Spatially varying distortions in optical elements—for instance prisms and progressive power lenses—modulate the visual world disparately in different visual areas. Saccadic eye movements in such a complexly distorted environment thereby continuously alter the retinal location of the distortions. Yet the visual system achieves perceptual constancy by compensating for distortions irrespective of their retinal relocations at different fixations. Here, we assessed whether the visual system retains its plasticity to distortions across saccades to attain stability. Specifically, we tapped into reference frames of geometric skew-adaptation aftereffects to evaluate the transfer of retinotopic and spatiotopic distortion information across saccades. Adaptation to skew distortion of natural-image content was tested at retinotopic and spatiotopic locations after a saccade was executed between adaptation and test phases. The skew-adaptation information was partially transferred to a new fixation after a saccade. Significant adaptation aftereffects were obtained at both retinotopic and spatiotopic locations. Conceivably, spatiotopic information was used to counterbalance the saccadic retinal shifts of the distortions. Therefore, distortion processing in a natural visual world does not start anew at each fixation; rather, retinotopic and spatiotopic skew information acquired at previous fixations are preserved to mediate stable perception during eye movements.

Introduction

Images on the retina are not an exact replica of the visual world. Instead, they are often distorted by either inherent optical properties of the eye or magnification effects of spectacles worn to correct refractive errors (Fannin & Grosvenor, 2013). In some cases, as in progressive addition lenses and prisms, the magnification axis varies across the surface of the spectacle (Meister & Fisher, 2008). Thus, the geometry of the distortions can even be complexly disparate in different parts of the visual field. On that condition, eye movements shift the retinal location of the distortions and disrupt retinotopic representations. Yet while people adapt to optical elements comprising spatially variable distortions, the visual system seems to compensate for the distortions regardless of their continuous retinal shifts. How this perceptual constancy is attained during eye movements in complexly distorted dynamic natural visual inputs is not well explored. To reveal the underlying visual process, it is vital to assess if visual plasticity to distortion is transferred across saccades in different coordinate systems.

The visual system retains information of several visual features across a saccade based on their location in retinal and in some cases spatial reference frames (Galletti, Battaglini, & Fattori, 1993; Melcher, 2005, 2007; Melcher & Morrone, 2003; Zimmermann, Morrone, Fink, & Burr, 2013; Zimmermann, Weidner, Abdollahi, & Fink, 2016). The retinotopic location of a stimulus brings perceptual advantages such as in tracking a moving object (Golomb & Kanwisher, 2012b; Howe, Pinto, & Horowitz, 2010). Spatiotopic representation of specific visual features in extraretinal reference frames has been previously demonstrated (Andersen, 1997; Andersen, Essick, & Siegel, 1985; Burr & Morrone, 2011; Crespi et al., 2011; Zimmermann et al., 2013; Zimmermann et al., 2016). The visual system uses
spatiotopic information to compensate for saccade-associated retinal shifts. The spatiotopic location of a visual stimulus is therefore important information for successful interaction with the external world (Andersen, 1997; Andersen et al., 1985; Burr & Morrone, 2011).

Examining the reference frames in which adaptation aftereffects occur is one of the approaches recurrently used to scrutinize transsaccadic transfer of visual information and the underlying coordinate system (Melcher, 2005, 2007; van Boxtel, Alais, & van Ee, 2008; Zimmermann et al., 2016). By introducing an eye movement after adapter presentation and before test-stimulus presentation, it is possible to separately test if any adaptation is retained across a saccade in a retinotopic and a spatiotopic reference frame. In retinotopic adaptation, an aftereffect occurs at the adapted retinal location after an eye movement, whereas in spatiotopic adaptation, an aftereffect occurs at the adapted spatiotopic location though the retinal location is altered after the saccade.

The input to the visual cortex from the natural visual world comprises complex stimulus attributes which potentially excite interactions of different cortical levels (Betsch, Einhäuser, Körding, & König, 2004; Bex, Dakin, & Mareschal, 2005; Bex, Marschal, & Dakin, 2007; Bex, Solomon, & Dakin, 2009; Billock, de Guzman, & Kelso, 2001; Dong & Atick, 1995). Although controlled studies with artificial stimuli elucidate feature-selective neural responses, they might not fully divulge how these mechanisms respond in a coordinated manner with other neural populations when stimulated by the rich natural-image content (David, Vinje, & Gallant, 2004; Felsen & Dan, 2005; Ringach, Hawken, & Shapley, 2002). Studying visual plasticity to stimuli that resemble the natural world thus not only mirrors real-life visual circumstances but even asserts potential coordinated responses of different cortical areas.

