Contextual effects on perceived contrast: Figure–ground assignment and orientation contrast

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Figure–ground segregation is an important step in the path leading to object recognition. The visual system segregates objects ('figures') in the visual scene from their backgrounds ('ground'). Electrophysiological studies in awake-behaving monkeys have demonstrated that neurons in early visual areas increase their firing rate when responding to a figure compared to responding to the background. We hypothesized that similar changes in neural firing would take place in early visual areas of the human visual system, leading to changes in the perception of low-level visual features. In this study, we investigated whether contrast perception is affected by figure–ground assignment using stimuli similar to those in the electrophysiological studies in monkeys. We measured contrast discrimination thresholds and perceived contrast for Gabor probes placed on figures or the background and found that the perceived contrast of the probe was increased when it was placed on a figure. Furthermore, we tested how this effect compared with the well-known effect of orientation contrast on perceived contrast. We found that figure–ground assignment and orientation contrast produced changes in perceived contrast of a similar magnitude, and that they interacted. Our results demonstrate that figure–ground assignment influences perceived contrast, consistent with an effect of figure–ground assignment on activity in early visual areas of the human visual system.

Introduction

A main purpose of the visual system is to recognize and locate objects in the visual scene. A key step in achieving these aims is to segregate objects from their background. The importance of this process, known as figure–ground segregation, has been highlighted by studies showing that regions which have been designated as figures are more deeply processed by the visual system, so that their shape is likely to be encoded in short-term memory (Driver & Baylis, 1996; S. Palmer, Davis, Nelson, & Rock, 2008). In

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FGM has therefore been suggested to be the neural correlate of figure–ground assignment. The source of FGM has been suggested to be feedback from higher visual areas (Lamme & Roelfsema, 2000; Self, Kooijmans, Supèr, Lamme, & Roelfsema, 2012; Self, van Kerkoerle, Supèr, & Roelfsema, 2013). This makes intuitive sense, as the visual system, in order to accurately segregate the visual scene, must integrate global cues from across the scene concerning the arrangement of objects with local cues concerning edges.

Given the relatively large changes in neuronal firing rates in early visual areas observed in monkeys, it is of interest to determine whether figure–ground assignment affects the perception of low-level features in humans. There have been relatively few studies addressing this question. Rubin (1915, 1958) noted that figures appeared closer to the observer, more saturated, and higher in contrast. Coren (1969) showed, using bistable stimuli and figure–ground stimuli defined by depth, that induced brightness contrast is greater on figures compared to backgrounds. Similarly, studies of illusory figures, in which there is no physical difference between the figure and the background, established that figures appear brighter (Jory & Day, 1979) and closer to the observer (Coren & Porac, 1983) than the background, suggesting that figure–ground segregation does change the perception of brightness. Indeed, more recent studies have shown that brightness perception is strongly influenced by the global interpretation of scene structure and illumination (Purves, Williams, Nundy, & Lotto, 2004). Other studies have found preferential processing of figures in temporal judgment tasks (Lester, Hecht, & Vecera, 2009) and a reduced luminosity threshold for figures (Bonato & Cataliotti, 2000), suggesting a general preferential processing of figures in the visual system. However, to our knowledge there have been no studies of whether the perception of luminance contrast is affected by figure–ground structure.

Here we used stimuli based on those used in the electrophysiological studies described previously to investigate whether figure–ground assignment affects the perception of luminance contrast. These stimuli were textures made from oriented line elements, and the figures were constructed from small regions of texture with the opposite orientation (Figure 2A). To determine how the perception of contrast differed between figure and ground, we asked participants to judge the contrast of Gabor probes placed on the figure and the ground. We hypothesized that if neural activity in early visual areas is enhanced on figure regions (compared with the ground), then the neural representation of a Gabor probe on a figure might also be enhanced, leading to a higher perceived contrast.
General methods

Stimuli

All stimuli were constructed in MATLAB (MathWorks, Inc., Natick, MA) using Cogent (developed by John Romaya at the Laboratory of Neurobiology at the Wellcome Department of Imaging Neuroscience, London, UK) and were presented on a linearized CRT monitor at a viewing distance of 0.54 m. The exact stimulus arrangement varied between the experiments, but all stimuli were made from textures composed of oriented line elements. Two full-screen (36.5° × 27.4°) textures, one consisting of 45° oriented lines and one of 135° oriented lines, were made by randomly choosing the center coordinate of each of 25,000 white (81.2 cd/m²) lines which were drawn on a black (0.07 cd/m²) background. The lines had a thickness of 1 pixel (0.035°) and a length of 0.8°. The figures were constructed by copying a square region (4° × 4°) of one texture onto the orthogonal texture. This creates figures with sharp boundaries defined by both the orientation difference of the texture and the occlusion.
of the underlying lines. We also created a “crossed” texture consisting of the same line elements as in the normal textures, but with each line randomly assigned to either the 45\(^\circ\) or the 135\(^\circ\) orientation. These textures were used in Experiments 2 and 4 as prestimulus screens to prevent changes in mean luminance upon presentation of the relevant stimulus. In Experiments 1–3, we measured perceived contrast using two Gabor patches presented on a luminance pedestal of 30 cd/ \(m^2\). One of these (the reference Gabor) was always presented at 50\% Michelson contrast. The other Gabor (test Gabor) was presented at various contrasts according to a staircase procedure. Both Gabors were presented in a circular aperture 1.8\(^\circ\) in diameter. The underlying sine wave of the Gabor had a spatial frequency of 3.3 c/\(\text{deg}\), and the Gaussian envelope had a standard deviation of 0.4\(^\circ\). The Gabors were cosine phase (phase of 180\(^\circ\), i.e., they had a dark stripe in the middle, and they had an orientation of 45\(^\circ\) except in Experiment 3, where they were vertically oriented. Both the Gabors and figures were presented at 6\(^\circ\) eccentricity from the fixation point at a polar angle of 45\(^\circ\), 135\(^\circ\), 225\(^\circ\), or 315\(^\circ\).

**Measurement of contrast discrimination thresholds**

In Experiments 1–3, contrast discrimination thresholds and perceived contrast of Gabor probes placed on figures or backgrounds was measured using a dual staircase technique under the control of QUEST (Watson & Pelli, 1983). In Experiment 4 we measured perceived contrast using the method of constant stimuli and a three-alternative forced-choice design. Full details are given in the Methods section of Experiment 4. Experiments 1 and 2 were two-alternative spatial forced-choice experiments in which participants had to indicate which of the two Gabors was highest in contrast. Experiment 3 was a two-interval forced-choice experiment; participants had to report whether the second Gabor was higher or lower in contrast than a standard.

For each experimental condition, we ran randomly interleaved descending and ascending staircases. Descending staircases started with a test-Gabor contrast of 60\%, and the contrast of the test Gabor moved towards the reference contrast of 50\% under the control of QUEST. Ascending staircases started with a test-Gabor contrast of 40\%, which increased towards the reference contrast. The staircases converged on the contrast level necessary to produce 79.4\% correct performance (i.e., the same level as a 3-down, 1-up staircase), which we refer to as the contrast discrimination threshold (CDT). We used these measures to derive a formal measure of perceived contrast (\(\Delta\text{Contrast}_p\)); see Appendix for details. The experiments were conducted in short sessions of approximately 25 min. Staircases were reset between sessions, but CDTs were always estimated using all trials across sessions. We estimated the threshold as the mean of the posterior probability density function of the threshold given by QUEST.

