Spatiotopic updating of visual feature information

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Saccades shift the retina with high-speed motion. In order to compensate for the sudden displacement, the visuomotor system needs to combine saccade-related information and visual metrics. Many neurons in oculomotor but also in visual areas shift their receptive field shortly before the execution of a saccade (Duhamel, Colby, & Goldberg, 1992; Nakamura & Colby, 2002). These shifts supposedly enable the binding of information from before and after the saccade. It is a matter of current debate whether these shifts are merely location based (i.e., involve remapping of abstract spatial coordinates) or also comprise information about visual features. We have recently presented fMRI evidence for a feature-based remapping mechanism in visual areas V3, V4, and VO (Zimmermann, Weidner, Abdollahi, & Fink, 2016). In particular, we found fMRI adaptation in cortical regions representing a stimulus' retinotopic as well as its spatiotopic position. Here, we asked whether spatiotopic adaptation exists independently from retinotopic adaptation and which type of information is behaviorally more relevant after saccade execution. We first adapted at the saccade target location only and found a spatiotopic tilt aftereffect. Then, we simultaneously adapted both the fixation and the saccade target location but with opposite tilt orientations. As a result, adaptation from the fixation location was carried retinotopically to the saccade target position. The opposite tilt orientation at the retinotopic location altered the effects induced by spatiotopic adaptation. More precisely, it cancelled out spatiotopic adaptation at the saccade target location. We conclude that retinotopic and spatiotopic visual adaptation are independent effects.

Introduction

Saccades are based upon rapid rotations of the eyeball, which relocate the retinal image relative to external space. In order to discriminate the retinal motion that is generated by a saccade from the one generated by an actually moving stimulus, information about the magnitude of a saccade must be taken into account and linked to a momentary visual representation. Many brain areas host neurons, which around onset of saccade execution shift their receptive field to the position that corresponds to the retinal stimulus position after the saccade (Duhamel, Colby, & Goldberg, 1992; Nakamura & Colby, 2002; Sommer & Wurtz, 2006; Umeno & Goldberg, 1997; Walker, Fitzgibbon, & Goldberg, 1995; for reviews see: Ross, Morrone, Goldberg, & Burr, 2001; Wurtz, 2008). This predictive shift of sensitivity might bridge the saccadic gap, a process referred to as remapping. To date, it remains controversial how this process is accomplished (Cavanagh, Hunt, Afraz, & Rolfs, 2010; Higgins & Rayner, 2015; Melcher & Morrone, 2015; Prime, Vesia, & Crawford, 2011).

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In addition to the problem of discriminating self-initiated versus external stimulus motion, saccades generate the problem of object correspondence: Because with each saccade objects change their position on the retina, the visual system has to match object information from before and after saccade execution for consistency (Gordon, Vollmer, & Frankl, 2008; Hollingworth, Richard, & Luck, 2008; Melcher & Colby, 2008). Solving the correspondence problem entails storing feature information of objects across saccades. Whether remapping is feature selective has been investigated behaviorally using the negative aftereffects of visual adaptation. In this context, adaptation is applied while the eye is fixating at one location and the aftereffect is tested following a saccade to another location. Melcher (2005) showed that adaptation of several primary visual attributes (i.e., tilt, form, and face) is represented spatiotopically (i.e., adaptation aftereffects relate to the same position in external space although an eye movement has been performed). Tilt adaptation that precedes saccades—that is to say during the phase where predictive remapping starts—has been used in various studies (Melcher, 2007; Zirnsak, Gerhards, Kiani, Lappe, & Hamker, 2011). When probed in this time period, tilt aftereffects are transferred to the saccade target. Cha and Chong (2014) showed with the same method that even the background is remapped, which suggests that figure and ground are processed similarly if the visual context remains stable across saccades.

