5. A comparison of Orientation- and Luminance-Contrast based retinotopy

Abstract

The abundance of orientation selective neurons throughout early visual cortex is well known. However, in human functional magnetic resonance imaging (fMRI) the assessment of orientation selectivity to study in the spatial organization of the visual cortex is still relatively uncommon. Given that many cortical neurons are orientation selective, the use of stimuli that tap into this property may provide more precise mapping information. Here, we use fields of oriented Gabor patches as a means to map and characterize properties of the human early visual cortex. Participants in our fMRI experiment viewed arrays of Gabor patches composing a foreground (a bar) and a background. These could only be distinguished on the basis of the difference in orientation of their patches. In our analyses, we compare the population receptive field (pRF) properties obtained using our new orientation contrast-based retinotopy (OCR) to those obtained using classic luminance contrast-based retinotopy (LCR). Our results show that BOLD responses obtained during OCR were lower than those for LCR. Nevertheless, visual field maps for LCR and OCR are highly comparable. The explained variance (EV) of the pRF models for OCR was lower than for those based on LCR. Yet, for OCR EV remained constant over eccentricity, while for LCR it tended to drop with increasing eccentricity, which was most marked in visual areas LO1 and LO2. For early visual areas (V1-V4), the eccentricity assigned to a voxel's pRF was comparable for LCR and OCR, yet OCR-based modeling resulted in smaller pRFs. For LO1 and LO2, both pRF eccentricity and size differed substantially between LCR and OCR, with lower eccentricity and smaller sizes estimated for OCR. We discuss why OCR may result in more accurate pRF property estimation and may therefore be the method of choice in particular for characterizing higher order visual areas.
5.1. Introduction

The discovery of orientation selective neurons in the early visual cortex is one of the milestones of visual neuroscience in the 20th century. Consecutive studies by Hubel & Wiesel (1959, 1962) showed that V1 neurons are selectively responsive to specific orientations and directions of motion. The abundance of orientation selective neurons throughout early visual cortex is by now well established. However, although previous studies have shown that orientation processing can be revealed using fMRI (Freeman, Brouwer, Heeger, & Merriam, 2011; Haynes & Rees, 2005; Kamitani & Tong, 2005; Swisher et al., 2010) the use of orientation information for characterizing visual areas and neuronal population characteristics is uncommon. Here, we do so, and compare the results to classic retinotopic mapping.

The most widely used stimuli in retinotopic mapping experiments are rings, wedges or bars containing a high-contrast polarity reversing pattern moving over a blank background. Retinotopic mapping uses the time-varying position of the patterns in the visual field to localize the borders and determining the spatial organization of visual areas. One of the reasons for the popularity of high luminance contrast patterns is that they tend to drive most neural populations – thus resulting in high signal-to-noise BOLD responses.

Recent approaches in fMRI analysis and retinotopic mapping have turned to using model-based analysis to reveal more detailed properties of visual areas and neuronal populations (Brewer, Barton, & Dumoulin, 2014; de Haas, Schwarzkopf, Anderson, & Rees, 2014; Dumoulin, Hess, May, & Harvey, 2014; Dumoulin & Wandell, 2008; Haak, Cornelissen, & Morland, 2012; Harvey & Dumoulin, 2011; Papanikolaou, Keliris, Papageorgiou, Shao, & Krapp, 2014; Schwarzkopf, Anderson, Haas, White, & Rees, 2014; Verghese, Kolbe, Anderson, Egan, & Vidyasagar, 2014; Zuiderbaan, Harvey, & Dumoulin, 2012). The most commonly used stimuli in this approach are bar-aperture stimuli containing high-luminance contrast reversing patterns (the carrier) presented on a blank background. However, other carriers can be used for characterizing pRF properties as well (Dumoulin et al., 2014). The ability to reveal more details may further be improved by also making the stimulus more selective.

We reasoned that we could use orientation as a carrier to define a bar-like aperture by placing similar small elements throughout the visual field albeit with elements having different orientations in bar and background (figure 1). As a consequence, both aperture and background will be continuously stimulated. However, the bar is visible because of the orientation-contrast creating virtual edges. Because of targeting a more selective population of orientation contrast neurons, we expect this approach to result in more selective activation and thus lower BOLD amplitudes – thus potentially avoiding non-linearities in the BOLD response. At the same time, we expect to retain the ability to map out the pRF properties of visual cortex. As an additional advantage, the continuous full field stimulation presumably more closely resembles natural stimulation. To our knowledge, our study is the first to use orientation-contrast in combination with population receptive field (pRF) modeling to map and characterize human visual cortex.
5.2. **Methods**

5.2.1. **Participants**

Prior to scanning, participants signed an informed consent form. The four participants (3 female, 1 male; average age: 24; age-range: 22-27) had normal vision. Our study was approved by the UMCG medical ethical review board.