**Results**

**Experiment 1**

In this experiment we investigated how figure–ground assignment affects contrast discrimination ability and perceived contrast. We determined contrast discrimination thresholds (CDTs) and the change in perceived contrast for a Gabor patch of constant physical contrast (reference Gabor) situated on a texture—either on a figure, the background, or a uniform texture—compared to a Gabor of variable contrast situated on a uniform texture (test Gabor; see Figure 2A, B). We used a test Gabor that was placed on a uniform texture (which is neither figure nor background) as the comparison stimulus so that we could independently measure the changes in CDT and perceived contrast produced by figure assignment or background assignment. We also orthogonally manipulated the orientation of the line elements surrounding the reference Gabor, as it is well-known from electrophysiological experiments that cross-oriented surrounds produce less inhibition than iso-oriented surrounds (Knierim & Van Essen, 1992; Levitt & Lund, 1997; Nelson & Frost, 1978) and from psychophysical experiments that orthogonal surrounds produce higher perceived contrast than iso-oriented surrounds (Cannon & Fullenkamp, 1991; Meese & Hess, 2004; Yu, Klein, & Levi, 2001). The textures in our experiment were either iso-oriented with respect to the Gabor (the Gabor was always oriented at 45\(^\circ\), so the line elements in this condition were also tilted at 45\(^\circ\) or cross-oriented (i.e., 135\(^\circ\)). The line elements surrounding the test Gabor (the one for which contrast was adjusted) were always iso-oriented. We therefore implemented a 3 \(\times\) 2 factorial design with two factors: figure–ground compartment (figure, ground, uniform) and orientation (iso- and cross-oriented). For each condition, we ran a descending and an ascending staircase in which the test Gabor was, respectively, higher and lower in contrast than the reference Gabor. This design yielded a total of 12 staircases, which were presented in an interleaved, pseudorandom order during the experiment.
Methods

Participants first viewed a gray screen (400 ms, 11.7 cd/m²) and were instructed to fixate on the fixation marker. We then presented two textures (Figure 2A). The screen was split horizontally, with the experimental texture (i.e., the texture on which the reference Gabor was situated) appearing in one half of the screen and the uniform texture appearing in the other half (we randomly determined whether the experimental texture appeared in the upper or lower half on each trial). In the figure and ground conditions, the experimental texture contained a figure that was located randomly to the left or right of fixation at 6° eccentricity from the fixation point. The orientation of the texture relative to the orientation of the Gabors was under experimental control. The Gabors were always oriented at 45°, and the orientation of the experimental texture was either iso-oriented (i.e., also 45°) or cross-oriented (135°) with respect to the Gabor. The participants were instructed to indicate via the keyboard arrow keys which Gabor appeared to have the highest contrast. The stimulus remained on the screen until the participant responded. A fixation dot was presented, but participants were instructed to move their eyes and foveate each Gabor in turn before making their response. Eight participants took part in this experiment (six women, average age = 25.5 years), including one of the authors (MWS); one was an informed participant, and the others were naive to the aims of the experiment. We presented 45 trials per staircase per session, and each participant completed 10 sessions, yielding a total of 450 trials per condition. CDTs were estimated using QUEST based on all 450 trials (see Appendix).

Results

The results are shown in Figure 2C, D. We used a novel dual-staircase approach that allowed us to simultaneously measure changes in CDTs and perceived contrast. We first examined the effect of figure-ground structure and orientation context on CDTs—the ability of observers to judge which Gabor was highest in contrast (Figure 2C)—using a factorial repeated-measures ANOVA. Although the effects of perceptual organization on CDTs were relatively small, we observed a significant main effect of figure-ground structure on CDTs, $F(2, 14) = 4.18, p = 0.038$. This was caused by lower CDTs (i.e., better performance) in the figure condition compared to the other conditions, although this difference was quite small (0.6%) and post hoc testing did not reach significance (figure vs. uniform and figure vs. ground: both $p$s > 0.05, t tests). There was no significant effect of orientation on the CDTs, and the two factors did not interact, both $Fs < 1$.

We then examined changes in perceived contrast (Figure 2D). The values in Figure 2D represent the difference in perceived contrast between the reference Gabor, which was subjected to the experimental manipulation, and the test Gabor, which was always presented on an iso-oriented uniform texture. We included one condition (Uni-Iso) in which the reference and test Gabors were presented on identical textures, and, as expected, the perceived contrast difference in this condition was not significantly different from zero ($t$ test, $p = 0.66$). There was a significant main effect of figure–ground structure, $F(2, 14) = 11.9, p = 0.001$, and of orientation, $F(1, 7) = 15.2, p = 0.006$, and a significant interaction between these effects, $F(2, 14) = 5.7, p = 0.015$. The main effect of figure–ground structure was the result of higher perceived contrast in the figure condition compared to the other two conditions. Simple effects analysis revealed significantly higher perceived contrast in the figure condition compared to the ground ($t$ test, $p = 0.022$, Bonferroni corrected) and uniform conditions ($t$ test, $p = 0.031$, Bonferroni corrected), but no difference between the ground and uniform conditions ($t$ test, $p = 0.915$. The difference in perceived contrast between the figure condition and the other conditions depended strongly on the orientation context. When the Gabors were surrounded by iso-oriented texture, there was a relatively large and significant (2.7% contrast, $p = 0.008$, paired $t$ test) difference between the figure condition and the ground condition. This difference was considerably less (0.76%), though still significant ($p = 0.03$, paired $t$ test), when they were surrounded by cross-oriented lines.

Discussion

The main goal of our experiment was to investigate whether figure–ground assignment influences perceived contrast. We found that the reference Gabor was perceived as being higher in contrast when presented on the figure compared to the background. We also included a condition with a uniform texture, which allowed us to examine whether the effect on perceived contrast was caused by contrast enhancement on the figure or by suppression on the background. Perceived contrast on the uniform texture was very similar to that in the ground condition, suggesting that figural enhancement was the dominant effect in this experiment.

We also examined the influence of orientation context on perceived contrast. In line with previous studies, we found that cross-oriented textures enhanced perceived contrast relative to iso-oriented textures (this can be seen by comparing the Uni-Cross condition with the Uni-Iso condition, in which no figure–ground structure was present; see Figure 2D). This result is not
in itself surprising, although it provides further validation for our dual-staircase technique; but perhaps more surprisingly, we observed a strong interaction between orientation context and the figure–ground structure. Figure–ground effects were much stronger on iso-orientated textures compared to cross-orientated textures, whereas the difference between iso- and cross-orientated surrounds was weakest on figures. What is the explanation for this interaction? One possibility is that the figure–ground modulation signal is feature specific. If the figure is composed of $45^\circ$ oriented elements, then theoretical studies have suggested that only the representation of neurons with preferred orientations close to $45^\circ$ will be enhanced (Poort et al., 2012; Roelfsema, Lamme, Spekreijse, & Bosch, 2002).

Feature-specific enhancement of the figure would explain why iso-oriented textures produce large enhancements, whereas cross-oriented textures produce less. When the Gabor was presented on an iso-oriented texture, it had the same orientation as the figure elements, and therefore neurons representing the Gabor may have received the same modulatory enhancement as the figure elements. It should be noted, however, that there may be a simpler explanation for these effects. We only controlled the orientation context that immediately surrounded the Gabor; the interaction we observed may have been due to a more remote effect of orientation context (Wolfson & Landy, 1999). If we consider the Fig-Iso condition, which produced large changes in perceived contrast, the reference Gabor on the figure was surrounded locally by a suppressive iso-oriented texture; but at greater distances (i.e., greater than 2$^\circ$ from the Gabor), the texture reversed to the less suppressive cross-oriented texture. In contrast, the test Gabor was surrounded by a large and homogeneous suppressive iso-oriented texture. Thus the reference Gabor on the figure may have been less suppressed than the test Gabor on the uniform texture; the remote orientation effect works in the same direction as the figure–ground effect, leading to an apparent interaction. The same argument can be made to explain why the orientation context effect appeared larger in the uniform and ground conditions. When the reference Gabor was on a figure, it was surrounded locally by only a small region of oriented texture before the orientation reversed; by contrast, Gabors on the background or uniform textures were surrounded by much larger regions of one orientation. Therefore the effects of orientation would have been enhanced for the ground and uniform conditions compared to the figures.