We and others have shown that spatiotopic aftereffects are generated actively and take time to build up (He, Mo, & Fang, 2017; Nakashima & Sugita, 2017; Zimmermann, Morrone, Fink, & Burr, 2013). The strength of the transsaccadic aftereffect scales with the time subjects have to prepare their saccade: With longer preview durations of a saccade target, adaptation is significantly stronger at the spatiotopic condition than at a nonspecific location. For instance, Nakashima and Sugita (2017) designed an elegant eye blink conditioning procedure in which a conditional tilt stimulus was followed by an unconditioned stimulus (i.e., an air puff to the eyelid). They then used tilt adaptation to make a neutral tilt orientation appear like the conditional tilt stimulus, thus evoking the conditioned eye blink response. After adaptation of the neutral stimulus, they found conditioned responses at the retinotopic and the spatiotopic position. Furthermore, Parwaga, Buckley, and Duke (2016) dissociated gaze- and head-centered coordinates and suggested that the tilt aftereffect is coded in a head-centered reference frame.

How might spatiotopic adaptation be implemented at the neural level? Three fMRI studies have recently investigated transsaccadic tilt adaptation. First, Dunkley, Baltaretu, and Crawford (2016) used fMRI adaptation and presented probes that were either identical to an adapter or tilted by 90° relative to the adapter orientation. They found a reduction in neural activation in the supramarginal gyrus of the anterior inferior parietal lobe for probes that were identical to the adapter, compared to probes that had a different orientation. Furthermore, they reported a summation of neural activation in V4 related to transsaccadic tilt adaptation. In our own study, we used fMRI adaptation to compare transsaccadic adaptation using adapters that deviated by either 90° or 15° from the adapter orientation (Zimmermann et al., 2016). Behavioral tilt adaptation is weak if probe and adapter differ by 90° in orientation while it is high for a 15° difference (Blake, Holopigian, & Jauch, 1985). Consistently, we found significantly weaker behavioral and neural responses for probe adapter differences of 15° than for 90°. Neural adaptation was located in areas V4 and VO. Furthermore, in a functional study Fairhall, Schwarzbach, Lingnau, Van Koningsbrugggen, and Melcher (2016) found transsaccadic tilt adaptation effects in frontoparietal regions: the superior parietal lobe, intraparietal sulcus, and frontal eye fields. They also reported spatiotopic, location-specific adaptation in visual areas. All three studies demonstrate gaze-invariant tilt representation in visual areas.

We previously probed aftereffects after a saccade was executed (Zimmermann et al., 2013; Zimmermann et al., 2016) and found aftereffects at the retinotopic and the spatiotopic location. One interpretation was that presaccadic remapping might have transferred neural activation induced by the adapter to a new cortical location, thereby generating spatiotopic aftereffects. Following saccade execution, the remapped receptive field will be set back to its initial position. Thus, aftereffects are expected to occur also at the retinotopic location where adaptation has originally been induced. Melcher (2007) investigated remapping of tilt adaptation by presenting probes precisely during the critical time window for receptive field shifts (i.e., 50–100 ms before saccade execution). Using this technique, Melcher (2007) observed decreasing aftereffects at the retinotopic location while at the same time aftereffects increased at the spatiotopic location. It has been argued that what is interpreted as a spatiotopic aftereffect may simply stem from a global spread of adaptation, emanating from the retinotopic location (Knapen, Rolfs, Wexler, & Cavanagh, 2010; Mathôt & Theeuwes, 2013). According to these authors, adaptation at the spatiotopic position is not significantly higher than at nonspecific locations. Therefore, we here investigated whether retinotopic and spatiotopic aftereffects result from a single global adaptation process or whether both effects coexist independently. To decide between these alternatives, we put both effects into competition. We used multiple adapters simultaneously, positioned at the retinotopic, spatiotopic, and

control locations, with retinotopic and spatiotopic adapters being presented with opposite orientations. Positions of the adapters were chosen such that the saccade would bring both aftereffects into the same position. As a consequence, the direction of the aftereffect should be indicative of which aftereffect is dominant. In addition, we prevented spatial spread of adaptation by adapting several locations with adapters of different orientation.

