6. On the contribution of contour mechanisms in early visual cortex to shape perception: an exploratory study

Abstract

The visual system tends to group clusters of similar parts into a single shape. The perceived shape of such an object – consisting of many similar small parts – can be manipulated by creating a perceptual conflict between the orientation and the position of the parts. This has the interesting consequence that the position of parts and intermediate illusory contours can appear displaced compared to their physical position. Here, we used this shape-dependent change in perceived position as a pointer to identify visual regions involved in shape perception. We hypothesized that if the percept of a shape is primarily evoked bottom-up through (illusory) contours generated at an early level in visual cortex, it should be possible to read-out the displaced contour activity in V1 and V2, as these areas have previously been associated with contour integration. On the other hand, if it is the perceived shape that drives the perceived positional change of the parts and contours, activity in early visual cortex should reflect the physical position of the parts and not differ depending on the perceived shape.

In the experiment, participants viewed relatively large shapes composed of gabor patches, while their brains were scanned using fMRI. Data was analyzed by determining shifts in the position of contour-evoked cortical activity. In early cortical areas (V1-V4, LO1), this position was independent of the perceived illusory shape. Only in visual region LO2, the data showed a trend to suggest that the peak's position changed in line with the perceived illusory shape. We conclude that early visual areas represent the physical position of stimuli only.

6.1. Introduction

The visual system has the tendency towards grouping clustered parts into a uniform single whole. The Gestalt school of thought defined three principles particularly for how the visual system organizes parts into wholes. Figures are seen as uniform and as simple
as possible (Pragnanz). Objects such a disorganized cable would be perceived as a single entity (Good Continuation). Nearby parts are grouped together (Proximity) (Korte, 1923). By using shapes of which the percept relies on some of these principles, we investigated where the brain processes are located that result in the perception of a shape.

In the study of Day & Loffler (2009), the contribution of position and orientation to the overall shape perception was modified by keeping the position of the parts the same and assigning their orientation based on that of a shape defined by a specific radial frequency (RF). They argued that the visual system “favors orientation signals and overrides the positional information” so that the perceived location of parts may differ from their physical position. The nature of the shape and the strength of the position illusion in this study depend on a number of factors such as position alignment and orientation continuity of the parts. The most powerful version of the illusion can be obtained by using both of these aspects in synchrony as shown by Day & Loffler (2009) and Wang & Hess (2005) For this type of stimuli, it is known that orientation information dominates the overall shape information (Day & Loffler, 2009).

In our study, the stimuli were composed of Gabor parts whose centers are aligned on an invisible circle while their orientations are sampled from certain points on either a circle or a pentagon (Figure 1). In this way, we kept the spatial layout of the holistic shape the same, while still evoking different percepts by varying the orientation of each single part. In a way, one can state that the position and orientation information are thus in conflict: the perception of the shape is determined largely by the orientation of the parts rather than their position, resulting in the perception of a pentagon rather than a circle.

It is an interesting question to determine where this illusion might originate. One possibility is that in early visual cortex, contour integration mechanisms influence the perceived part position and consequently this affects the perceived shape. Hypothetically, if the activity pattern in the visual cortex solely depends on the parts’ positions in space, changing their orientation should not change the cortical representation of their position. However, according to association field theory of Field, Hayes, & Hess (1993), neurons processing a specific orientation have excitatory connections with aligned neurons with similar orientation sensitivity. Therefore, we expect that the stimulus used here will also activate neurons in their vicinity. This – in turn – would result in the formation and perception of illusory contours, which in turn may lead to a specific shape percept. Hence, we predict very specific displacements of contour related activation in V1 and V2 in case the shape illusion is evoked through the illusory contour-dependent activity.

Alternatively, the shape is perceived more holistically based on the orientation information only. For this reason, among our regions of interest (ROI), we also include areas that have previously been implicated in shape perception, namely the lateral occipital cortex (LOC) regions. These may also respond depending on the perceived shape.