Importantly, while these long-range orientation effects can explain the interaction observed in this experiment, they cannot fully explain the effect of figure–ground organization on perceived contrast. Consider, for example, the Fig-Cross and Gnd-Cross conditions (Figure 2D). If our results were entirely due to remote orientation effects, then the reference Gabor in the Fig-Cross condition would be suppressed compared to the reference Gabor in the Gnd-Cross condition, as the Gabor in the Gnd-Cross condition is surrounded for a larger distance by the less suppressive cross-oriented texture. We observed the opposite result: Perceived contrast was significantly higher in the Fig-Cross condition than the Gnd-Cross condition. This shows that while remote orientation does have an influence, it cannot account for the increase in perceived contrast of figures compared to ground.

We also considered alternative explanations for the effect of figure–ground organization on contrast perception that are unrelated to figural enhancement. Firstly, it is possible that participants may have had an intrinsic bias to report the Gabor on the figure as higher in contrast when they were uncertain about the answer. Such a bias would lead to apparent increases in perceived contrast, as it would lead to worse performance on descending staircases (where the Gabor on the figure is the incorrect choice) and better performance on ascending staircases (where the Gabor on the figure is the correct choice). This would result in a higher $\Delta$Contrast$_{wp}$ (see Appendix). In Experiment 3 we addressed this concern by decoupling the contrast response judgment from the location of the figure, and in Experiment 4 we used an alternative approach to measure perceived contrast that provides strict control over response bias. Secondly, it is possible that the figure region captures attention (Nelson & Palmer, 2007), and as previous studies have demonstrated that attention increases perceived contrast (Carrasco, Ling, & Read, 2004; Ling & Carrasco, 2006; Stormer, McDonald, & Hillyard, 2009; but see J. Palmer & Moore, 2009; Prinzmetal, Long, & Leonhardt, 2008; Schneider, 2006; Schneider & Komlos, 2008), it is possible that attentional capture underlies the effects we observed.

This explanation is highly unlikely, though, for several reasons. Firstly, the figures we used were task irrelevant and have previously been demonstrated in studies of inattentional blindness to be poor in automatically capturing attention (Scholte, Witteveen, Spekreijse, & Lamme, 2006). More importantly, in this experiment the participants were not forced to make a speeded choice and were instructed to fixate both Gabors before making a behavioral choice. Reaction times (RTs) in this experiment were long (all participants had median RTs of greater than 1 s in all conditions), suggesting that participants obeyed these instructions. In such a situation it is highly unlikely that attention directed to the task-irrelevant figure would affect the results. In Experiment 3 we addressed this concern further by presenting all figures at fixation in a temporal alternative forced-choice experiment.
We also observed a significant effect of figure-ground structure on CDTs in this experiment. This effect was very small (0.6%), and not significant when post hoc tests were applied. Nevertheless, the result raises the possibility that participants may be more accurate in judging the contrast of Gabors placed on figures compared to backgrounds. We investigated this effect further in Experiment 2 but did not observe any effect of local orientation context on CDTs. This result is in line with previous studies which have found no effect of adding oriented surrounds on above-threshold contrast discrimination ability in the fovea (Snowden & Hammett, 1998).

### Experiment 2

In Experiment 1 we observed that a Gabor situated on a figure was perceived as higher in contrast than a Gabor on a background. We also observed a small decrease in CDTs when the reference Gabor was placed on a figure, suggesting that perceptual decision making is improved on figure regions compared to backgrounds. This difference in CDT was very small and at the limits of statistical significance. This may be because in Experiment 1 only one of the two Gabors being judged was subject to experimental manipulation. The test Gabor was always presented on a uniform texture, whereas the reference Gabor was placed on a figure, background, or uniform texture. It seems likely, therefore, that if the contrast of Gabors on figures can be judged more accurately, then we may observe larger effects if both Gabors are placed on figures. In Experiment 2 we included situations in which both Gabors were presented on figures or backgrounds, maximizing our sensitivity to changes in discrimination thresholds (Figure 3A). If figure regions are processed more accurately than ground regions, then CDTs will be lower on figures compared to backgrounds. We also included conditions in which both Gabors were presented on cross-oriented textures, and both on iso-oriented textures, to allow us to study the effects of orientation context on discrimination ability.

### Methods

Eight participants (five women, average age = 26 years) took part in this experiment, including two of the authors (MWS and AM). The experiment therefore contained six new, naïve participants. We implemented a factorial design with the figure–ground structure and the local orientation context (iso- or cross-oriented) as the parameters of interest (Figure 3B). Each condition contained a driving factor and a contextual factor. For example, in the Cross-Iso (CI) conditions, the driving factor behind changes in perceived contrast was a difference in local orientation contrast: The reference Gabor was situated on a cross-oriented texture, whereas the test Gabor was on an iso-oriented texture. However, there were two variations of this condition, which differed by their contextual factor: CI\textsubscript{fig}, where both Gabors were presented on figures, and CI\textsubscript{gnd}, where both Gabors were presented on the background. In the Figure-Ground (FG) conditions, the driving factor was a difference in figure–ground compartment, whereas the contextual factor was the local orientation contrast (both Gabors presented on cross-oriented, FG\textsubscript{crs}, or iso-oriented textures, FG\textsubscript{iso}). We ran two versions of each condition, with the location of the reference and test Gabor swapped (bottom row of conditions in Figure 3B). These different versions measured the same effect but with reversed polarity. This design therefore required a total of 16 staircases: the four main conditions shown in Figure 3B (CI\textsubscript{fig}, CI\textsubscript{gnd}, FG\textsubscript{crs}, FG\textsubscript{iso}) and with the test and reference Gabors swapped in location (IC\textsubscript{fig}, IC\textsubscript{gnd}, GC\textsubscript{crs}, GC\textsubscript{iso}), with each condition comprising both an ascending and descending staircase. There were 40 trials per staircase per session, and each participant completed 10 sessions, yielding a total of 400 trials used for each threshold estimate.

