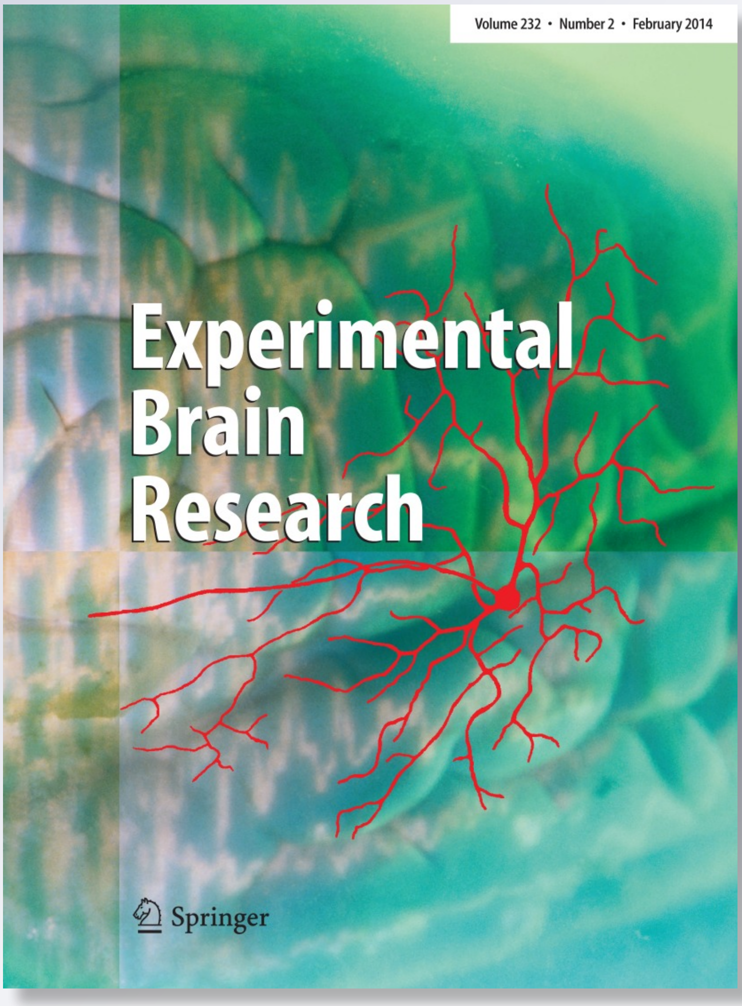
The background is remapped across saccades

Oakyoon Cha & Sang Chul Chong

Experimental Brain Research

ISSN 0014-4819
Volume 232
Number 2

Exp Brain Res (2014) 232:609-618
DOI 10.1007/s00221-013-3769-9



Springer

Exp Brain Res (2014) 232:609–618
DOI 10.1007/s00221-013-3769-9

RESEARCH ARTICLE

The background is remapped across saccades

Oakyoon Cha · Sang Chul Chong

Received: 17 December 2011 / Accepted: 9 November 2013 / Published online: 26 November 2013

Abstract Physiological studies have found that neurons prepare for impending eye movements, showing anticipatory responses to stimuli presented at the location of the post-saccadic receptive fields (RFs) (Wurtz in Vis Res 48:2070–2089, 2008). These studies proposed that visual neurons with shifting RFs prepared for the stimuli they would process after an impending saccade. Additionally, psychophysical studies have shown behavioral consequences of those anticipatory responses, including the transfer of aftereffects (Melcher in Nat Neurosci 10:903–907, 2007) and the remapping of attention (Rolfs et al. in Nat Neurosci 14:252–258, 2011). As the physiological studies proposed, the shifting RF mechanism explains the transfer of aftereffects. Recently, a new mechanism based on activation transfer via a saliency map was proposed, which accounted for the remapping of attention (Cavanagh et al. in Trends Cogn Sci 14:147–153, 2010). We hypothesized that there would be different aspects of the remapping corresponding to these different neural mechanisms. This study found that the information in the background was remapped to a similar extent as the figure, provided that the visual context remained stable. We manipulated the status of the figure and the ground in the saliency map and showed that the manipulation modulated the remapping of the figure and the ground in different ways. These results suggest that the visual system has an ability to remap the background as well as the figure, but lacks the ability to modulate the remapping of the background based on the visual context, and that different neural mechanisms might work together to maintain visual stability across saccades.