Here, we evaluated whether distortion adaptation is transferred across fixations during eye movements in a distorted natural environment. Reference frames of geometrical skew-distortion adaptation were tested with natural-image contents. After a saccade, skew adaptation was partially transferred to a new fixation only at retinotopic and spatiotopic locations. No aftereffect was obtained at a control location which was neither retinotopic nor spatiotopic. Thus, during eye movements in a skewed visual world, retinotopic as well as spatiotopic distortion information is conceivably used to mediate stable perception.

Materials and methods

Here, we assessed the coordinate frames in which skew-adaptation information was transferred across fixations. The measurements encompassed four conditions: no saccade, retinotopic, spatiotopic, and control.

Participants

In total, 12 observers participated in the study. All partook in the no-saccade adaptation condition, eight in the spatiotopic condition, and eight in the retinotopic and control conditions (four of whom also participated in the spatiotopic condition). All except one were unaware of the purpose of the study. Participants had normal or corrected-to-normal vision.

Study protocol

The ethics committee at the Medical Faculty of the Eberhard Karls University of Tübingen and the University Hospital approved the study. In adherence to the Declaration of Helsinki, participants’ informed written consent was collected prior to their participation in the study.

Setup

Psychophysical experiments were designed and stimuli were generated in MATLAB (MathWorks, Natick, MA) using the PsychToolbox routines (Brainard, 1997) on an Apple computer (Apple Inc., Cupertino, CA). The stimuli were displayed on a ViewPixx/3D monitor (VPixx Technologies Inc., Saint-Bruno, Canada) at a resolution of 1,920 × 1,080 pixels and vertical refresh rate of 100 Hz in an otherwise darkened room. A chin and head rest was used to maintain the viewing distance of 60 cm at which the display subtended visual angles of approximately 47° horizontally × 27° vertically. The lateral position of the stimuli was controlled gaze contingently by recording the right eye’s position in real time at a sample rate of 1 kHz with the EyeLink 1000 Plus eye tracker (SR Research, Ontario, Canada) and the Eyelink toolbox (Cornelissen, Peters, & Palmer, 2002). Participants’ responses were recorded using the left, right, and space keys of a keyboard.

Stimuli

Geometrical transformation matrix $M$ was used to skew images by a shear angle of $\theta$, wherein the pixel
positions $x$ and $y$ of the undistorted image were remapped to distorted positions $x_d$ and $y_d$:

$$
\begin{pmatrix}
x_d \\
y_d
\end{pmatrix} = M \times \begin{pmatrix} x \\ y \end{pmatrix} \quad (1)
$$

$$
M = \begin{pmatrix} 1 - \tan \theta & -\tan \theta \\ -\tan \theta & 1 \end{pmatrix} \quad (2)
$$

The adapting stimuli were skewed natural-image sequences. Two groups of oppositely skewed adapting stimuli were generated, containing left-skewed ($\theta = +25^\circ$) and right-skewed ($\theta = -25^\circ$) natural-image sequences. Distortion information from sheared boundaries was removed by weighting each image with a Hanning window weighting function of the second order (Harris, 1978). Each image subtended $10^\circ \times 10^\circ$ of visual angle at zero eccentricity. The image content was identical in the positive- and negative-skewed adapting image sequences. These image sequences were rendered at a rate of 20 frames/s. A white cross image on a black background, skewed at different angles, was used as a test stimulus to examine the aftereffect. At $0^\circ$ skew, the cross subtended $10^\circ \times 10^\circ$ of visual angle when viewed at zero eccentricity. Viewing was monocular with the right eye while the left eye was patched. Illustration of a skew geometrical distortion with examples of adapting and test stimuli are shown in Figure 1.

### Procedure

Participants were informed about the procedure and trained on how to adjust a skewed cross until they perceive it to be undistorted.