5.2.2. **Stimulus presentation**

Visual stimuli were created using MATLAB and the Psychtoolbox (Brainard, 1997; Pelli, 1997). Stimuli were presented on a BOLD screen 24 MR compatible display screen (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. Screen size was 36 x 23 degrees of visual angle.

5.2.3. **Stimulus Design**

5.2.3.1. **Luminance-contrast defined retinotopy (LCR)**

For the retinotopy scan, we presented a drifting bar aperture defined by high-contrast flickering texture (Dumoulin & Wandell, 2008; Harvey & Dumoulin, 2011; Zuiderbaan et al., 2012). The bar aperture moved in 8 different directions (four bar orientations: horizontal, vertical and the two diagonal orientations), with for each orientation two opposite drift directions. The bar consisted of alternating rows of high-contrast luminance checks drifting in opposite directions. The bar moved across the screen in 16 equally spaced steps each lasting 1 TR. After each pass and a half, 12 seconds of a blank stimulus at mean luminance was presented full screen.

5.2.3.2. **Orientation contrast defined retinotopy (OCR)**

The orientation-contrast defined retinotopy stimulus (OCR) was designed in such a way that the aperture size and shape and movement of the aperture approximately corresponded to that of the conventional LCR stimulus. By doing so, we preserved the spatial attributes of the visible larger-scale object (the bar aperture). However, instead of a blank grey background and a luminance contrast-defined bar, both the background and the aperture bar consisted of small oriented Gabor patches. Bar and background could be distinguished from each other on the basis of their different base orientations (Figure 1). The OCR stimulus consisted of a field of small Gabor patches (GB) that filled the entire screen. Gabors were positioned in a [90 x 56] grid covering the entire screen. The width of the gabor patches was 0.33 deg. They were 0.07 deg apart from each other. Absolute orientation of the Gabors varied randomly and was refreshed every 125 ms. A relative difference in base-orientations between fore- and background of 45° revealed the bar aperture from the background. The position of each Gabor's center varied randomly between 0-0.08 degrees of visual angle to reduce adaptation.
Figure 1: A: Example bar aperture stimuli for Luminance-Contrast (LCR) and B: Orientation-Contrast (OCR) defined Retinotopy. C: Stimulus model matrices used in the LCR and OCR-field (OCRf) and D: OCR-edge (OCRf) population receptive field (pRF) analyses.
5.2.4. MRI scanning

Scanner
Scanning was carried out on a 3 Tesla Philips Intera MR-scanner using an 8-channel receiving SENSE head coil. A T1-weighted scan covering the whole-brain was recorded 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.

5.2.5. Experimental procedure

Participants were scanned using both the standard luminance-contrast defined retinotopy (LCR) and our new orientation contrast-defined retinotopy (OCR) in two different sessions of approximately 1 hour. For LCR (OCR) a single run consisted of 136 (188) functional images (duration of 204 s and 270 s respectively). Eight prescan images (duration of 12 s) were discarded. In the first session, the anatomical scan and the LCR experiment (8 runs) were performed. In the second session, the OCR experiment (10 runs for three and 11 runs for one subject) was performed. During scanning, participants were required to perform a fixation task in which they had to press a button each time the fixation point turned from green to red. The average performance over participants for the fixation task was 82%.

5.2.6. Preprocessing

Analysis of the functional imaging data was performed using the mrVista software package from Stanford University (http://white.stanford.edu). 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. The functional scans were motion corrected and the anatomical and functional scans were aligned.

5.2.7. Population Receptive Field (pRF) modelling

For both stimulus types (LCR and OCR), population receptive field analysis was performed on the functional MRI data (Dumoulin & Wandell, 2008). For each voxel, a 2D-gaussian model was fitted with parameters x0, y0, and σ where x0 and y0 are the receptive field center coordinates and σ is the spread (width) of the Gaussian signal, which is also the pRF size. All the parameter units are in degrees of visual angles and stimulus-referred.