Keywords Saccadic remapping · Saccadic eye movements · Tilt aftereffects · Orientation-specific adaptation · Shifting receptive field · Saliency map

Introduction

Saccades refer to ballistic eye movements that are usually intended to bring objects of interest into a fovea, where the visual resolution is best among the retinal regions. Saccadic eye movements are pre-programmed before execution and take less than a second. During saccades, images projected onto the retina undergo radical changes, resulting in the counterintuitive idea that we may lose track of the object while the eyes are moving toward it. Physiological studies have found a potential mechanism that resolves this problem, allowing the visual system to track objects of interest over saccades. Neurons in the lateral intraparietal area (LIP) of monkeys showed anticipatory responses to a stimulus presented in the post-saccadic receptive field (RF) prior to saccadic onset (Duhamel et al. 1992). As neurons respond to the stimuli which they will process after an impending saccade, they process the same stimuli over the course of a saccade. Similar anticipatory responses were also found in many brain regions related to vision, eye movement, and attention, including the visual cortices (Nakamura and Colby 2002; Tolias et al. 2001), frontal eye field (FEF) (Sommer and Wurtz 2006; Umeno and Goldberg 1997, 2001), superior colliculus (SC) (Walker

O. Cha · S. C. Chong (✉)
Graduate Program in Cognitive Science, Yonsei University,
50 Yonsei-ro, Seodaemun-gu, Seoul 120-749, Korea
e-mail: scchong@yonsei.ac.kr