Methods

Participants

Eight subjects (five female, two male, naive to the purpose of the experiment and one male author; mean age 28 years) participated in the experiments. All had normal or corrected-to-normal vision. Experiments were carried out in accordance with the Declaration of Helsinki. The study was approved by the ethics committee of the German Society of Psychology.

Eye movement measurements

Eye movements were monitored using the Eyelink 1000 system (SR Research, Ltd., Mississauga, Ontario, Canada), which samples gaze positions with a frequency of 2000 Hz. Viewing was binocular, but only the dominant eye was recorded. The system detected start and end of a saccade when eye velocity exceeded or fell below 22°/s and acceleration was above or below 4000°/s^2. At the beginning of each experimental session, a nine-point calibration and validation procedure was conducted. If the calibration did not meet the specified criteria, calibration was repeated until it was successful.

Procedure

The experiment consisted of three kinds of trials, which were presented in separate sessions. The trials differed only with regard to the number of adapters presented. Baseline trials contained no adapters, four adapters for spatiotopic/retinotopic competition trials, and three adapters for purely spatiotopic trials. Baseline trials were applied to measure tilt perception without any adaptation (see Figure 1A). They started with the simultaneous presentation of the fixation point and the saccade target (both red and with a size of 0.75° × 0.75°; see Figure 1A). The fixation point was shown 17° to the left of screen center and the saccade target 3° to the right. The required saccade amplitude therefore was 20°, in accordance with earlier studies (Melcher, 2005; Zimmermann et al., 2013). Although 20° saccades were large with regard to natural vision, they still do not involve head movements (Freedman & Sparks, 1997). Subjects were instructed to direct their gaze to