We analyzed the responses to the OCR stimuli using two different models to explain how the bar-aperture may be processed by the visual system. In the first (field) model, we include the aperture’s surface in between the borders in the definition of the stimulus. In the second (edge) model, we assume that only neurons in a narrow region near the
(virtual) border between the fore- and background of Gabor patches are activated by the stimulus.

5.2.8. **Statistical analysis**

Data was thresholded by retaining the pRF models that explained at least 20% (10% for the maps shown in figure 2) of the variance in the BOLD response and that had an eccentricity in the LCR analysis in the range of 2-9 degrees. Unless mentioned otherwise, for the analyses, results (i.e. pRF model parameters) were binned over eccentricity, in 1-degree bins, separately for each hemisphere. Statistical analysis was performed using repeated measures ANOVA, with ROI, pRF model (LCR, OCR-edge, OCR-field), hemisphere (LH, RH) and eccentricity-bin as within subject parameters. A p-value of 0.05 or less was taken to indicate significant results.

5.3. **Results**

In this study, we compare retinotopic mapping results obtained with Luminance- and Orientation-contrast defined stimuli (abbreviated as LCR and OCR respectively) and use population receptive field (pRF) modeling to analyze the data. To preview our main results, we find that LCR and OCR derived maps of visual cortex are highly comparable. In general, pRF sizes obtained with OCR are smaller than those obtained with LCR. While there are small shifts in the voxel based pRF location in early visual cortex (V1-V4), in higher order ventral cortex (LO1 and LO2) we find lower eccentricities assigned to the pRFs of voxels as well as substantially smaller pRFs. EV as a function of eccentricity tended to be lower but more stable for OCR than for LCR.

5.3.1. **Comparison of BOLD signals evoked by LCR and OCR stimuli.**

Figure 2a shows representative time-series for LCR and OCR stimuli. Figure 3b shows the average standard deviation of the signal in various ROIs. It is clear that the signal modulation evoked by OCR stimuli is smaller than that evoked by LCR stimuli. Remarkably, the stimulus induced signal variation (standard deviation) for LCR stimuli is markedly smaller for higher (LO1, LO2) than for lower order (V1-4) areas. For OCR stimuli, signal variation is comparatively lower but stable over areas (and even shows a slight increase).

5.3.2. **Comparison of LCR and OCR derived retinotopic maps**

Figure 3 shows polar angle, eccentricity and pRF size maps obtained for LCR and OCR stimuli projected onto the inflated hemisphere of a representative participant. This visualization shows that overall, the maps and ROI borders obtained with OCR and LCR are very comparable. For OCR, it can be appreciated that in the extrastriate regions, pRF sizes are generally smaller (less red).
Figure 2: (a) A representative voxel's pRF field coverage and time series for LCR (blue) and OCR (red) stimuli, (b) Time series of percentage BOLD modulation for a representative subject.
5.3.3. Comparison of voxel-wise pRF eccentricities for LCR and OCR

Figure 4 compares the eccentricities assigned to each voxel based on the results of the pRF analysis in the LCR and the two OCR model conditions. In early visual cortex (V1-V4) the eccentricities assigned are quite comparable, evident from the relatively small deviation from the oblique line. For LO1 and LO2, the eccentricities assigned differ much more substantially, with most eccentricities being smaller in the OCR conditions. There is only a very small difference between the eccentricities assigned by two OCR model conditions.

There was a significant interaction between ROI and eccentricity (F(35, 105)=5.67, p<0.01). ROI, condition and eccentricity did not show a three-way interaction (F(35, 105)=1.37, p>0.05).
Figure 3: Polar angle, eccentricity and pRF size maps for the right hemisphere of participant S04 obtained with luminance- and orientation-contrast (field) defined stimuli. In all cases, the explained variance threshold was set to 0.1 Dark blue lines indicate ROI borders. The maps for the field and edge analysis of the orientation-defined stimuli were nearly identical and are therefore not shown separately.
5.3.4. Comparison of voxel-wise pRF sizes for LCR and OCR

Figure 5 shows pRF sizes based on the results of the pRF analysis in the LCR and the two OCR model conditions, as a function of the eccentricity assigned by each of the respective model analyses. As is commonly observed, pRF size increases with eccentricity. This was comparable for all conditions and ROIs. In general, the pRF sizes determined based on the OCR analyses were somewhat smaller than those determined based on the LCR analysis. The difference in pRF size between conditions was most prominent for V4, LO1 and LO2. There was a significant interaction between condition and eccentricity (F(14, 42)=4.75, p<0.05) and condition and ROI (F(10, 30)=9.46, p=0.01), indicating the difference is larger for higher order areas.
Figure 5: Average pRF size plotted as a function of pRF eccentricity (as assigned by each respective model analysis) for six different ROIs. Eccentricity was binned in bins of 1 degree of visual angle. Average results for 4 participants, 2 hemispheres each. Error bars indicate the standard error of the mean over hemispheres.