O. Cha
e-mail: oakyoon@gmail.com

S. C. Chong
Department of Psychology, Yonsei University, 50 Yonsei-ro,
Seodaemun-gu, Seoul 120-749, Korea

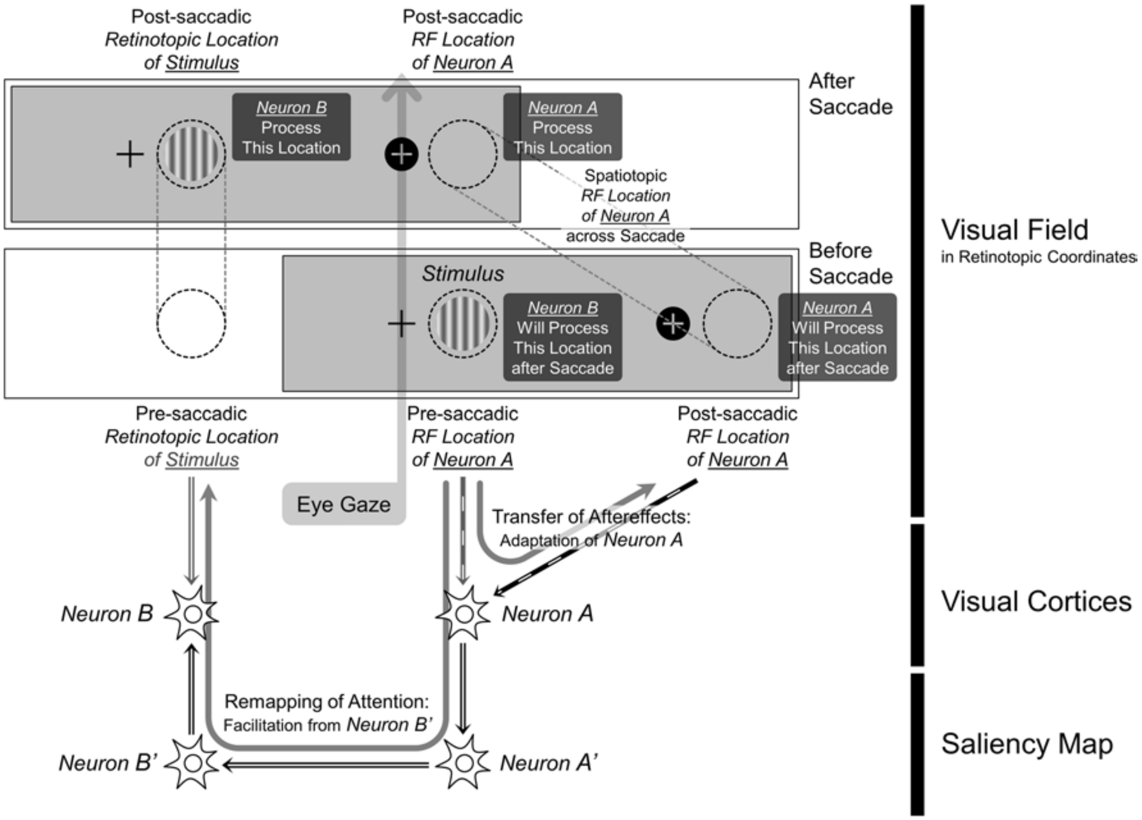


Fig. 1 Proposed neural mechanisms accounting for the transfer of aftereffects and the remapping of attention. In this figure, a saccade will occur from the black cross to the black circle containing the white cross. The visual field is drawn in the retinotopic coordinates, and thus, eye gazes are at the same vertical line both before and after saccades. The first mechanism, the shifting of the RFs, accounts for the transfer of the aftereffects. When Neuron A has been adapted to the stimulus, aftereffects from the stimulus are transferred to the post-saccadic RF location of Neuron A, where Neuron A will process after an impending saccade. This transfer implies that if there is an object at the post-saccadic RF location of Neuron A, Neuron A prepares for the upcoming object by shifting its RF to the location of the object. In the same manner, the shifting RF mechanism predicts that the stimulus would be processed by Neuron B prior to saccadic onset. The second mechanism, activation transfer via a saliency map, accounts for the remapping of attention. The activation of Neuron A is reflected in Neuron A′ in the saliency map, and the activation of Neuron A′ is transferred to Neuron B′. Neuron B′, in turn, facilitates Neuron B, which will process the stimulus after the saccade. Thus, the processing of the stimulus is facilitated by transferring the activation from Neuron A to Neuron B via the saliency map

et al. 1995), and LIP (Batista et al. 1999; Colby et al. 1996; Duhamel et al. 1992; Heiser and Colby 2006; Kusunoki and Goldberg 2003).

While physiological studies have focused on the neurons' ability to respond to the same object across a saccade, psychophysical studies have shown behavioral consequences of these anticipatory responses, specifically a transfer of aftereffects and a remapping of attention. Melcher (2007) found that tilt aftereffects were transferred to the post-saccadic location corresponding to the future RFs where adapted neurons would process after an impending saccade was completed (post-saccadic RF location). This finding was considered as behavioral evidence of neurons with shifting RFs (Wurtz 2008). These neurons shift their RFs to the location they will process after an impending saccade to prepare for the upcoming stimuli (Fig. 1). Other researchers investigated the remapping of attention at the time of a saccade. For example, Rolfs et al. (2011) found that attention to a saccadic target was remapped to the post-saccadic location of the saccadic target in the retinal coordinates (post-saccadic retinotopic location). Attention could remain on the same object over saccades as attention was remapped from the current location to the post-saccadic retinotopic location of the object (Fig. 1). Cavanagh et al. (2010) suggested that learned horizontal connections in the LIP (saliency map) transfer the activations of the neurons processing the current location to those processing the post-saccadic retinotopic location. In turn, those transferred activations facilitate the neurons in the visual cortices, resulting in the remapping of attention.