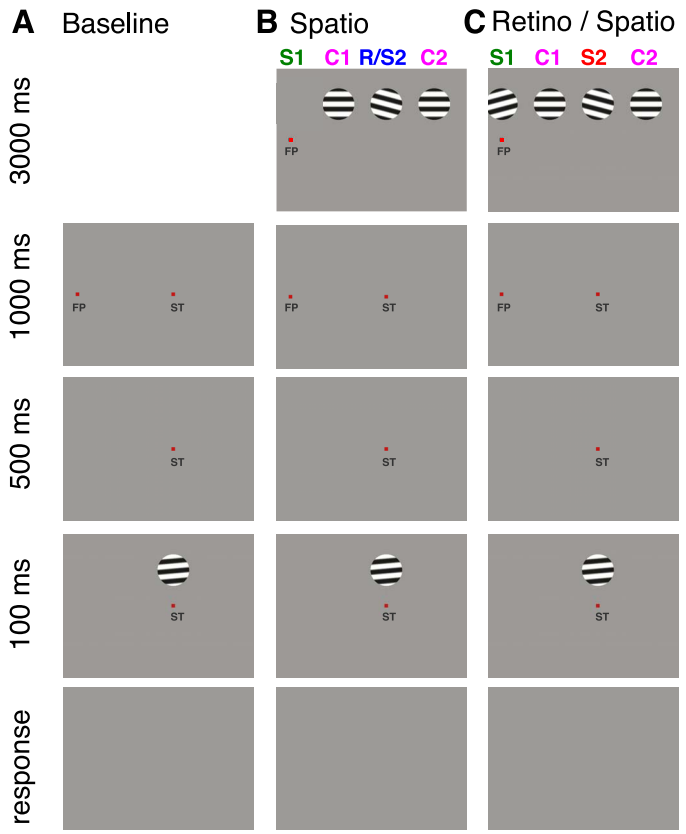

Figure 1. (A) Graphical sketch of an experimental baseline trial. A trial started with the presentation of a fixation point (FP) and a saccade target. After 1000 ms the fixation point disappeared, and the subject was required to perform a saccade. After execution of the saccade, a test grating appeared and subjects had to judge whether the grating was oriented clockwise or counterclockwise relative to the horizontal. The position of the test grating corresponded to one of the adapter positions. Test gratings presented at the third position (R/S) tested what happened if retinotopic and spatiotopic adaptation were set into competition. In this condition, counterclockwise tilt adaptation from the first position (S) was carried retinotopically through the saccade to the third position. However, the third position was itself adapted by an adapter with clockwise orientation. In baseline trials, no adapters were presented and trials started with the presentation of the fixation point and the saccade target. (B) Purely spatiotopic trials started with the presentation of three adapter stimuli. These trials served to measure the magnitude of spatiotopic adaptation at position S2. The adapters were presented for 3000 ms. The rest of the trial was identical to baseline trials. (C) In spatiotopic/retinotopic competition, four adapter stimuli were presented for 3000 ms at trial start. In these trials, adaptation magnitude was measured at all four positions. The rest of the trial was identical to baseline trials.

the fixation point and to execute a saccade to the saccade target as soon as the fixation point disappeared. After 1000 ms, the fixation point was removed so that only the saccade target was visible. After another 500 ms, in which the screen remained blank, a probe grating was flashed for 100 ms. The probe grating was shown at one of four positions and was presented with one out of seven equiprobable orientations (−12 to +12° in seven steps of 4°). After offset of the grating, the screen remained blank until subjects judged the orientation of the grating by pressing the left or right arrow key. Subjects had to indicate tilt orientation by reporting whether the patch appeared tilted clockwise or counterclockwise relative to the horizontal. Participant's response initiated a new trial.

Purely spatiotopic trials were shown to measure adaptation magnitude at position S2 (see Figure 1B). Three adapters were shown at trial start (see Figure 1B). Tilt-adapter stimuli were grating patches of 100% contrast with 0.4 cycles/degree, vignetted within a circular envelope of 7° diameter. The adapters were centered 7.5° above screen center. The spatiotopic adapter (S2) was shown 3° to the right, flanked by two control adapters (C1 and C2), which were presented −7° and 13° to the right of the screen center. Their orientations varied across positions. Adapter S2 had a tilt of −15° while adapters C1 and C2 had a tilt of 0°. The adapters were presented for 3000 ms. After adapter offset, the trial structure was identical to that of baseline trials except that the probe grating was shown always at the location of the saccade target (spatiotopic position S2).

In spatiotopic/retinotopic competition trials, adaptation magnitude was measured at two probe and two control locations (see Figure 1C). Trials started with the presentation of a fixation point and four adapter patches (see Figure 1C). Tilt-adapter stimuli positions were −17° to the left (S1), −7° to the left (C1), 3° to the right (S2), and 13° to the right (C2) of the screen center. Their orientations varied across positions. Adapter S1 was shown with a tilt of 15°, adapter S2 with a tilt of −15°, and adapters C1 and C2 with a tilt of 0°. The adapters were presented for 3000 ms. The remaining trial structure was again identical to the baseline trials. As in baseline trials, the probe grating was shown at one of four positions and was presented with one out of seven equiprobable orientations (−12° to +12° in seven steps of 4°). For each psychometric function, 70 trials were measured (10 repetitions for each data point). Trials were run in a block design to ensure that adaptation builds up at only one spatial position. Randomization of the different conditions within blocks would have led to adaptation at several positions simultaneously. Experimental blocks were counterbalanced across subjects.

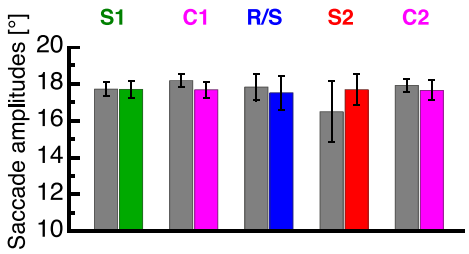

Figure 2. Average saccade amplitudes from each of the five conditions for baseline trials (shown in gray) and adaptation trials (shown in colors). Error bars represent *SEM*.