Figure 6 shows the average pRF sizes in each ROI. The pRF size determined for the three different conditions differed for the various ROIs (F(10, 30)=9.46, p=0.01). While pRF size increased monotonically from lower to higher order visual areas for both LCR and OCR, this effect was most pronounced for LCR.

5.3.5. Comparison of Explained Variance for LCR and OCR-based analyses

Figure 8 shows the average VE in each ROI as a function of model-specific eccentricity. VE is higher for LCR than for OCR. For LCR, in most areas, VE tends to decrease with increasing eccentricity. For OCR, in most areas, VE is stable over eccentricity. Figure 8 shows the average VE in each ROI. The average VE determined for the three different conditions differed for the various ROIs. For LCR, VE decreased for higher order areas compared to V1-V3. For OCR, VE increased slightly from V1 to V3, and peaked in LO1.
Figure 6: Comparison of pRF sizes for each ROI and for all three analysis. For each observer and ROI, pRF size was averaged over the eccentricity bins as shown in figure 5. Error bars indicate the standard error of the mean over observers.

Figure 7: Explained variance as a function of pRF eccentricity for six different ROIs. Model-specific eccentricity was binned in bins of 1 degree of visual angle. Each bin shows the average results for 4 participants, 2 hemispheres each. Error bars indicate the standard error of the mean over hemispheres.
Figure 8. A: Comparison of the average explained variance in each ROI and for all three models. For each ROI, explained variance was averaged over the eccentricity bins as shown in figure 7. B: Average slope of explained variance against eccentricity for each ROI. Error bars show standard error of the mean over observer.
5.4. Discussion

The main finding of this study is that orientation-contrast defined retinotopy (OCR) is feasible and provides pRF estimates that – in particular for higher order ventral areas – are distinctive and – as we will discuss below – most likely more accurate compared to those obtained using luminance-contrast retinotopy (LCR). For LO1 and LO2, the voxel-wise estimated pRF eccentricities were substantially lower for OCR than for LCR. For early visual areas (V1-V4), the voxel-wise estimated pRF eccentricities showed small but systematic shifts between OCR and LCR. In general, estimated pRF sizes were smaller for OCR than for LCR. The explained variance (EV) of the pRF models was lower for OCR than for LCR. However, for OCR, it remained constant over eccentricity, while for LCR it tended to drop with increasing eccentricity. This was most marked in visual areas LO1 and LO2. Visual field maps derived from OCR and LCR were qualitatively highly similar. Below, we discuss these results in more detail.

5.4.1. Lower signal amplitude and explained variance for OCR compared to LCR

Signal amplitude and EV of pRF models of OCR were both lower compared to those of LCR. This is not entirely surprising since high luminance contrast stimuli have historically been preferred for retinotopic mapping because they stimulate the majority of visually sensitive neurons and thus evoke large BOLD responses.

Evident from the standard deviation of the raw BOLD signal, for LCR, both LO1 and LO2 showed a drop in signal compared to V1-V4. In OCR, the signals remained as high in the higher order areas. This might be an indication of a stronger involvement of high-level visual areas for processing the orientation contrast boundaries compared to the luminance contrast stimuli. This finding corroborates a patient study that indicated that V1 is sufficient to process simple orientation discrimination tasks but that ventral extrastriate regions are required to properly detect texture boundaries (Allen, Humphreys, Colin, & Neumann, 2009).

A feature of OCR was that EV of the pRF models – while lower than for LCR – remained relatively stable over eccentricity (with the exception of LO2). The LCR pRF models tended to show a decrease in EV with eccentricity, most markedly in LO1. Hence, although the EV of OCR models is lower, most likely due to lower signal-to-noise, the models tended to retain their explanatory value at all eccentricities.