As a point of interest, in addition to classic luminance-contrast defined retinotopy (LCR) for the visual field mapping we also used orientation-contrast derived retinotopy (OCR) (see chapter 5). Compared to LCR the stimulus used in this technique uses parts (i.e. gabor parts) that are very similar to those used in the main experiment. We used this
method in combination with population receptive field (pRF) modeling to determine the eccentricity and polar angle information for each voxel.

6.2. Methods

6.2.1. Participants

Prior to scanning, participants signed an informed consent form. The four participants (3 female, 1 male; average age: 24.25 age-range: 22-27) had normal vision. Our study was approved by the UMCG medical ethical review board.

6.2.2. Stimulus presentation

Visual stimuli were created using MATLAB and the Psychtoolbox (Brainard, 1997; Pelli, 1997). Stimuli were presented on a BOLD screen 24 MR Safe display screen (Cambridge Research Systems; 52cm x 32.5cm). The screen was located at the head-end of the MRI scanner. Participants viewed the screen through a tilted mirror attached to the 16-channel SENSE head mounted coil. Distance from the eyes to the screen (measured through the mirror) was 80 cm. Maximum stimulus radius was 10.2 degrees of visual angle.

6.2.3. Shape stimulus

The shape stimuli we used were composed of 10 gabor parts. The orientation of the Gabor was sampled from a shape in which the radial frequency (RF) was modulated according to a sinusoidal modulation of the radius of a circle (Day & Loffler, 2009; Wilkinson, Wilson, & Habak, 1998). We used either a circle (0 amplitude modulation) or a pentagon shape (5 cycles, Figure 1). The standard deviation of the gabor envelope was 0.2 deg. The Gabor parts making up the shape were flickering at 8 Hz.

6.2.4. Visual field mapping

For the visual field mapping procedures, the reader is referred to chapter 5. Mapping was performed using both Luminance Contrast Retinotopy (LCR) and Orientation Contrast Retinotopy (OCR).
Figure 1: Example stimuli. The gabor parts composing both the circle and pentagon shapes occupied exactly the same positions on a circle. However, the orientations of the parts were sampled from RF modulated shapes (left) (a circle and a pentagon respectively).

Figure 2: Stimuli. A, B and C correspond to the stimuli used in the upward pointing pentagon, the circle and the downward pointing pentagon shape conditions, respectively. The gabor parts that make up the shape were flickering at 8 Hz and were presented for 6 seconds, followed by a mean luminance screen lasting 4.5 seconds. Participants were required to fixate throughout the run.
Figure 3: Analysis: Grouping of regions of interest in terms of outward and inward pointing direction of the (virtual) contour connecting the gabor parts (Note that this division is reversed for the downward pointing pentagon (left) compared to the upward pointing pentagon (right) condition). In the experiment, we specifically test the hypothesis that the stimulus driven BOLD response is shifted to higher eccentricities in the outward compared to the inward classified sectors (sector label determined on the basis of the RF shape that was used to derive the orientations).

6.2.5. MRI scanning

6.2.5.1. Scanner

A T1-weighted whole-brain scan was acquired to chart each participant’s cortical anatomy. The functional scans were collected using T2*-weighted echo-planar imaging sequences, with a flip angle of 80°, a TR of 1.5 second and a TE of 30 ms, and a voxel size of 2.3 mm isotropic. Each functional scan consisted of 24 slices aligned parallel to the calcarine sulcus.

6.2.6. Experimental procedure

Participants were scanned using both LCR and OCR and the shape stimuli in three different sessions of approximately 1 hour. In the first session the anatomical scan and LCR experiment was performed. In the second session, OCR was performed. In the third session, the shape experiment was performed. In the shape session, each run consisted of 119 functional images (duration of 178.5 s). 12 runs were performed. The Gabor parts making up the shape were shown for 4.5 s (3 TR) followed by a blank screen with mean luminance that was presented for duration of 6.0 s (4 TR). This sequence was repeated 7 times in a run.