Results

We first analyzed saccade parameters in order to confirm that eye movement performance did not significantly differ between conditions. Saccade amplitudes pooled across conditions were almost identical between baseline (17.62; $SEM = 0.44$) and adaptation trials (17.64; $SEM = 0.39$). The required amplitude size was 20° and subjects thus missed the target position by ~11%, which is within the usual range of saccade undershoot (e.g., Nuthmann, Vitu, Engbert, & Kliegl, 2016). Figure 2 shows average saccade amplitudes for all experimental conditions. There were no striking differences in saccade behavior between conditions. A two-way repeated measures analysis of variance (ANOVA) with the factors Adapter Presentation (baseline/adaptation) and Probe Position (five conditions) did not reveal any significant main effect. Saccade amplitudes therefore were statistically indistinguishable.

We also analyzed saccade latencies since transsaccadic adaptation magnitude takes time to build up (Nakashima & Sugita, 2017; Zimmermann et al., 2013). Differences in latencies between conditions could, at least in principle, explain differences in aftereffect strength. Pooled across all conditions, saccade latencies from baseline trials (243.19 ms; $SEM = 10.56$) were very similar to latencies from adaptation trials (248.36 ms; $SEM = 10.28$). A two-way repeated measures ANOVA with the factors Adapter Presentation (baseline/adaptation) and Probe Position (five conditions) did not reveal any significant main effect.

In a next step, tilt discrimination performance was analyzed. To this end, we determined perceptual tilt biases for each subject by fitting Gaussian distributions to the mean responses at every increment. We used the Akaike information criterion, which is a relative measure for the goodness of fit. We calculated a two-way repeated measures ANOVA with the factors Adapter Presentation" (baseline/adaptation) and Probe Position (five conditions). No significant difference between conditions was revealed. Figure 3 shows the respective psychometric functions for one subject. Psychometric functions derived from baseline sessions