These two mechanisms, a shifting RF and activation transfer via a saliency map, emphasize different aspects of the remapping. According to the shifting RF mechanism, the visual features of figures and the ground are remapped because the neurons in the early visual cortices process the same stimuli over a saccade, regardless of whether the stimuli are figures or the ground. To help visual neurons anticipate the upcoming stimuli, this remapping has to precede saccadic onset. Meanwhile, the activation transfer mechanism predicts that the location information about attended objects is maintained over a saccade. This activation transferred from the saliency map requires time to reach the visual cortices and then facilitates the processing of attended stimuli after the saccade.

To maintain visual stability, not only the location of important objects, but also the background information in which the objects are embedded, should be conveyed over a saccade. Joiner et al. (2011) found that RFs of the FEF neurons showing anticipatory responses were equally distributed throughout the eccentricity. More importantly, only 30 % of these neurons were modulated by stimulus saliency. These results suggest that FEF neurons have an ability to remap stimuli in the periphery, and only some of those neurons are influenced by saliency. Furthermore, FEF neurons are known to detect trans-saccadic location and feature changes, and their responses reflect the degree of those changes (Crapse and Sommer 2012), which suggests that FEF neurons are capable of comparing visual environments over saccades with more than just a locational map of the attended objects. This remapping process can start prior to saccadic onset (Melcher 2007, 2008, 2009) and still works after the completion of the saccade (Golomb et al. 2008, 2010). Thus, the remapping process deals with figures and the ground throughout the entire period of a saccade. We need both the shifting RF and activation transfer mechanisms, as they are complementary in determining what is to be remapped and emphasized based on the visual context.

We hypothesized that the remapping serves several roles during eye movements: helping neurons to anticipate an upcoming stimulus and indicating which objects were to be processed immediately after the saccade. The main purpose of our study was to show different aspects of the remapping, which represent different underlying neural mechanisms: a remapping based on shifting RFs and a remapping of attention via a saliency map. Moreover, our study investigated how those mechanisms interact depending on the visual context. To achieve these goals, we examined the remapping of the background and compared them with the remapping of the figure. We predicted that the figures and the ground were remapped in a similar manner, unless the top-down signals from a saliency map modulated the remapping of them differently. It is known that the activities in the visual cortices evoked by the background are influenced less by a saliency map (Qiu et al. 2007).

In Experiment 1, we used the same method as Melcher (2007), although we used a different type of adapter to investigate the transfer of tilt aftereffects from both the figure and the ground. Tilt aftereffects from both the figure and the ground were transferred to the post-saccadic RF location, and the amount of the transfer was noted to be similar between the figure and the ground. Experiment 2 extended the findings of Experiment 1 in two ways. We found a similar amount of transfer in another type of aftereffect (orientation-specific adaptation) and at a different time point (during an eye movement). The amount of transfer was also similar between the figure and the ground. The results from Experiments 1 and 2 suggest that a figure and the ground are processed similarly if the visual context remains stable. In Experiment 3, we showed that top-down signals modulate the transfer of aftereffects. Changes in the saliency map influenced the amount of transfer differently, depending on whether the adapter was represented as a figure or as the ground during the adaptation process.

Experiment 1

In Experiment 1, we investigated whether the tilt aftereffects of stimuli presented as a background were transferred to the post-saccadic RF location prior to saccadic onset. The paradigm and stimuli were similar to those in Melcher (2007), except that the adapter consisted of sine-wave gratings on both the figure and the ground, which were tilted at opposing orientations (Fig. 2). A probe was presented at the post-saccadic RF location for either the figure or the ground. Participants reported the orientation of the probe [clockwise (CW) or counterclockwise (CCW)]. The proportion of 'clockwise' responses was fitted to a cumulative Gaussian function to acquire the point of subject equality (PSE). Significant differences in PSEs, depending on the orientation of the adapter grating, indicated that the tilt aftereffects were transferred to the location of the probe. We hypothesized that the predictive transfer of tilt aftereffects occurs for the background as well as for the figure.