6.2.7. fMRI preprocessing

Analysis of the functional imaging data was performed using the pipeline of the mrVista software package from Stanford University (http://vistalab. stanford.edu/software/). The T1-weighted whole-brain anatomical images were re-sampled to a 1 mm isotropic resolution. Automatic gray and white matter segmentation was carried out with FSL
software (Smith et al., 2004) and subsequently edited manually if necessary. The functional scans were motion corrected and the anatomical and functional scans were aligned. Data for runs of the same conditions were averaged. To improve sensitivity, only data from gray-matter voxels were analyzed for activity.

6.2.8. fMRI data analysis

For analyzing the visual field maps, population receptive field analysis was performed on the functional MRI data (Dumoulin & Wandell, 2008). The borders of visual areas V1, V2, V3 and V4v, L01 and L02 were determined based on the LCR-based retinotopic maps of each participant. In the analyses of the shapes, each voxel’s eccentricity and polar angle was determined based on the OCR. We restricted the data analysis to voxels with pRF centers between 1 and 9 degrees of eccentricity.

6.2.9. Analysis of shape-induced activations

This analysis (Engel, 2012)(Engel, 2012) fits a sinusoidal signal to the repetition of the stimulus block and returns the coherence of the fitted signal, as well as its amplitude. The data were then displayed on a 3D representation of the boundary between white and gray matter. Based on the activation patterns obtained for the circle shape condition, the average phase of the peak response in V1 was determined individually for each participant. Next, for all experimental conditions, fMRI activation was expressed as the amplitude of the blood oxygenation level-dependent modulation (BOLD), projected on the phase of the V1 peak response to the circle stimulus. This procedure assures that activations with a fixed temporal relationship to the stimulus presentation are used under all circumstances. In addition, this procedure takes small individual variations in BOLD delay into account (Cornelissen, Wade, Vladusich, Dougherty, & A., 2006).

6.2.10. Sector ROI-based analysis

ROIs were created by dividing the visual field into 10 equally sized sectors (Figure 1) with the borders of each sector aligned with the location of the gabor parts. Each voxel was assigned to a ROI-sector based on the polar angle of its associated pRF center (as determined using OCR).

Separately for each individual and each visual area, for each combination of stimulus condition (upward, downward, circle) and sector ROI type (upward, downward), we fit a cumulative gaussian distribution curve to the projected amplitude as a function of log eccentricity. This distribution was characterized by a baseline and a mean, a standard deviation and amplitude for the cumulative gaussian. To minimize the number of fitting parameters, only the mean was left to vary between sector types and conditions. Fitting was done using the Solver of Excel 2011 (Mac Version; set to “GRG non-linear engine”) by minimizing the mean squared error between the fit and the data. The fitted mean thus indicated the position of the peak response for a specific condition and sector type. To derive the relative shift of the peak response for each shape condition, for each combination of pentagon shape condition and sector type, the fitted mean for the circle condition was subtracted. Depending on the stimulus (either the upward or downward
pointing pentagon), a sector was either classified as "pointing" inward or outward (hence, the final sector ROI classification differed for the two stimulus types; see figure 3). Finally, the relative shift in position of the peak response was calculated by averaging the inward and outward sectors obtained for the two stimulus types.

6.2.11. Statistical analysis

To test for differences between areas in their way of responding to the illusory shapes, repeated-measures ANOVA was performed on the shifts in peak position, with area (V1, V2, V3, V4, LO1, LO2) and ROI label (inwards, outwards). Moreover, given our very specific expectation about the direction of the effect, one-sided paired t-tests were performed to determine in which visual areas the position of the response was shifted to higher eccentricities for the outward compared to the inward sectors. A p-value of 0.05 or less was taken to indicate a significant result.