### Results

**Effect of orientation contrast on contrast perception:** We will first examine the results from the CI condition, in which we investigated the effect of local orientation contrast on contrast discrimination thresholds and perceived contrast. The Gabors were presented under two different contexts, both on figures (CI\textsubscript{fig}) and both on grounds (CI\textsubscript{gnd}). We first calculated CDTs (Equation 1 of the Appendix; Figure 3C). We did not observe any significant differences in CDTs between the figure and ground contexts (paired t test), t(7) = 0.54, p = 0.6, indicating that in this experiment the figure–ground compartment did not affect the participants’ sensitivity in making contrast discrimination judgments. To investigate the effect of local orientation contrast on perceived contrast, we computed \( \Delta \text{Contrast}_o \) (Equation 3 of the Appendix; Figure 3D). \( \Delta \text{Contrast}_o \) measures the difference in perceived contrast between the test and reference Gabors. Its value was positive when the reference Gabor was surrounded by a cross-oriented texture and negative when the reference Gabor was surrounded by an iso-oriented texture. The CI and IC conditions were identical except that the position of the reference and test Gabors were swapped. This means that \( \Delta \text{Contrast}_o \) in the iso- and cross-oriented conditions should be opposite in sign but equal in magnitude, as can be seen in Figure 3D. For statistical analysis we calculated \( \Delta \text{Contrast}_o \), which is a single measure, by inverting the sign of the \( \Delta \text{Contrast}_o \) values.
Figure 3. Stimuli and results from Experiment 2. (A) A screenshot from Experiment 2 showing the split screen with the reversal in the orientation of the texture across the horizontal meridian. A trial from a descending staircase from the FGcrs condition is shown, with the reference Gabor on the figure and the test Gabor on the ground. The two figures are outlined in red (not present in the experiment). Note that the local orientation of the texture elements surrounding the Gabors is the same. (B) The design of Experiment 2. The top row shows the four main conditions of the experiment. The gray and green conditions explore the effect of local orientation contrast under two different contextual environments: both Gabors presented on figures (CIfig) and both on the background (CIgnd). The pink and purple conditions examined the effect of figure–ground structure under two different orientation contexts (FGcrs, FGiso). Four paired conditions, in which the position of the reference and test Gabors were swapped, are shown below the dashed line. These were predicted to produce equal results of opposite polarity. The test Gabor is shown as higher in contrast here. (C) Contrast discrimination thresholds (CDTs) averaged across eight participants from the CI and IC conditions. No significant differences were observed. Conventions as in Figure 2C. (D) Differences in perceived contrast ($\Delta$Contrast$_v$) in the CI and IC conditions, showing a strong effect of local orientation context on perceived contrast. The differences are grouped according to whether both Gabors were presented on figures (left) or the background (right). Perceived contrast differences were, as expected, equal and opposite in the CI and IC conditions. (E) As the CI and IC conditions measure the same effect with reversed sign, we averaged the $\Delta$Contrast$_v$ values of these conditions together (after reversing the sign of the IC conditions) to produce $\Delta$Contrast$_{orient}$. This measure is positive if perceived contrast is higher on cross-oriented than iso-oriented backgrounds, as was the case in this experiment. The effect was significantly larger when both Gabors were presented on the ground compared to the figures. (F) CDT values from the FG...
and GF conditions; no significant differences were observed. (G) $\Delta$Contrast$_{figgnd}$ values from the FG and GF conditions grouped according to whether the Gabors were surrounded by cross- or iso-oriented textures. (H) We estimated $\Delta$Contrast$_{figgnd}$ by reversing the sign of perceived contrast values in the GF conditions before averaging with the FG conditions. This measure is positive if perceived contrast is higher on figures compared to backgrounds. This effect was strongest when the Gabors were surrounded by iso-oriented textures.

from the IC conditions and then averaging across the CI and IC conditions. Thus, $\Delta$Contrast$_{orient}$ is positive if perceived contrast is higher on cross-oriented textures and negative if the reverse is true. The mean $\Delta$Contrast$_{orient}$ values across participants are shown in Figure 3E. $\Delta$Contrast$_{orient}$ was significantly different from zero for both figure and ground contexts [paired $t$ tests: figure context, $t(7) = 3.7, p = 0.007$; ground context, $t(7) = 4.8, p = 0.002$]. We also observed a significant difference between $\Delta$Contrast$_{orient}$ under figure and ground contexts (paired $t$ test), $t(7) = 3.8, p = 0.007$. In other words, perceived contrast was higher on cross-oriented textures, and the effect of local orientation context was stronger when the Gabors were on the background compared to when they were on the figures.

**Effect of figure–ground structure on contrast perception:**

In the FG conditions we investigated the effect of figure–ground structure on CDTs and perceived contrast while holding the local orientation contrast constant. We found no significant effect of local orientation contrast on CDT, $t(7) = 0.6, p = 0.6$, indicating that orientation contrast did not affect contrast discrimination ability in this experiment (Figure 3F). On the other hand, we found consistent and large effects of figure–ground organization on $\Delta$Contrast$_{figgnd}$ (Figure 3G). The perceived contrast of the reference Gabor was higher when it fell on a figure compared to when it fell on the background. Accordingly, $\Delta$Contrast$_{figgnd}$ was positive for the FG conditions and equal but opposite for the GF conditions. We therefore calculated a single measure by reversing the sign of $\Delta$Contrast$_{figgnd}$ for the FG conditions and averaging the resulting values with those of the FG conditions to produce $\Delta$Contrast$_{figgnd}$, which is positive if perceived contrast is higher on the figure (Figure 3H). $\Delta$Contrast$_{figgnd}$ was significantly greater than zero for both iso-oriented and cross-oriented contexts [Iso: $t(7) = 4.3, p = 0.002$; Cross: $t(7) = 2.1, p = 0.04$].

**Discussion**

The main results of this experiment are clear: Perceived contrast was higher when the Gabor was on the figure compared to the background and also when it was surrounded by a cross-oriented texture compared to an iso-oriented texture. These effects were not accompanied by changes in the participants’ sensitivity to contrast, as we found no significant differences in CDT values. The effects of figure–ground context and orientation context on perceived contrast appeared to be similar in magnitude in this experiment (compare Figures 3E and 3H). These effects confirm the findings on perceived contrast of Experiment 1 in a largely new group of participants and show at the same time that CDTs are not affected by either orientation contrast (Snowden & Hammett, 1998) or figure–ground structure. The failure to replicate the small reduction in CDT we observed in Experiment 1 indicates that this effect is not particularly robust.

As in Experiment 1, we observed interesting interactions between the effects of figure–ground assignment and orientation differences on perceived contrast. The effect of the local orientation context was always greater when the Gabors were on the background, and conversely, the effect of figure–ground assignment was greater when the Gabors were surrounded by an iso-oriented texture. This interaction is consistent with feature-specific feedback and also with the effects of more remote orientation context (see the Discussion section of Experiment 1), and we distinguish between these hypotheses in Experiment 3.

The most straightforward interpretation of the results of this experiment is that the perceived contrast of the Gabor stimuli was modulated by both the figure–ground context and the orientation context. However, we have to consider a possible alternative explanation for our results. Participants may have been biased towards reporting the Gabor situated on the figure as highest in contrast. This bias would only affect the results of figure–ground trials (i.e., FG and GF conditions) but might lead to a pattern of results similar to those actually obtained in Experiments 1 and 2. To see why this is the case, consider the FG condition of Experiment 2. On a descending staircase, the correct answer is to choose the test Gabor, as it is always highest in contrast. If the participant, when in doubt, tends to choose the figure location, then he or she will appear to have very low CDTs (as his or her guesses will tend to be correct). Exactly the opposite pattern would be expected on ascending staircases, where the reference Gabor is the correct answer. This pattern of results would be interpreted as an increase in perceived contrast of the test Gabor in the figure condition, although it actually would reflect a response bias. Although it may seem unlikely that such a bias exists (as the figures were irrelevant to the task), we
wished to rule out this possible confound in two further experiments.

Experiment 3

In this experiment we addressed the possibility that response bias could explain our results. To this end, we decoupled the perceptual decision from the location of the figure. We used a temporal forced-choice design in which the figure (if present) was always presented at fixation. We presented two textures which both contained a Gabor. The participants first viewed a Gabor presented at 50% contrast at fixation on a uniform texture (the standard Gabor). They then viewed a second texture which, on 50% of trials, contained a figure presented at fixation. On the remaining 50% of trials a uniform texture was presented. The second texture also contained a Gabor (the test), which could appear at different contrasts. The participants’ task was to determine whether the test Gabor was higher or lower in contrast than the standard. Thus, now the perceptual decision did not depend upon the location of the figure, which was always presented at fixation. The higher/lower contrast judgment was also not coupled to the presence or absence of the task-irrelevant figure. This experiment therefore controls for response biases that participants may have had in Experiments 1 and 2.