Methods

Participants

Three participants, including both authors, participated in Experiment 1. All participants, including those for Experiments 2 and 3, gave informed consent, and every aspect of the study was carried out in accordance with the Institutional Review Committee of Yonsei University.

Experimental setup

Stimuli were presented using MATLAB software (MathWorks) with the Psychophysics Toolbox extension

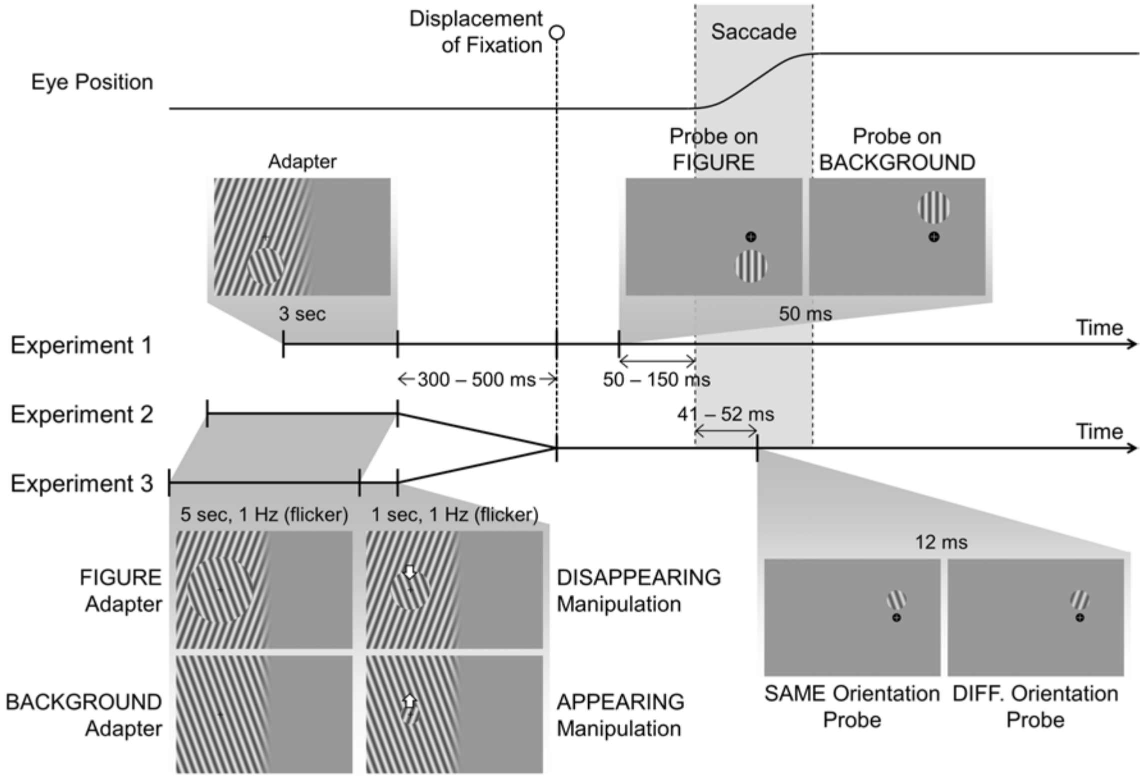


Fig. 2 Stimuli and procedures of Experiments 1 through 3. Different types of adapters and probe timings are plotted on separate timelines, according to the experiment. In Experiment 1, the adapter grating was presented for 3 s. In Experiments 2 and 3, the adapter grating was counter-phase flickered for 5 s. Experiment 3 contained 1 additional second of manipulation. The timing of a probe was targeted 50–150 ms before the saccadic onset in Experiment 1, whereas it was targeted 41–52 ms after saccadic onset (during a saccade) in Experiments 2 and 3

(Brainard 1997; Pelli 1997). A gamma-corrected CRT monitor (HP P1230; refresh rate 85 Hz) was placed at a viewing distance of 90 cm in a dark room.