6.3. Results

Figure 4 shows the response amplitude for a single observer in V1 as a function of eccentricity combined over all conditions and sectors. The peak of the response lies at approx. 4 deg which corresponds to the location were the Gabor parts were presented. This result indicated that our stimuli, despite being relatively small, evoked a substantial BOLD response with a clear peak. In our analysis approach, we verify whether this response has been shifted towards higher eccentricities for the "outward" compared to the "inward" designated sectors (see figure 3).

Subsequently, we explored the possibility of early visual cortical contour mechanisms contributing to the illusory shape perception. For this, the signals evoked by the oriented Gabors as well as any possible intermediate (illusory) contour signals were compared between the two different pentagon shapes. The circle stimulus served as a reference signal. Figure 5 shows the shift in the response for the individual participants in different visual areas for the "outward" and the "inward" designated sectors. Figure 6 shows the same data expressed in terms of the average difference in shifts between sectors.
Figure 4: Projected amplitude in V1 for the circle condition and plotted as a function of eccentricity. Data averaged over all participants. Error bars indicate 1 s.e.m. over participants. Eccentricity was binned in bins of 0.5 deg.

Repeated measures ANOVA indicated that there was no difference between areas (F(5,15)=1.5; p=0.23). In the individual areas V1, V2, V3, V4 and LO1, paired t-tests showed that there was no evidence for an outward shift of the peak response (p-values of 0.41, 0.43, 0.26, 0.32, 0.45, respectively). In LO2 there was a trend indicating a possible shift (p=0.08).
Figure 5: Relative displacement of the cumulative gaussian fit shown for individual participants for the different ROIs.

Figure 6: Average difference in shift of the peak of the response between 'outwards' and 'inwards' sectors in all ROIs. Error bars indicate 1 s.e.m. over participants.
6.4. Discussion

The main finding of this study is that a powerful shape illusion did not evoke observable shifts in contour responses in early visual cortex. This suggests that this specific illusion is not based on illusory contours that arise in early visual cortex. More likely, therefore, it arises from integrating orientation information in a more holistic manner. We have some evidence for this. The only area that showed a notable trend in its shift in response that coincided with the expected direction was LO2. This region has previously been implicated in object perception.

In our experiment, we used different shapes that were created by modulating the orientation of constituting parts only, while keeping the location of each part intact. While this resulted in clearly observable differences in percept, visual spatial activity in various occipital regions did not vary significantly, even though tested one-sided. We tested the assumption that the shape illusion is based on contour integration, by classifying sectors in the visual field according to whether the (illusory) contour appeared to point away or towards the center of the stimulus. This also corresponded to the position of the lobes of the shape from which the part orientation was derived. We hypothesized that if shifts in (illusory) contours were underlying the illusory shape percept, we should be able to observe this in the form of shifts in the BOLD responses particularly in V1 and V2 (because of their relative size, as well as V2’s previous implication in illusory contour perception (von der Heydt & Peterhans, 1989)). In none of the occipital regions examined we found proof that the shape illusion is contour-based. However, in LO2, a high-level area, there was a trend towards a significant shift.

Importantly, the lack of finding a shift was not due to a lack of response. Despite being relatively small, our stimuli evoked a substantial BOLD response with a clear peak. Moreover, the determination of the shift was based on the entire response between 2 and 9 deg of eccentricity, and not just on the location of the peak. Our present analysis included the activations evoked by the Gabor parts. This was done, as the orientation information of the Gabor was considered to contribute to the shape perception. However, reducing the sector width to exclude most of the BOLD activity evoked by the Gabors did not change our overall results.

6.4.1. Previous contour integration and illusory contour studies

A large body of literature has addressed how signals can be spatially extended to form contours (for a review, see Loffler, 2008). Biologically plausible models such as based on the association field theory, suggest that connections in neural fields are strong along the axis of orientation given by the target element (Field et al., 1993) and weak in orthogonal directions. Based on these ideas, we had expected contour signals to fill-in between the oriented Gabors that make up the pentagon shapes.

