attentional phenomenon but may result from sensory-driven processing within visual cortex due to the global organization of the stimulus, possibly related to exogenous bottom up attention and/or figure-ground segregation.
2. Enhanced activity at retinotopic locations in V1 corresponding to the surface of a figure is indicative of whether that figure is seen or not.