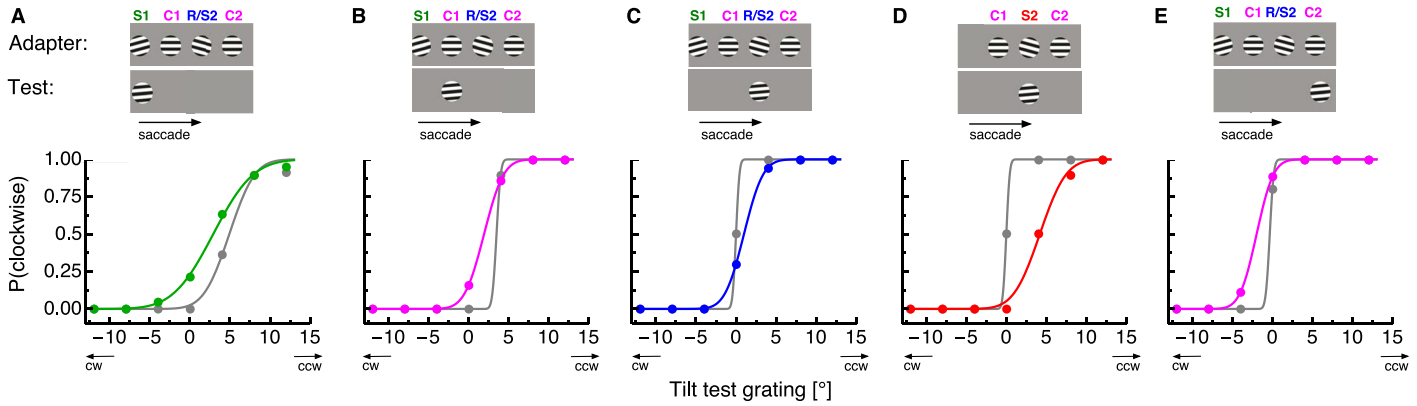

Figure 3. (A) Tilt judgements measured at the spatiotopic position S1. Data shown in black result from baseline trials and data in color from adaptation trials. (B) Tilt judgements measured in baseline and adaptation trials at the control position C1. Same conventions as in (A). (C) Tilt judgements measured in baseline and adaptation trials at the control position R/S. Same conventions as in (A). (D) Tilt judgements measured in baseline and adaptation trials at the control position S. Same conventions as in (A). (E) Tilt judgements measured in baseline and adaptation trials at the control position C1. Same conventions as in (A).

are shown in gray and those from adaptation sessions in color. Please note, Figure 3A shows results from spatiotopic/retinotopic competition trials, in which four adapters were shown and adaptation magnitude was measured at position S1. After adaptation, the tilt of the probe was perceived shifted in clockwise direction (i.e., the green curve was offset to the left relative to the gray curve). This result is consistent with a negative aftereffect relative to the counterclockwise orientation of the adapter. Adapters C1 at the second position and C2 at the fourth had a neutral orientation of 0°. The aim of these adapters was to avoid any spreading of adaptation from the location of the first adapter to the third position. No adaptive shift in apparent tilt was expected for probes presented at positions two and four since adapter orientation (0°) and the average probe orientation 0° were identical (Blake et al., 1985). In order to prove that the adapters C1 and C2 were effective in neutralizing adaptation from adjacent regions, we also measured aftereffects for briefly presented probes at the control positions.

The data shown in Figure 3B result from spatiotopic/retinotopic competition trials where adaptation magnitude was measured at the control position C1. This particular subject perceived the probe's tilt slightly more clockwise after adaptation than in baseline trials. Figure 3C shows results from spatiotopic/retinotopic competition trials where adaptation magnitude was measured at position R/S2. The adapter at the third position had an opposite orientation compared to that at position S1. Since the saccades started at position S1 and ended at position R/S2, two different types of adaptation were pitted against each other. In particular, retinotopic adaptation as induced by the adapter at position S1 was carried over, hence spatially coinciding with spatiotopic adaptation induced by the adapter at position R/S2. Accordingly, this allowed testing the relative strength of retinotopic as compared to spatiotopic adaptation. Equally strong adaptation effects should cancel each other out (i.e., no aftereffect should be seen). For the subject shown in Figure 3C, the tilt perception shifted slightly in counterclockwise direction. This corresponds to a negative aftereffect of the spatiotopic S2 adapter at the first position, which was oriented in a clockwise direction. Thus, the subject shown in Figure 3C demonstrated a slight dominance of spatiotopic over retinotopic adaptation. In separate sessions, we also measured the magnitude of the purely spatiotopic adaptation at the third position. We therefore presented only three adapters in the adaptation trials. The leftmost adapter was such that no retinotopic adaptation could interfere with the spatiotopic adaptation at the third position. Figure 3D shows results from purely spatiotopic trials, which were measured with only three adapters. The spatiotopic adapter at position S2 shifted tilt perception of the individual subject considerably in counterclockwise direction. Thus, without the interference of an adapter at position S1, strong adaptation was observed at position S2 (see Figure 3D). By contrast, when an adapter was shown at position S1, no adaptation was observed (see Figure 3C). These data indicate that retinotopic and spatiotopic adaptation interfered with a slight tendency for this subject to push tilt perception in the direction that is expected if retinotopic adaptation was stronger than spatiotopic adaptation (compare Figure 3C and D). Finally, the adapter at position C2 served again—like the adapter at position C1—to neutralize spreading adaptation. The tilt aftereffect measured for this subject showed a shift in clockwise direction (see Figure 3E). This shift can be explained by retinotopic adaptation from the first position carried over by the saccade to the third position.