Experiment 3 had an additional aim, which was to study whether the increase in perceived contrast observed in Experiments 1 and 2 depends critically on feature-specific feedback or long-range orientation effects. In Experiments 1 and 2, we observed the largest increases in perceived contrast when the texture elements surrounding the Gabor patch had the same orientation as the Gabor. We hypothesized that this interaction could be due to two different effects, as was mentioned earlier (see the Discussion section of Experiment 1). Firstly, it could be explained by feature-specific feedback signals. It has been theorized that figure–ground modulation arises due to orientation-dependent feedback from higher visual areas (Roelfsema et al., 2002). These models predict that the representation of the Gabor patch would be targeted by the same modulatory signals that boost the representation of the figure surface. Secondly, it could be explained by long-range orientation effects (Wolfson & Landy, 1999; see the Discussion section of Experiment 1 for more details). In Experiment 3, the Gabor was always vertically oriented (i.e., 90°), while the textures were oriented at either 45° or 135°. This effectively rules out contributions from either feature-specific feedback or long-range orientation effects, as the Gabor was not aligned with the underlying texture elements of either the figure or the ground.

Methods

Nine participants took part in this experiment, including MWS and one further participant who also took part in Experiment 2. The other participants had not taken part in the other experiments and were naïve to the aims of the experiment (six women, average age = 24.5 years). The details of the textures were identical to those of the textures used in the previous experiments, except that in this experiment the textures covered the entire screen. There were eight conditions (staircases) in this experiment, which form a 2 × 2 factorial design. The two factors were figure/uniform and orientation of the texture (45° or 135°), and a descending and ascending staircase were run for each condition. The trial structure was as follows (Figure 4A): Participants viewed a central red fixation dot for 200 ms; the first texture was then presented for 400 ms. This texture was randomly selected to be composed of either 45° or 135° orientation line elements. After a further 400 ms, the standard Gabor (50% contrast and vertical orientation) was presented at fixation on top of the texture. The texture was then removed from the screen and replaced by the fixation dot for 200 ms. There then followed the second texture interval of 400 ms. On figure trials, the texture contained a 4° figure presented at fixation; on the remaining 50% of trials the texture was uniform. The orientation of the second texture was chosen so that the orientation of the line elements at fixation was the same as for the standard Gabor. After a further 400 ms, the test Gabor was presented at a contrast that was determined by the QUEST algorithm in an identical fashion to Experiments 1 and 2. We ran descending and ascending staircases as described before. After the second texture interval, the participants were presented with a grey screen and were asked to press the up arrow on the keyboard if they judged the test Gabor to be higher in contrast than the standard, and the down arrow if they judged the opposite. They were provided with feedback if their choice was incorrect. Each session contained 50 repeats of each condition, yielding 400 trials, and each participant completed two sessions. Final threshold estimates were made using QUEST based on 100 trials per condition.

Results

We again converted the threshold measurements into CDT and δContrast,ω (see Equation 4 of the Appendix for how we determined δContrast,ω). We observed no significant difference in CDT value (Figure 4B) between the figure and uniform conditions (paired t test), p = 0.23. On the other hand, we observed significantly higher perceived contrast in the figure condition compared to the uniform condition (paired t test), p = 0.006 (Figure 4C). Perceived contrast was approximately 1% higher on the figure compared to the
uniform texture. Note that the absolute value of $\Delta \text{Contrast}_{\psi}$ is not informative in this experiment, as the test Gabor was always presented second. This ordering effect can lead to response biases which may affect the measurement of $\Delta \text{Contrast}_{\psi}$. Critically, however these ordering effects were the same for the figure and uniform conditions and so did not affect the difference in $\Delta \text{Contrast}_{\psi}$ between these two conditions.

**Discussion**

In this experiment we removed possible sources of response bias that were present in Experiments 1 and 2. In the first two experiments, the participants had to indicate the location of the Gabor with the highest contrast, and it is possible that they may have been biased to select the figure location. In Experiment 3, the figure was always presented at fixation and during the second interval of a two-interval forced-choice paradigm. This procedure makes it unlikely that the perceptual decision could be biased by the presence of a figure. Yet we still observed an increase of perceived contrast of approximately 1% for the test Gabor when it was presented on the figure compared to a uniform texture. In Experiment 3, the Gabors were always vertically oriented, and the results are compatible with those in Experiment 1 because the change in perceived contrast of the vertical Gabors fell in between the change caused by the iso- and cross-oriented contexts of the previous experiment. Although changing the paradigm from a two-location to a two-interval forced-choice design with a limited exposure time of the Gabor might have had an effect, the magnitude of the difference in perceived contrast between a figure and a uniform texture was similar to that observed in the other experiment. It therefore also seems unlikely that the influence of perceptual organization on perceived contrast measured in Experiments 1 and 2 was caused by a response bias.

In this experiment, the orientation of the Gabor patch was not aligned with the orientation of the underlying texture elements, of either the figure or the ground. The fact that we still observed an increase of perceived contrast on the figure compared to a uniform surface suggests that this increase is not due to an orientation-specific feedback signal targeting the representation of the Gabor.

**Experiment 4**

In Experiment 3 we used a temporal alternative forced-choice paradigm in which the figure was presented at fixation. This approach controls for several possible sources of response bias, but the possibility remained that participants, when uncertain, tended to select the “higher” response, i.e., the second interval, when the Gabor was presented on a figure. Note that this explanation is only viable if subject have a stronger bias to give this higher response in figure trials than in uniform trials. In this experiment we used an alternative technique for measuring perceived contrast, in which participants were allowed to indicate that they were uncertain as to whether a test grating had a lower or higher contrast than a reference grating. On these uncertain trials, the participants reported that they perceived no difference in contrast between the gratings, and the maximum of the distribution of these trials provides a direct measure of the point of subjective equality. Recent work has demonstrated that adopting such a design provides strict control over response bias (Garcia-Perez & Alcala-Quintana, 2011a, 2011b, 2013).
In this experiment, we also examined further the possibility of suppression on the background. In Experiment 1 we did not find any evidence for a reduction in perceived contrast for Gabors presented on the background. However, in Experiment 1 the Gabors were presented at large distances from the figure, and previous work has suggested that ground suppression may be strongest close to the figure (Poort et al., 2012). We therefore reexamined the possibility of ground suppression by placing the probe stimuli closer to the figures (2° separation). Furthermore, in this experiment we switched from using Gabor probes to sine-wave gratings. A possible concern with using Gabors to judge perceived contrast is that changes in contrast may also affect the perceived size of the Gabor stimulus. Participants may therefore base their responses on perceived size rather than contrast. This concern can be avoided by using grating stimuli which are not multiplied by a Gaussian envelope.

Methods

Eight participants took part in this experiment, including two of the authors (MWS and NT); none of the other participants had taken part in the other experiments, and they were naïve with respect to the aims of the experiment (six women, average age = 23.5 years). The experiment consisted of two factors: figure/ground and upper/lower, yielding a total of four conditions. The figure/ground factor determined whether the reference grating was presented on a figure or on the background (close to the figure; Figure 5A). The upper/lower factor controlled whether the reference grating was presented on the upper or lower half of the screen.