5.4.2. Qualitatively similar retinotopic maps, but smaller pRFs for OCR compared to LCR

When the ROIs that were drawn based on the OCR data are projected onto those based of the LCR data, they were very comparable. Only small and no systematic differences in border locations were present. Hence, for determining the general layout of visual cortical maps OCR appears to hold no advantage over LCR. There appears, however, to be a difference in estimated pRF size between the methods. OCR generally assigned smaller pRF sizes to voxels, with the edge-based analysis resulting in the smallest estimates. Smaller pRFs imply that each voxel more selectively processes a region of the visual field. There might be a couple of reasons for this. First of all, signal amplitude was
smaller in OCR. Moreover, unlike in LCR, in OCR the background image was also dynamic, resulting in perpetual activity in visual cortex. This may have limited BOLD spread, and as such further resulted in smaller pRF size estimates. Estimating smaller pRF sizes is not necessarily a bad feature: as we will argue below, it may actually be better for accurately estimating pRF location in the visual field.

5.4.3. Differences in Lateral Inhibition between LCR and OCR explains lower BOLD amplitude and small pRF sizes

Lateral inhibition is the reduction of the activity of a neuron by the activity of other neurons in its vicinity. This mechanism increases the contrast and sharpness of the neural response. In OCR, – unlike in LCR in which the background is not stimulated – the stimulation between the bar and the background was continuous and identical (except for orientation). Thus, contrary to an on-off type of stimulus such as used in LCR, the activity evoked by the OCR bar is inhibited by the activity evoked by the background. This may both explain the lower response amplitude in OCR, but also the reduced pRF size.

5.4.4. OCR more accurately estimates pRF eccentricity

We observed systematic differences in the voxel-wise assigned eccentricities between LCR and OCR models. In early visual cortex (V1-V4), differences in eccentricities were rather modest. The OCR-based eccentricity values are slightly higher for the lower eccentricities (2-~5 deg), and slightly lower for the higher eccentricities (~5-9 deg). In areas LO1 and LO2, the estimated eccentricity difference was much more marked. In these areas, the eccentricity assigned during OCR to a specific voxel was ~on average~ about half that for the LCR stimuli. This difference in assigned eccentricity is one of the more intriguing and puzzling aspects of our present study. Figure 9 provides a possible explanation for the larger pRFs and more eccentric pRF locations observed for LCR compared to OCR. The standard pRF method estimates pRF size and location based on the BOLD time-series signal of a voxel. This signal is the combination of BOLD activity evoked locally and activity that "leaked" into the voxel from neighboring voxels (due to BOLD spreading). While the influence of BOLD leakage will be symmetric at the level of the visual cortex, it exerts an asymmetric effect on the pRF at the level of the visual field (see lower part of figure 9). Hence, BOLD signal leakage will increase both the pRF's estimated size and force its location towards a higher eccentricity. Compared to LCR, OCR stimuli activate a more selective neuronal population and result in smaller amplitude signals and smaller estimated pRFs. By continuously stimulating each part of the visual field, OCR may also be limiting BOLD leakage. As depicted in figure 9, smaller pRF sizes result in a smaller shift in eccentricity. The effect may be most obvious in LO1 and LO2 as these areas contain neurons with larger receptive fields (moreover, such ventral areas may have a higher cortical magnification (Harvey, Klein, Petridou, & Dumoulin, 2013; Brewer, Liu, Wade, & Wandell, 2005; but see Larsson & Heeger, 2006).

It implies that OCR, despite its lower-amplitude BOLD signal, may result in more accurate estimates of pRF eccentricity.
Figure 9. An explanation for the difference in pRF size and eccentricity between OCR and LCR based on BOLD spreading and cortical magnification. The picture shows a row of voxels that encode consecutive sections of the visual field (due to cortical magnification the section of visual field represented by each voxel expands with eccentricity). Bold activity evoked in neighboring voxels (green and blue) will leak into the target voxel (red) and mimic BOLD activity evoked locally. Based only on activity evoked in the voxel itself, the red indicates the pRF size and eccentricity. In case BOLD spreading is limited, only leakage from immediately neighboring voxels (green) will occur, slightly increasing the pRF size and eccentricity estimate. If spreading is more pronounced (blue), also more remote voxels will influence the target voxel’s BOLD signal and an even larger pRF size and eccentricity will be estimated (note how the dots that indicate the position of the pRF’s center shift towards higher eccentricity). While leakage is symmetrical at the level of the cortex, its effect on the pRF will be asymmetrical as it considers the visual field.