In each condition, the baseline was first raised by exposure to a positively skewed image sequence for 8 min. Subsequently, the test stimulus appeared on the screen. The test stimulus was a cross skewed at a random angle between $3^\circ$ and $-3^\circ$. The observers’ task was to adjust the skewed cross until it was perceived as undistorted, that is, until the two edges appeared perpendicular. The left and right keys of a keyboard were used to increase or decrease the skew angle with a step size of $0.5^\circ$, and the space key was used to confirm the perception of the undistorted cross. Then the negatively skewed image sequence was presented for another 8 min, followed by similar adjustment task. Fifteen trials of adjustment were performed in each aftereffect-measurement step. The point of subjective equality (PSE) was used as an aftereffect-measurement parameter. It was defined by the skew angle of the adjusted cross at which the subjective undistorted perpendicular cross was perceived.

In all conditions, skewed adapting stimuli were presented in the upper right visual field $2^\circ$ from the fixation dot. In the no-saccade condition, gaze position remained fixed throughout the adaptation-measurement procedure, as presented in Figure 2a. In all the other conditions, aftereffects were tested after a saccade, as shown in Figure 1b. Just after each adaptation and before the appearance of the test stimuli, observers made a saccade to a new fixation marker located $14^\circ$ to the left of the previous fixation marker. The transferred adaptation to the new fixation was measured at retinotopic, spatiotopic, or control null locations separately (Figure 2b). In the retinotopic condition, the spatial location of the test stimuli was altered, maintaining its retinal location as the adapting stimuli; whereas the spatiotopic condition was assessed by varying the retinal location of the test stimuli while preserving its spatial location as the adapting stimuli. The control measurement was performed at neither a retinal nor a spatial matching location, to make sure that the measured aftereffects were confined to retinotopic and spatiotopic locations.

Observers’ gaze was tracked in real time during the whole measurement procedure. Around every fixation target, a circular boundary of radius $1^\circ$ was defined. Whenever gaze was positioned outside of this circular boundary, the stimuli vanished from the screen gaze contingently. At the selected refresh rate of the screen and the sampling rate of the eye tracker, this was achieved in a delay of less than $40 \text{ ms}$ (Saunders & Woods, 2014). This assured exclusive presentation of
the stimulus at the intended retinal and spatial position. Thus, in all nonretinotopic conditions, there was no retinal overlap of the adapting and test stimuli. Eye movements within a radius of 1° from the fixation marker were ignored, to account for microscopic saccades during fixation.

Data analysis

For every observer, the aftereffects measured in the 15 trials after each adaptation were binned into three by averaging Trials 1–5 into Bin 1, Trials 6–10 into Bin 2, and Trials 11–15 into Bin 3. The PSEs of the right skew-adaptation aftereffects in each bin were subtracted from those in the corresponding bin for the left skew-adaptation aftereffects to compute the aftereffect magnitude—the ΔPSE. In the retinotopic, spatiotopic, and control conditions, the transferred adaptation across saccade was quantified by the first-bin ΔPSE of each condition as a proportion of the first-bin ΔPSE of the no-saccade adaptation condition.

The overall data were computed by averaging the magnitudes of the aftereffects and the percentage values measured from all the observers. A t-test was performed on each aftereffect.

Results

The adaptation aftereffects of all the observers in each condition are presented in Figures 3 and 4. Figure 3 shows the shift in perception of an unskewed cross after alternate exposure to oppositely skewed image sequences measured in the no-saccade condition. During fixation, the adaptation aftereffect measured at the adapted retinal and spatial location showed a significant positive ΔPSE, decaying within the 15 test trials ($p_{\text{trials}1-5} < 0.01$, $p_{\text{trials}6-10} < 0.05$, $p_{\text{trials}11-15} > 0.05$). Thus, after exposure to skewed stimuli, observers perceived a cross that is skewed in the adapting skew direction to be unskewed.

Since the aftereffect decayed as the trials progressed, transfer of adaptation to a new fixation location was estimated by the magnitude of the aftereffects in the first five trials. The aftereffect magnitude measured in the saccadic conditions is shown in Figure 4a. In the
saccade conditions, similar to the no-saccade condition, positive ΔPSE occurred in the retinotopic (p_{trials1–5} < 0.05) and spatiotopic (p_{trials1–5} < 0.01) conditions. No significant aftereffect was measured in the control condition at a location that was neither retinotopic nor spatiotopic (p_{trials1–5} = 0.81). After a saccade, 91% of the magnitude of adaptation was transferred to the retinotopic position and 82% to the spatiotopic position at a new fixation (p < 0.01 and p < 0.05, respectively). This is shown in Figure 4b.