The textures used were identical to those of Experiment 1. The screen was split in half horizontally, with two different textures appearing in the top and bottom half of the screen. In the figure condition, a 4° square figure was presented on either the upper or lower texture at 4° vertical separation from the fixation point and at a horizontal location that was drawn with a random jitter of ±4° (drawn from a uniform distribution yielding final eccentricities ranging from 4°, jitter = 0°, to 5.7°, jitter = ±4°). The reference grating (vertically oriented, 40% contrast, 3 c/°) was then placed in the center of the figure. On ground trials, the figure was displayed as described, but the reference grating was presented on the upper or lower half of the screen.

The perceived contrast of the reference grating was taken as the maximum of the averaged psychometric function for the uncertain decisions (arrows; 1.35% indicates that the reference was perceived as being higher in contrast than the test).
right). The reference grating was therefore situated on the background at 2° separation from the figure edge (Figure 5A). The test grating was always presented on the uniform texture. The contrast of the test grating was pseudorandomly chosen from a specified set of contrast values including two easy trials (25% and 55% contrast) and a set of linearly spaced values ranging from 30% to 50% in steps of 2.5 percentage points. This gave a total of 11 contrast values. The local orientation of the texture elements was the same for the test and reference gratings.

Each trial began with the presentation of a crossed texture in both halves of the screen for 200 ms with a central fixation dot, as described in Experiment 2. The experimental textures and gratings then appeared simultaneously and were presented for 600 ms. After this, the crossed texture was presented again for 200 ms. Participants were instructed to fixate on the central dot and maintain fixation throughout the trial. They were instructed to press the up and down arrow keys on the computer keyboard with their right hand to indicate the location of the grating with the highest contrast. However, if they were uncertain which grating was higher in contrast, they were instructed to press the S key with their left hand.

Participants received initial training in the use of the uncertain response. They were presented with the same stimuli as described, except that both gratings were presented on uniform textures. The training session was used to test the participants’ veridical perception of the gratings with no experimental manipulation. Two different reference grating contrasts were used, 36% and 44%, and trials of each reference contrast were pseudorandomly intermixed. Participants performed one training session consisting of 440 trials (20 trials at each test contrast value for each reference contrast). We derived the perceived contrast of the reference grating separately for each reference contrast (see later) and only allowed participants to proceed if the mean deviation from the physical contrast of the reference was less than 2%. If the mean deviation was greater than 2%, the participants were allowed to complete one more training session.

Participants completed 1,760 trials in the main experiment, yielding 40 trials at each test grating contrast value per condition. We calculated the proportion of trials on which the participants responded up, down, or uncertain for each contrast value of the test grating. These proportions were calculated separately for trials on which the figure was presented on the upper and lower textures, to yield six data sets. We then fitted the difference with indecision model (Garcia-Perez & Alcala-Quintana, 2013) to these data using maximum likelihood estimation. In this variant of signal detection theory, the representation of the difference in contrast between the upper and lower grating for a given contrast value of the test grating is assumed to be normally distributed (with the parameters mean \( \mu \) and standard deviation \( \sigma \)). If figure–ground structure affects perceived contrast, this is assumed to shift the mean of this distribution away from zero. On individual trials, the participants are assumed to respond according to two internal criteria: If the signal difference falls below criterion \( d_1 \), then they respond down; if it falls above \( d_2 \), they respond up. For signal differences that fall in between \( d_1 \) and \( d_2 \), they respond uncertain. Unbiased participants should place these criteria symmetrically around zero; response biases are therefore captured by shifts in these criteria. The model simultaneously fits four parameters \((\mu, \sigma, d_1, \text{ and } d_2)\) to generate six psychometric functions; critically, the mean parameter \( \mu \) describes effects on the perceived contrast of the reference grating, with positive (negative) values indicating that the experimental manipulation increases (decreases) the perceived contrast of the grating. This parameter determines the maximum of the psychometric function of the uncertain responses when averaged across the upper and lower conditions. At this point the participants are maximally uncertain about their response, and we use this parameter as an estimate of the difference in perceived contrast between the test and reference grating. This approach has been shown to control for biases that participants may have in responding to a particular spatial location or temporal interval (Garcia-Perez & Alcala-Quintana, 2013).

**Results**

One participant was excluded, as that participant only responded uncertain on less than 2% of trials, which made estimation of the psychometric function unreliable. The remaining seven participants responded uncertain on between 5% and 51% of trials (mean = 21%). The psychometric functions generated by fitting the difference with indecision model to the data of one example participant are shown in Figure 5B. The red and blue curves in Figure 5B show the proportion of trials where the participant judged the test grating to be higher in contrast relative to the reference grating on trials with the figure in the upper and lower field, respectively. Similarly, the cyan and green curves show the proportion of trials where the subject was uncertain in trials with the figure in the upper and lower field, respectively. The difference between these curves provides an estimate for the participant’s decision bias. The black curve (with a Gaussian shape) shows the average of the cyan and green curves and is uninfluenced by decision bias (Garcia-Perez & Alcala-Quintana, 2013). We took the contrast value at the peak of this curve (the parameter \( \mu \)) as our estimate of the
difference in perceived contrast between the test and reference grating.

The difference with indecision model provided an excellent fit to the data of all participants (all $R^2 > 0.95$). The perceived contrasts in the figure and ground conditions from all seven participants are shown in Figure 5C, and the differences between the figure and ground conditions in Figure 5D. We observed a significant increase in perceived contrast on the figure compared to the grating on the uniform texture, $p = 0.049$ (t test). The magnitude of this effect was 0.8%, very similar to that observed in Experiment 3. In addition, we observed a comparable decrease in perceived contrast when the grating was placed on the background (magnitude = $-0.74\%$); this difference was consistent across participants and was significant, $p = 0.007$ (t test). Notably, we observed that in all seven participants, perceived contrast was higher on the figure compared to the ground. This highly reliable difference had an average magnitude of 1.55% and was significant, $p = 0.001$ (t test). The indecision model also allowed us to measure the sensitivity ($\sigma$) and bias ($\delta 1 + \delta 2$) of the participants; however, neither effect showed any significant difference between figure and ground (sensitivity: $\sigma_{\text{fig}} = 6.5\%, \sigma_{\text{gnd}} = 6.3\%, p = 0.40$; bias: $\delta 1_{\text{fig}} + \delta 2_{\text{fig}} = 0.01\%, \delta 1_{\text{gnd}} + \delta 2_{\text{gnd}} = -0.33\%, p = 0.39$, t test).

Discussion

The results indicate that perceived contrast was approximately 1.5% higher on the figure compared to the ground. The magnitude of this result was comparable to that observed in Experiment 3 despite our use of very different stimulus paradigms and psychophysical techniques. This makes us confident that the differences in perceived contrast between figure and ground are due not to response biases but rather to a real perceptual effect. The effect could be divided into two components: figure enhancement and ground suppression relative to a uniform texture.

In Experiment 1 we found that perceived contrast was similar on the background compared to uniform textures, whereas in this experiment we observed a significant decrease of perceived contrast on the background. What could account for the difference between Experiment 4 and Experiment 1? Firstly, the apparent discrepancy may reflect a difference between central and (near) peripheral vision. In Experiment 4, the grating stimuli were presented briefly (0.6 s) at 4.0°–5.7° eccentricity from fixation. Participants were instructed to maintain fixation, and the short exposure did not allow enough time to make saccades to both gratings. This contrasts with Experiment 1, in which participants were allowed to fixate both Gabor elements. Secondly, in the background condition the gratings were presented close to the figures, and previous evidence has suggested that background suppression is strongest close to figures (Poort et al., 2012). This could account for the differences in ground suppression relative to Experiment 1.