Eye movement recording

The electrooculogram (EOG) was recorded using Neuroscan NuAmps Express (Compumedics). A ground electrode was placed on the forehead, and a reference electrode was placed 1 cm outside the left canthus. Signals from an electrode 1 cm outside the right canthus were used to record EOG signals. This configuration canceled out signals caused by eye blinks and vertical saccades, leaving only the signals caused by horizontal saccades.

Each participant, including those recruited for Experiments 2 and 3, underwent a pre-experimental EOG recording session, which consisted of 30 trials of horizontal rightward saccades. We marked the saccadic onset by hand on every EOG recording. Using a real-coded genetic algorithm technique (Michalewicz et al. 1996), a 9-point convolution kernel, which yielded strong positive values at the saccadic onset, was optimized for each participant. Optimized convolution kernels were very similar between participants (Fig. 3a), and a descriptive sample of the EOG recording and filtered signal were shown in Fig. 3b. We defined saccadic onset as the time point at which the filtered signal first exceeded a certain threshold. Average differences between hand-picked saccadic onsets and those calculated based on the convolution kernel were −0.99 ± 2.17 ms for five participants.

Main experiment

The participants started each trial by pressing a space bar. Trials began with a 3-s adaptation period. A fixation cross was presented at 5° to the left of the center of the screen. A sine-wave grating of 1 cpd, tilted either 20° CW or 20° CCW from the vertical position, was presented on the left half of the screen (background adapter). A 5° circular grating, tilted toward an orientation opposite to that of the background (figure adapter), was presented either 4° above or 4° below the fixation point (Fig. 2). Note that both the figure and ground adapters were presented at the same time. After the adapter gratings disappeared, the fixation cross was displaced 5° to the right of the center of the screen with a random latency between 300 and 500 ms. Participants made a

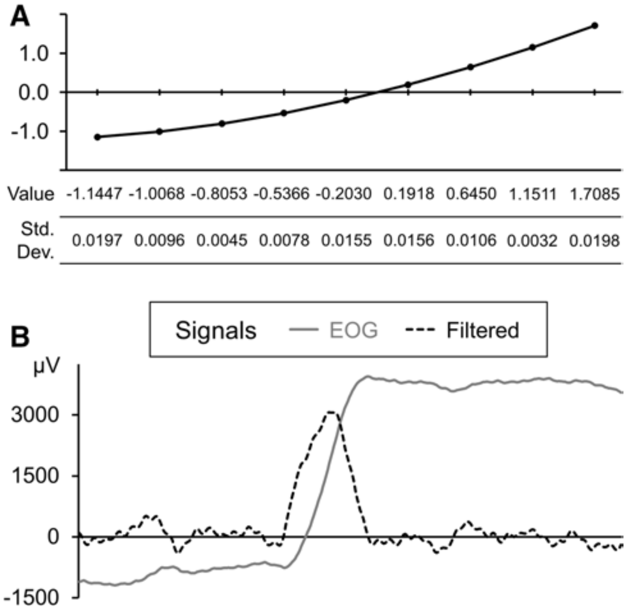


Fig. 3 **a** Averaged convolution kernel for the five participants. Each kernel was normalized to have an average of 0 and a standard deviation of 1 after optimization. Optimized convolution kernels were very similar between the participants. Standard deviations for each of the 9 points between different kernels were shown at the bottom of the graph. As the kernels were very similar, we plotted an averaged kernel. **b** Example of EOG (*gray solid line*) and filtered (*black dashed line*) signals using an optimized convolution kernel. Filtered signals were to yield a value of 0 at random fluctuations in EOG signals, because the kernel was normalized to have an average of 0. When there was a sudden rise in the EOG signal, filtered signals yield strong positive values, which could be thresholded to detect saccadic onset