Thus, during eye movements, both spatiotopic and retinotopic mechanisms preserve distortion information acquired at previous gaze positions.

**Discussion**

Reference frames of adaptation aftereffects were assessed to reveal the neural mechanisms that compensate for skew distortions in dynamic natural scenes during eye movements. While the gaze was varied between adaptation and test tasks, adaptation significantly transferred to retinotopic and spatiotopic locations but not to a null location—that is, neither retinotopic nor spatiotopic.

In this study, we elucidated that the visual system transfers retinotopic and spatiotopic skew distortion information across a saccade. Retinotopic and spatiotopic reference frames were decoupled by an eye movement just before the test task. Accordingly, retinotopic and spatiotopic effects were dissociated and measured at different positions. Partially transferred adaptation in a retinotopic as well as a spatiotopic reference frame was shown. In the retinotopic condition, the aftereffect was measured at an identical retinotopic position after a saccade. In the spatiotopic condition, the aftereffect was measured at a retinally novel but spatially constant location. Plasticity of neurons in higher cortical areas with large receptive-field sizes leads to retinal-location-invariant aftereffects (Afraz & Cavanagh, 2008; Gattass et al., 2005; Leopold, O’Toole, Vetter, & Blanz, 2001; Mather, Pavan, Campana, & Casco, 2008; Meng, Mazzoni, & Qian, 2006; Suzuki, Clifford, & Rhodes, 2005; Van Essen & Anderson, 1995; Zimmer & Kovacs, 2011). Thus, general position invariance was excluded in a control condition. If the measured adaptation aftereffect at the spatiotopic position were a result of general position invariance, an aftereffect would have occurred at a separate location as well (Ezzati, Golzar, & Afraz, 2008; Mathot & Theeuwes, 2013; Zimmermann et al., 2016). Accordingly, in our control condition the aftereffect was measured at a novel retinal location, which was neither retinotopically nor spatiotopically matched. No significant aftereffect was found. This ascertained that the measured significant spatiotopic
effect did not originate from plasticity of position-invariant mechanisms.

Spatiotopic transfer of visual information can be achieved by neurons either remapping the retinotopic organization of their receptive fields during a saccade (Duhamel, Colby, & Goldberg, 1992; Kusunoki & Goldberg, 2003; Nakamura & Colby, 2002) or comprising receptive fields whose coordinate system is in extraretinal reference frames (d’Avossa et al., 2007; Duhamel, Bremmer, BenHamed, & Graf, 1997; Galletti et al., 1993). In the case of receptive-field remapping, saccadic eye movements trigger changes in the receptive-field location of neurons. If a stimulus initially appeared outside the neuron’s receptive field and a saccade which will bring the stimulus into the receptive field is intended, the neuron changes its receptive-field location to the stimulus location before saccade execution. It starts firing at the initial gaze position and keeps this sensitivity after the saccade when the stimulus appears in its receptive field. Accordingly, the stimulus’s spatial correspondence will be maintained. In purely spatiotopic neurons, on the other hand, receptive-field organization is based on an extraretinal reference frame and codes the visual stimulus with its location in space. Hence, the neurons keep responding to a preferred feature at any gaze position and retain information during eye movements as long as the stimulus is stationary in space.

Either one or both of the aforementioned spatiotopic mechanisms could account for the reported transfer of spatiotopic skew information across saccades. In a receptive-field remapping mechanism, skew-information-coding neurons should be sensitive to eye-movement-related signals, such as efference copy and proprioceptive information, to remap their receptive fields before the saccade (Andersen et al., 1985; Backus, Banks, van Ee, & Crowell, 1999; Wexler, Panerai, Lamouret, & Droulez, 2001; Wexler & Van Boxtel, 2005; Wolpert & Flanagan, 2001). In the other case, neurons selective to the skew information would have pure spatiotopic receptive fields. This way, the same neurons process the skewed adapting and test stimuli before and after the saccade, respectively, by maintaining spatial correspondence.