Although we found evidence for ground suppression in this experiment, the main outcome of Experiment 4 is that we reproduced the difference in perceived contrast between figure and background with a design controlling for decision biases by providing the option to subjects to report that they were uncertain. We found, once more, that the figure–ground structure in the scene has a reliable effect on the perception of contrast; probe stimuli placed on figures are perceived as higher in contrast than those on backgrounds.

General discussion

We have found that figure–ground structure influences the perception of contrast. The perceived contrast of a Gabor patch (or grating in Experiment 4) that was placed on a region perceived as figure was increased relative to that of the same Gabor placed on the background or a uniform texture. The effect was approximately equivalent in magnitude to the effect of orientation contrast in Experiments 1 and 2. On the other hand, we did not find strong evidence for enhanced contrast sensitivity for Gabors on figures relative to Gabors on the background; contrast discrimination thresholds were only slightly lower for figures in Experiment 1, and we could not replicate this effect in Experiment 2. Sensitivity was unchanged by figure–ground structure in Experiment 4. Our results suggest that the neural representation of a Gabor probe is enhanced in the visual cortex when the probe is situated on a figure texture compared to a background, leading to greater perceived contrast of the probe.

Mechanisms underlying the enhancement of perceived contrast of the Gabor probe

Our experiments did not measure the perceived contrast of the texture itself. Instead, we measured the effect of the texture on the perceived contrast of a Gabor element (or grating in Experiment 4). Given that the dominant effect of high-contrast textures is to reduce perceived contrast (Cannon & Fullenkamp, 1991, 1993; Chubb, Sperling, & Solomon, 1989), it might have been envisaged that an enhanced neuronal response in the figure region causes an increase in suppression and hence a decrease in the perceived contrast of the Gabor. Our results show the opposite effect, because the figure increased the perceived contrast of the reference Gabor. Thus, the neural...
representation of the reference Gabor appears to be subject to the same enhancement as the underlying figure. It remains an open question why the influence of perceptual organization, which enhances the representation of texture elements of the figure, is also inherited by the Gabor.

We initially considered that the Gabor may be targeted by an orientation-specific feedback signal that serves to boost the representation of the texture elements on the figure. Models of figure–ground modulation have proposed that the orientation of the figure elements is extracted at high levels of the visual system and that the representation of this orientation is then enhanced through feature-specific feedback to earlier visual areas (Roelfsema et al., 2002). In line with this view, we found that figure–ground effects on perceived contrast were largest when the Gabor orientation was aligned with the orientation of the underlying texture elements. This interaction between the orientation of the texture elements and figure–ground structure can be explained by long-range interactions between orientation filters (Wolfson & Landy, 1999). Yet this cannot be the only mechanism causing the increase in perceived contrast elicited by the figure, because we also observed the effect when the Gabor orientation was orthogonal to the texture elements in Experiments 1 and 2, and even in Experiments 3 and 4, where we excluded possible contributions from feature-selective feedback and long-range orientation effects by using vertical Gabor/grating elements that did not align with either figure or background. In Experiments 3 and 4, perceived contrast was still higher on figures compared to uniform surfaces. What then explains this change in perceived contrast?

We propose that figure–ground structure affects the perceived contrast of the Gabor through a modulatory signal that labels the entire figure region with enhanced neuronal activity and thereby groups all the texture elements that fall within the boundaries of the figure (Roelfsema, 2006; Roelfsema & Houtkamp, 2011). Such a modulatory signal may also target the representation of the Gabor probe when it falls within the boundaries of the figure. Thus, we identify the influence on contrast perception with the modulatory signals observed in primary visual cortex of awake-behaving monkeys when they perform a figure–ground segregation task (Lamme, 1995; Zipser et al., 1996).

This view would suggest that measuring perceived contrast could be a useful tool to study the underlying processes of figure–ground segregation in humans. However, more work needs to be done to determine whether the changes in perceived contrast obey the same rules as figure–ground modulation in early visual cortex.

We also considered the possibility that the increase in perceived contrast we observed on figures was due to attentional capture by the figure rather than figure–ground segregation per se. There are several reasons why this is highly unlikely. Firstly, the figures were task irrelevant, because the participants were always concentrating on the Gabor patches to make their contrast judgment and could entirely ignore the figure–ground structure. Secondly, participants were instructed to fixate each Gabor in turn (in Experiments 1 or 2), and RTs in these experiments were long—much longer than the time course of perceptual benefits of automatic attentional capture, which typically lasts less than 400 ms (Posner & Cohen, 1984). Thirdly, in Experiment 3 the Gabor probes and figures were presented at fixation in different temporal intervals, which makes a contribution from attentional capture unlikely. Finally, the textured figure stimuli were not very salient, as can be seen in Figures 2A and 3A. Figures of this type have been used in inattentional blindness experiments (Scholte et al., 2006) and have been shown not to automatically capture attention if their onset coincides with the onset of the entire texture stimulus.

**Effects of orientation context on perceived contrast**

In Experiments 1 and 2 we demonstrated that the relative orientation of the texture elements and the Gabor probe also strongly affected perceived contrast of the Gabor. We observed a relative increase in perceived contrast when the Gabor was situated on a cross-oriented texture compared to an iso-oriented texture. These findings replicate previous studies that have examined the effect of textured or grating surrounds on perceived contrast (Cannon & Fullenkamp, 1991; Chubb et al., 1983; Eji & Takahashi, 1985; Meese & Hess, 2004; Snowden & Hammett, 1998; Yu et al., 2001). Interestingly, we also observed an interaction between the effects on perceived contrast of the orientation of the local texture and the figure–ground structure. However, this interaction does not necessarily reflect a genuine interaction between the mechanisms for surround suppression and figure–ground modulation at the neural level. Instead, our results are also compatible with orientation-selective surround suppression effects that operate over large distances (Wolfson & Landy, 1999). Indeed, there is considerable evidence from the neurophysiological literature that separate neural processes underlie orientation-tuned surround suppression and figure–ground segregation, and that these do not interact. In the visual cortex, the effects of orientation-tuned surround suppression occur on average 10 ms after the response to the onset of the visual stimulus (Bair,
Background suppression

We did not observe strong suppression of perceived contrast on the background of a figure–ground texture (compared to a uniform texture) in Experiment 1. This is in line with neurophysiological data which suggest only weak suppression of the background (Poort et al., 2012), but contrasts with recent fMRI findings which have found predominantly decreases in BOLD signal in V1 using figure–ground stimuli (Likova & Tyler, 2008). The difference between these findings may be due to the difference in stimulus design. Likova and Tyler used large strip-like figures defined by dynamic visual noise, whereas we used small texture-defined figures. Indeed, imaging studies which have used stimuli similar to the ones of the present study have typically reported enhanced activity at the location of the figure in V1 (Scholte, Jolij, Fahrenfort, & Lamme, 2008). Furthermore, the BOLD signal is not necessarily reflecting spiking activity, as it is thought to be more sensitive to subthreshold synaptic effects, which may not result in large changes in spiking activity (Maier et al., 2008). Nevertheless, there is also behavioral evidence for suppression of stimuli presented on the background. Salvagio, Cacciamani, and Peterson (2012) examined the ability of participants to discriminate the orientation of small line probes when they were situated on the background close to a high-competition or low-competition edge. The level of competition was manipulated by shaping the ground side of the edge to form either a familiar object (high competition) or a novel object (low competition). They found that the orientation of the probe was more difficult to discriminate in the high-competition case, suggesting that high competition increases the level of suppression of the background. A key difference from the current study is that our Experiment 1 measured perceived contrast at background locations situated a large distance from the figure boundaries. It is therefore possible that suppression may be stronger close to the figure (Poort et al., 2012), and this could explain the lack of strong suppression in Experiment 1. In line with this hypothesis, we observed decreases in perceived contrast on the background compared to a uniform texture in Experiment 4 when the probe was placed close to the figure. This result is suggestive of a suppressive process that increases in strength close to figure boundaries, and future work should focus on this suppressive mechanism.