Visual illusory contour responses in the visual cortex have been reported in several previous studies (Kok & de Lange, 2014; McMains & Kastner, 2011; Murray & Herrmann, 2013). While some studies reported an enhancement of activity in early visual cortex associated with the percept of the illusion (Lee, Nguyen, 2011), others
suggested that V1 and V2 activations in response to illusory contours are a consequence of feedback from higher order areas such as LOC (Stanley and Rubin, 2003). A previous study (Kok and De Lange 2014) claimed to have found illusory contour-related activity in V1 based on showing participants a Kanizsa triangle stimulus. However, in this study, the inducing and control stimuli had different shapes. An additional issue raised concerned that the effect might have been caused by neural adaptation to perceptually stable input (Moors, 2015). Similar concerns cannot be raised for our study as – except for the orientation information – our shape and control stimuli were identical.

6.4.2. Shape versus contour information processing

Human neuroimaging studies have found activations in V1 and V2 evoked by illusory contours (Ffytche & Zeki, 1996; Lee & Nguyen, 2001; Montaser-Kouhsari, Landy, Heeger, & Larsson, 2007; Ramsden, Hung, & Roe, 2001). There are also studies that support the involvement of higher order visual areas (V3, hV4, V01, V3A/B, V7, LO1 and LO2) as well as early cortical areas (V1 and V2) in illusory contour processing (Mendola, Dale, Fischl, Liu, & Tootell, 1999; Montaser-Kouhsari et al., 2007). Mendola et al (1999) also found that responses to contour-defined shapes consistently increased across higher regions throughout the visual cortical hierarchy. They concluded that higher order areas including the LO region were specifically responsive to illusory induced contours. Those areas may be responsible for figure-ground segmentation as well. Montaser-Kouhsari et al, (2007) used an event-related adaptation paradigm to assess orientation selectivity for illusory contours. They demonstrated that adaptation strength to illusory induced lines increased systematically towards higher-level visual areas. There is additional evidence for high-level areas dealing with processing information of shapes rather than with the segmentation of contours (Grill-spector, Kourtzi, & Kanwisher, 2001). fMRI adaptation has shown that higher-order visual areas show adaptation when presented objects with the same shapes but different contours but not when objects with the same contours but different shapes are shown. Somewhat corroborating the importance of higher order visual areas, in our experiment, only visual area LO2 showed a notable shape-dependent response (albeit not significant). The lack of differences in contour-related activation in early visual areas in our study also suggests that contour integration and shape perception are distinct processes.

6.4.3. Limitations

The present study only included 4 participants, whose responses were analyzed in great detail. In particular, the trend in LO2 might be confirmed by including additional participants. At the same time, given even the absence of a trend in earlier areas, it is unlikely that including additional participants would result in significant and relevant effects.

Another limitation is arisen by the incompetent stimulus size and the spatial resolution of fMRI detected receptive fields. Let us define the effect size of illusion in terms of the maximum and minimum eccentricity of the stimulus edges given in figure 1 (left column). If we assume that the observers perceived the Gabors along with the illusory contours just as the radial frequency shapes, the effect size could be quantified as the
difference between these two eccentricities. This results in lower than 1 degrees of visual angle. Given the receptive field sizes are barely less than one degree of visual angle around the stimulus presentation eccentricity (see chapter 5 figure 5), this is a limited interval to look for a prominent effect of eccentricity shifts.

By including stimuli with physical shapes similar to the illusory shapes future studies could consider establishing the maximal effect that could have been measured in early visual cortex.

6.4.4. Conclusion

In a shape illusion, we did not find any evidence of illusory contour related responses in early visual cortex. This suggests that this specific illusion is not based on illusory contours that arise in early visual cortex. We suggest that the illusion may arise from integrating orientation information in a more holistic manner. According to this view, higher-order areas would present activity related to the shifts in shape perception. We found a notable trend in LO2 following the direction of the illusion's shift. This region has previously been implicated in object perception.
6.5. References