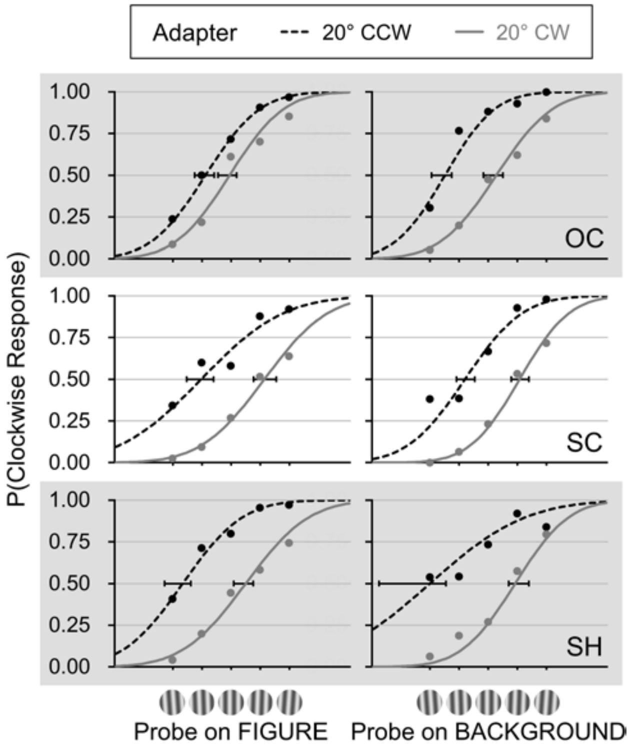


Fig. 4 Fitted cumulative Gaussian curves and estimates of PSEs from Experiment 1. The *dashed curves* represent the cumulative Gaussian functions after adaptation to the 20° CCW adapter, and the *solid curves* represent those after adaptation to the 20° CW adapter. *Error bars* indicate 90 % confidence intervals. Significant differences between PSEs indicate that aftereffects are transferred to the location of the probe

saccade to the new fixation cross. A probe was flashed for 50–150 ms before saccadic onset, depending on the mean saccadic latency of each participant. Participants reported whether the probe (a 4.5° circular grating tilted either −2°, −1°, 0°, 1°, or 2° from vertical) was tilted CW or CCW. Experiment 1 consisted of 20 blocks of 100 trials each. On average, the participants completed three to four blocks a day, therefore requiring 6–8 days for a participant to finish 20 blocks. The orientation of the adapter (20° CW or 20° CCW) and the location of the probe (post-saccadic RF for the figure adapter or the background adapter) were blocked. The orientation of the probe was randomly intermixed within each block.

Results

Trials with a probe onset outside the window of −150 to −50 ms relative to saccadic onset were discarded from further analysis. The mean percentage of the accepted trials was 37.43 %. The proportion of 'clockwise' responses was fitted to a cumulative Gaussian function to acquire the PSE. Figure 4 depicts the fitted curves and estimates of the PSEs. A bootstrapping comparison (Wichmann and Hill 2001) revealed significant PSE differences for the post-saccadic RFs for both the figure and the ground in all three participants (all *ps* < .05).

Discussion

We found a predictive transfer of tilt aftereffects in the post-saccadic RF location for both the figure and the ground. Our new finding was that the tilt aftereffects caused by the background as well as the figure were transferred to the post-saccadic RF location prior to saccadic onset. The underlying neural mechanism for this type of remapping (predictive transfer of aftereffects) might reside in the earlier visual areas, which process figures and the ground in the same manner. One might argue that the probe could be shown at the post-saccadic RF location for the ground adapter, and thus, the ground adapter containing the task-relevant region could be perceived as a figure. Nonetheless, the figure and the ground adapters should have different representational strengths in the saliency map because of the large difference in area between them (figure: circle of 4.5° in diameter;

ground: rectangle of 6.34° in width and 9.46° in height). It is known that processing a large area decreases the efficiency of attention (Castiello and Umiltà 1990).