Mean tilt aftereffect magnitude is shown in Figure 4. We subtracted all individual adaptation data from each

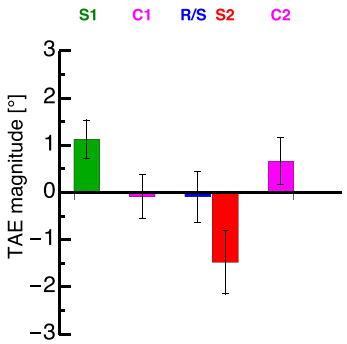

Figure 4. Average tilt aftereffect magnitude measured in each of the five conditions. Tilt aftereffect magnitude is defined as the difference between adaptation and baseline trials. Error bars represent *SEM*.

condition by the data from the respective baseline conditions and averaged within each condition over all subjects. A spatiotopic tilt aftereffect occurred at positions S1 and S2. The directions of these aftereffects were opposite to the directions of the adapters at the corresponding positions. A smaller amount of adaptation was observed at the control location C2. The direction of this aftereffect suggests that it results from retinotopic adaptation induced at position S1, which is carried over to position C2 through execution of the saccade. Particularly interesting was the position R/S, since at that location spatiotopic adaptation had to compete with retinotopic adaptation from position S1. The aftereffect at that position was almost absent. Thus, retinotopic and spatiotopic adaptation, which induced aftereffects in opposite directions, efficiently cancelled out each other, suggesting that none dominated the other. We calculated a two-way repeated measures ANOVA with the factors Adapter Presentation (baseline/adaptation) and Probe Position (five conditions). A significant main effect for the factor Probe Positions, $F(4, 28) = 3.561$, $p = 0.018$, and a significant interaction effect, $F(4, 28) = 4.471$, $p = 0.009$, was revealed. Post hoc tests revealed a stronger adaptive aftereffect at the spatiotopic position S1 than at the control location C1; a stronger aftereffect at the spatiotopic position S2 than on the retinotopic/spatiotopic location R/S; and a stronger aftereffect at the spatiotopic position S2 than at the control location C2.

Discussion

Our results show that transsaccadic adaptation resides in two reference frames (i.e., the retinotopic and the spatiotopic frame) and that functionally both stand on equal footing. We applied two strategies to rule out that spatiotopic adaptation is merely the result of a retinotopic adapter activity that spreads globally across visual cortex. First, we adapted the fixation and the saccade target location simultaneously with opposite tilt orientation, and second, we presented a neutral adapter between both positions that stopped spreading of adaptation.

When we set retinotopic and spatiotopic adaptation in competition, with both involving opposite orientation, we found that they annulled each other. This finding implies that adaptation can simultaneously exist in retinotopic and spatiotopic reference frames. Importantly, the data indicate that these two independent frames of reference and the aftereffects do not emerge from a spreading of adaptation. In order to prevent adaptation from spreading from the position of the adapter to other locations, four adapters were presented adjacently. Adaptation was spatially selective, as verified by the strength of the aftereffect at all four possible adapter locations. Transsaccadic remapping implies that before saccade onset a neural cell becomes transiently responsive to those retinal locations that an object will cover after the saccade has landed. If transsaccadic remapping is the mechanism that establishes spatiotopic adaptation, one would expect the aftereffect to decrease at the retinotopic location in parallel to being build up at the spatiotopic position. However, this reasoning applies only to the short time window of remapping. After the saccade is finished, the neural cell will have fallen back again to its standard retinotopic position. Our probes were all presented after saccade execution. Under the assumption of remapping of adapter activity, it is therefore to be expected that adaptation builds up at both the retinotopic and the spatiotopic position.