Figure–ground modulation in human visual cortex

One of the aims of this study was to investigate whether we could find psychophysical evidence in humans of the kinds of neuronal enhancements found in figure–ground segregation tasks in macaque monkeys. To this end, we presented figure–ground stimuli that were very similar to those used in electrophysiological experiments in awake-behaving monkeys (Lamme, 1995; Zipser et al., 1996). These studies found that figural regions evoked stronger neuronal activity in area V1 than background regions. This figure–ground modulation has generated much interest, as it is an example of a relatively global process affecting neuronal firing rates at a very early stage in the visual system. Several studies using EEG and fMRI have demonstrated differences in the representation between figures and homogeneous textures in early visual areas in humans (Appelbaum, Wade, Vildavski, Pettet, & Norcia, 2006; Likova & Tyler, 2008; Scholte et al., 2008; Scholte et al., 2006; Skiera, Petersen, Skalej, & Fahle, 2000), suggesting that similar modulations of activity occur in human early visual areas, although a number of early studies failed to find such differences (Kastner, De Weerd, & Ungerleider, 2000; Schira, Fahle, Donner, Kraft, & Brandt, 2004). In our study,
we provide further evidence that early visual representations in humans are affected by figure–ground organization. We used a contrast discrimination task because activity in early visual areas is closely linked to contrast perception (Ress, Backus, & Heeger, 2000; Ress & Heeger, 2003), and we found that figure–ground organization indeed influences contrast perception.

Conclusion

We have demonstrated an increase in the perceived contrast of Gabor probes placed on figures compared to backgrounds or uniform textures, and a suppression of perceived contrast on ground regions close to the figure. We propose that the neural representation of the Gabor is enhanced in human visual cortex by the same modulatory signals which have been demonstrated to exist in the primary visual cortex of awake-behaving monkeys performing figure–ground segregation tasks. The measurement of perceived contrast may therefore provide a useful tool to investigate the mechanisms of figureground segregation in humans.

Keywords: contrast perception, figure–ground, contextual modulation, orientation context, perceptual organization

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References


Roelfsema, P. R., Lamme, V. A., Spekreijse, H., & Bosch, H. (2002). Figure-ground segregation in a recurrent network architecture. *Journal of Cognitive Neuroscience, 14*, 525–537.


Appendix

Derivation of perceived contrast in Experiments 1–3

For each experimental condition, we obtained two measurements: the contrast discrimination threshold (CDT) for the descending and the ascending staircase. From these two measurements we derived two orthogonal measures: the mean CDT and the perceived contrast difference between the test and reference Gabors (ΔContrast). CDT was calculated as the geometric mean:

\[ \text{CDT} = \sqrt{da}. \]  

Perceived contrast, at a first approximation, can be assumed to lie halfway between the descending and ascending CDTs. However, this approach ignores the effects of Weber’s law, which will ensure that performance is better on ascending stairs than descending stairs (as the average contrast of the two Gabors is lower on ascending staircases). To derive a formal measure of perceived contrast from our measurements of CDT, we first considered the veridical situation in which both reference and test Gabors are presented on a homogeneous luminance field. In this situation, the physical contrast of the test Gabor at threshold performance levels on descending and ascending staircases follows Weber’s law:

\[ \frac{\Delta I}{I} = k, \]

where \( I \) is the baseline intensity, \( \Delta I \) is the intensity at threshold, and \( k \) is a constant.

On descending staircases this becomes

\[ \frac{\text{CDT}_{\text{des}} - \text{ref}}{\text{ref}} = k. \]

On ascending staircases, the reference Gabor is always higher in contrast than the test Gabor, and therefore the test Gabor can be viewed as the baseline:

\[ \frac{\text{ref} - \text{CDT}_{\text{asc}}}{\text{CDT}_{\text{asc}}} = k. \]

As performance levels are, by definition, identical at both thresholds, we can assume that the underlying signal difference between the representations of the test and reference Gabors is the same for both the descending and ascending CDTs (assuming the observer is unbiased); therefore,

\[ \frac{\text{CDT}_{\text{des}} - \text{ref}}{\text{ref}} = \frac{\text{ref} - \text{CDT}_{\text{asc}}}{\text{CDT}_{\text{asc}}}. \]  

Now we add an unknown contrast change (\( \Delta c \)) to the reference Gabor, representing the influence of the texture stimuli on the perceived contrast of the reference Gabor. The change in reference contrast will cause a change in the level of contrast of the test Gabor required to reach threshold. Equation 2 then becomes

\[ \frac{\text{CDT}_{\text{des}} - (\text{ref} + \Delta c)}{\text{ref} + \Delta c} = k = \frac{(\text{ref} + \Delta c) - \text{CDT}_{\text{asc}}'}{\text{CDT}_{\text{asc}}'}, \]

where CDT_{des}' and CDT_{asc}' are the CDTs measured after the addition of \( \Delta c \). Rearranging, we obtain

\[ \Delta c^2 - 2\text{ref}\Delta c + \text{ref}^2 - \left(\text{CDT}_{\text{des}}' \cdot \text{CDT}_{\text{asc}}'\right) = 0, \]

which is a quadratic equation:
The positive root gives the correct value for $\Delta c$. This situation is applicable to Experiment 1, in which only the reference Gabor was subject to experimental manipulation; the test Gabor was always presented on a uniform texture. In this case, the change in perceived contrast difference between the test and reference Gabors, which we refer to as $D_{\text{Contrast}}$, is equal to $\Delta c$. Using Equation 3, we can therefore estimate the perceived contrast change of the reference Gabor given the CDTs from the descending and ascending staircases and the known contrast of the reference Gabor. In Experiment 2, the perceived contrast of both the test and reference Gabors was experimentally manipulated. In these experiments, it was therefore impossible to individually determine the changes in perceived contrast of each Gabor. Instead, we used Equation 3 to calculate the perceived contrast difference between the two Gabors, $D_{\text{Contrast}}$. The values that we report in the article are the difference in perceived contrast between the test and reference Gabors from the perspective of the reference Gabor, i.e., positive values indicate that the reference Gabor is being perceived at a higher contrast than the test Gabor. In Experiment 3, the test Gabor was subject to experimental manipulation, whereas the reference Gabor (called the standard Gabor in this experiment) was always presented on a uniform texture. We therefore derived $\Delta c$ for the test Gabor (Equation 4). This equation is identical to Equation 3 except for the change in sign of the first term; the positive root again gives the correct value for $\Delta c$.

$$
\Delta c = \frac{-2\text{ref} \pm \sqrt{2\text{ref}^2 - 4(\text{ref}^2 - \text{CDT}_{\text{des}}' \text{CDT}_{\text{asc}}')}}{2}
$$

(3)

$$
\Delta c = \frac{2\text{ref} \pm \sqrt{2\text{ref}^2 - 4(\text{ref}^2 - \text{CDT}_{\text{des}}' \text{CDT}_{\text{asc}}')}}{2}
$$

(4)