5.4.5. Comparison of edge- and field-based pRF analyses provides no evidence for object-specific signal processing

In real life, the scenes we are exposed to are generally much more complex than a single object against a blank background. Moreover, objects are often build up of smaller elements. For this reason, it is worthwhile to study how the brain processes and decides on the presence of more complex objects (e.g. Nordhjem, Kurman, Renken, & Cornelissen, 2015; Silson et al., 2013). Orientation-contrast defined stimuli may potentially inform about the early stages of object-related processing. In the OCR edge analysis, the assumption was that the primary signals are evoked by the local differences in orientation at the edges. In this model, we assumed that only a narrow region near the (illusory) border between the fore- and background of Gabor patches aroused visual activity. In the OCR field analysis, the assumption is that fore- and background are based
on stronger grouping for similarly oriented Gabors (Parkes, Lund, Angelucci, Solomon, & Morgan, 2001). In this model, we also included the aperture’s surface in between the borders in the definition of the stimulus. By varying these model assumptions, we expected to find out how the brain is organized for processing objects that consist of smaller elements than the whole of the bar aperture (gabor patches) where the integrative aspect is orientation.

We compared if either model used in the analysis of OCR (edge and field models) resulted in a different estimation of pRF parameters. A difference in model fit (EV in particular) could indicate figure or object selective processing in a specific area. EV was highly similar between the two OCR models, indicating that neither provided a superior explanation for the signals evoked by the orientation-contrast stimuli. Neither did we find significant differences in the maps for the two OCR models. Voxel-wise pRF eccentricity estimates were highly comparable between models, while pRF size estimates were somewhat smaller for the edge model. Consequently, we find no evidence for object-specific or selective signals in the areas studied.

5.4.6. Limitations

The Gabor patches in the current experiment were all of similar size. In a recent study, eccentricity scaling had a significant effect on goodness of fit and pRF size estimates (Alvarez, de Haas, Clark, Rees, & Schwarzkopf, 2015). Future experiments could consider scaling the Gabor patches with eccentricity. It also remains to be determined conclusively whether the eccentricity differences for OCR and LCR are a consequence of signal leakage. More accurate pRF models, that take BOLD leakage into account could also prove useful in this realm.

For logistic reasons, the LCR and OCR paradigms presently used were very similar, but not identical in terms of scan and run duration. Future experiments could consider using identical spatio-temporal profiles for both stimulus types. The signals evoked by LCR and OCR differed in BOLD amplitude. The lower amplitude signal for OCR was somewhat offset by a longer overall sampling duration for OCR than for LCR. Nevertheless, even though there were a few more and somewhat longer OCR sessions, this still resulted in models with lower explained variance. Future experiments could consider using lower contrast LCR stimuli to equalize this aspect and evaluate the consequences thereof on EV and pRF property estimates.

5.4.7. Future studies

Our current pRF analyses were based on the assumption that orientation contrast of the Gabor forms illusory edges or that Gabors are grouped into objects based on the orientation differences. More detailed – and therefore potentially more informative – models could be created that take the actual orientation of each Gabor in each frame into account when modeling the BOLD responses. In that case, also periods of blank backgrounds (i.e. Gabors only present in the bar aperture or no Gabors present at all) could be included to enable modeling this aspect of the response as well. This could result in an integrated stimulus that combines the properties of the current OCR and LCR stimuli.

73
Other visual aspects could be tested for using Gabor patch stimuli that could be generated at various levels of orientation contrast, various spatial or temporal frequencies, chromatic differences or other aspects that could result in figure-ground segmentation. By varying Gabor similarity and inter-Gabor distance, the Gabor fields could also be used to study feature integration and crowding. At higher fMRI field strengths, it could be examined at what laminar layer the OCR evokes BOLD responses, and whether this differs from classical LCR (De Martino et al., 2013; Muckli et al., 2015).

5.4.8. Conclusion

Visual field maps could be defined with orientation-contrast defined stimuli. Receptive field properties obtained using orientation-contrast defined stimuli differ from those obtained using luminance contrast defined stimuli. We conclude that despite the lower evoked signal amplitude, OCR’s more natural – texture-like – characteristics, and relatively stable EV behavior may render it an additional method of choice in particular for characterizing higher order visual areas and for comparing pRF estimates between higher and lower order areas. Our new versatile approach opens new ways to explore the functional organization of visual cortex based on well-defined stimuli that bear a relatively close resemblance to natural stimuli.

Acknowledgments

FY was supported by The Graduate School of Medical Sciences (GSMS), University of Groningen, The Netherlands. FWC was supported by the Netherlands Organization for Scientific Research (NWO Brain and Cognition grant 433-09-233).
5.5. References