In a previous fMRI study we demonstrated that spatiotopic tilt adaptation is accomplished by remapping of visual feature information in visual areas V3, V4, and VO (Zimmermann et al., 2016). We found reductions in neural activity when adapter and probe were presented at the same position in external space but a saccade was executed. Due to execution of the saccade, adapter and probe were processed in opposite hemispheres. In order to observe neural adaptation, adapter activity processed in the left hemisphere had to be transferred interhemispherically and to become effective in the right hemisphere. By also measuring the visual aftereffect, we could show that this interhemispheric transfer was the neural correlate of spatiotopic adaptation.

This raises the question of how this transfer of activity is generated neurally? An electrophysiological study found receptive field shifts in area V3 (Nakamura & Colby, 2002). This result indicates that neurons at early stages of the visual hierarchy update visual signals and thereby provide a putative basis for the transfer of visual feature information that we observed. Another

possibility is that feature transfer is organized by higher level saccade areas that reach down to visual areas. For instance, area V4 is modulated by input from the frontal eye field (Moore & Armstrong, 2003; Tolias et al., 2001). The involvement of the frontal eye field in transsaccadic updating of visual feature information has been demonstrated by an fMRI and a transcranial magnetic stimulation study (Dunkley et al., 2016; Prime et al., 2011). There are principally two possibilities transsaccadic adaptation might work. The first is the transfer of adapter activity and the second transfer of the adapted state. Indeed, transfer of adapter activity presupposes—as the reviewer points out—that the adapter signal is still present. After a delay of 1 s between adapter offset and saccade onset, this signal will be extinguished. However, we suppose that part of the remapping process starts already with the presentation of the saccade target. We and others have reported evidence that prolonged preview of the saccade target enhances transsaccadic adaptation (He et al., 2017; Nakashima & Sugita, 2017; Zimmermann et al., 2013). We can only speculate about the neural origin of the preview effect since electrophysiological studies on remapping have only used reactive saccades with short latencies of ~180 ms. However, we find the possibility that remapping of the adapter activity can start earlier when saccade initiation is delayed, more likely than a remapping of the adapted state. Remapping of adapter activity requires to store the spatial coordinates of a certain feature (i.e., orientation) and shift the coordinates around saccade execution. Remapping of the adapted that would require to store feature information plus the neuron's adaptation to that feature and the corresponding spatial coordinates. The first strategy is computationally more efficient compared to the former.

Our study confirms recent evidence for feature information in transsaccadic remapping. Harrison and Bex (2014) demonstrated spatiotopic feature integration in transsaccadic crowding. In this task, performance of postsaccadic target discrimination depended on what subjects had seen before the saccade. Thus, feature information was actively transferred across the saccade. Nonretinotopic effects in perceived orientation have also been suggested by Wutz, Drewes, and Melcher (2016), who showed that in a Ternus-Pickler display, the temporal integration of orientation was biased towards a nonretinotopic reference frame for stimulus presentations longer than around 150–200 ms. Transsaccadic integration of orientation information is also indicated by the finding that discrimination performance is best when an oriented target is visible both before and after a saccade (Ganmor, Landy, & Simoncelli, 2015; Wijdenes et al., 2015). Feature transfer of shape- (Demeyer et al., 2009) and motion-specific information (Fabius et al., 2016; Fracasso et al., 2010; Melcher & Fracasso, 2012; Turi & Burr, 2012) has also been reported. Evidence for transsaccadic motion integration has been provided by Szinte et al. (2016). They demonstrated that the visual system predictively integrates motion signals between the current and the postsaccadic retinotopic location during the period of saccade preparation. Finally, also higher level features as facial expressions are remapped across saccades (Melcher, 2005; Wolfe & Whitney, 2015). All these studies suggest that transsaccadic remapping takes into account visual feature information rather than shifting only abstract position information. Storing visual feature information across the execution of saccades might be important to solve the correspondence problem—that is, to connect objects that were seen before saccade initiation with those visual features seen after the saccade has finished.

In conclusion, our data is consistent with the claim that transsaccadic remapping has access to feature information.

Keywords: spatiotopic, transsaccadic adaptation, remapping, visual feature information

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