In addition to stimulation of receptive-field remapping, eye-motion signals alter firing patterns of neurons in the cortical visual hierarchy (Andersen, 1997; Andersen et al., 1985; DeSouza, Dukelow, & Vilis, 2002; Trotter & Celebrini, 1999). Gaze-contingent perceptual changes to distortions of a wedged prism have been previously demonstrated (Pick & Hay, 1966). In the present study, the partial transfer of adaptation to a new gaze direction might be explained by changes of neural mechanisms whose responses are modulated by the gaze direction (Nishida, Motoyoshi, Andersen, & Shimojo, 2003; Parwaga, Buckley, & Duke, 2016).

Aftereffects originate from response changes in specific neural populations tuned to the adapting stimuli’s attributes (Clifford et al., 2007; Roach, Webb, & McGraw, 2008; Webster, 2011, 2015). Thus, adjustments in neural substrates processing the altered spatiotemporal features of the skewed natural-image content would have led to the measured aftereffects. These include neurons affected by skew effects such as tilt in contour orientations, dimension asymmetry due to oblique magnification, shift in the angle between the contours, and change in the distribution of motion signals in the direction of the skew.

Although studies argue that visual coding is purely retinotopic (Gardner, Merriam, Movshon, & Heeger, 2008; Golomb & Kanwisher, 2012a), spatiotopic adaptation at different visual areas has repeatedly been demonstrated in classical feature-selective adaptation paradigms (Melcher, 2005, 2007; Zimmermann et al., 2016). Lower level contrast and contour-orientation processing mechanisms in early stages like V1 exhibit fully retinotopic reference frames (Bao & Engel, 2012; Dekel & Sagi, 2015; Dickinson & Badcock, 2013; Wilkinson, Wilson, & Habak, 1998; Zhao, Series, Hancock, & Bednar, 2011). Electrophysiological and imaging studies have confirmed behavioral evidence on spatiotopic coding through receptive-field remapping in visual areas such as V2, V3, and V4 (Melcher, 2005; Nakamura & Colby, 2002; Zimmermann et al., 2016). These areas are well suited to encode intermediate shape information, such as orientation, aspect ratio, symmetry, and angle (Boynton & Hegdé, 2004; Gegenfurtner, Kiper, & Levitt, 1997; Hégédus & Van Essen, 2000; Ito & Komatsu, 2004; Laursen & Rasmussen, 1975; Loffler, 2008; Regan & Hamstra, 1992; Suzuki & Cavanagh, 1998; Wilson & Wilkinson, 2002; Zimmermann et al., 2016). Moreover, motion-processing neural mechanisms in MT+ exhibit pure spatiotopic receptive fields (Melcher & Morrone, 2003; Wexler et al., 2001). Their possible interactions with form-processing mechanisms could contribute to the measured spatiotopic aftereffects (Pavan, Marotti, & Mather, 2013).

The present study extended these findings to a naturalistic stimulation of the visual system—that is, when the visual system is exposed to dynamic natural-image content. Unlike classical feature-selective adaptation with artificial stimuli, such adaptation from a stimulus containing a variety of attributes potentially involves dynamic interactions between multiple levels in the hierarchy of the visual cortex and coordinated responses of several neural populations stimulated during adaptation (Berkley, Debruyn, & Orban, 1994; Dakin, Williams, & Hess, 1999; Pavan et al., 2013; Poirier & Frost, 2005; Smith, Clifford, & Wenderoth, 2001). In line with the aforementioned feature-selective adaptation studies, our results assert spatiotopic as well
as retinotopic visual-coding mechanisms during ecological viewing conditions. Furthermore, our methodology provides a tool to address the contribution of these mechanisms in real-life scenarios—for example, adaptation to optically induced distortions.

Therefore, during a saccade in a distorted natural environment, distortion processing does not start anew at every fixation. Rather, the visual system preserves distortion information acquired at previous fixations. This is specifically efficient in vision with progressive additional lenses, where the distortions are complexly distributed across the visual field. Specifically, during vision accompanying eye movements, spatiotopic mechanisms might facilitate habituation in this application scenario, since they retain the distortion’s spatial layout of the spectacles though their retinal position is varied.

**Keywords:** visual adaptation, spatial distortions, transsaccadic adaptation, natural vision

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**References**