We replicated Melcher (2007) in that the tilt aftereffects caused by a figure were transferred to the post-saccadic RF location. In addition, our results suggest that tilt aftereffects are transferred to a specific location (post-saccadic RF location), rather than having spilled over from adjacent locations. If the transfer was not location-specific or there was a spillover of aftereffects, aftereffects from the large background adapter enclosing the figure would have canceled out those from the figure adapter.

Experiment 2

Experiment 2 extended the findings of Experiment 1 in two ways. First, we measured the amount of threshold elevation caused by orientation-specific adaptation. This new measure was done to generalize our results to different types of adaptation in an efficient fashion (by reducing the number of trials). Second, a probe was presented during an eye movement instead of before saccadic onset. Neurons, which shifted their RFs to the post-saccadic RF location prior to saccadic onset, should process the same stimuli over a saccade to maintain visual stability. Therefore, we expected to find aftereffects at the post-saccadic RF location during a saccade.

Methods

Five participants, including the three from Experiment 1, participated in Experiment 2. The experimental settings were identical to those in Experiment 1, with the exception that the viewing distance modified to 45 cm. The EOG was monitored online, and a probe was presented during a saccade. Participants started each trial by pressing a space bar. At the beginning of each trial, adapting stimuli were presented for 5 s. A fixation cross was placed 15° left from the center of the screen. A sine-wave grating of 1 cpd, tilted either 20° CW or 20° CCW, was counter-phase flickered at the left half of the screen (background adapter). In the other condition, a 15° circular grating tilted at an orientation opposite to that of the background (figure adapter) was flickered with the background grating (Fig. 2). The flicker rate for both the figure and the background adapters was 1 Hz. After a random delay of 300–500 ms following the adaptation period, the fixation cross was displaced to the right by 30°, and the participants made a saccade to the new location. The saccade distance was much longer than it was in Experiment 1 because we wanted the saccade duration to be long enough to present a probe during the saccade. A 4.5° circular grating was presented as the probe either 4° above or 4° below the new fixation point 41–52 ms after saccadic onset. As 30° saccades took 70–124 ms (90.42 ± 5.84 ms) on average, probe onset always occurred during a saccade. The probe could be tilted in the same (same orientation probe) or the opposite (different orientation probe) direction relative to the orientation of the adapter grating. The task of the participants was to determine whether the probe was presented either above or below the new fixation cross. The contrast of the probe was adjusted using the QUEST procedure (Watson and Pelli 1983) to yield 75 % accuracy. Experiment 2 consisted of eight blocks of 90 trials each. The orientation of the adapter (20° CW or 20° CCW), the type of adapter (figure or ground), and the type of probe (same or different orientation) were blocked. The order of the blocks was randomized across participants. One block contained three interleaved QUEST procedures, each having 30 trials. In addition, two baseline blocks were conducted to measure the contrast threshold of the probe (oriented 20° CW or 20° CCW) without adaptation.

Results

Trials with a saccadic latency time of less than 200 ms or longer than 1.5 s were not reflected in the threshold estimation. On average, 3.32 trials were rejected per block. The ratio between the threshold after adaptation and the threshold without adaptation (threshold elevation index, TEI) indicates the amount of transfer during a saccade. The left part of Fig. 5a depicts the threshold elevation indices for four conditions (two types of adapter × two types of probe). A repeated-measures ANOVA revealed that the TEIs with the same orientation probes were significantly higher compared to the different orientation probes in both the figure adapter and the ground adapter conditions (main effect of the probe: $F(1, 4) = 144.144$, $p < .01$). The amount of transfer caused by both the figure and the ground adapter did not differ (main effect of the adapter: $F(1, 4) = .089$, $p = .781$; interaction between the adapter and the probe: $F(1, 4) = .093$, $p = .775$).

Discussion

In Experiment 2, the aftereffects were also found at the post-saccadic RF location during an eye movement, where they were transferred prior to saccadic onset. The amount of transfer was similarly maintained during an eye movement between the figure adapter and the ground adapter conditions. The similar amount of transfer suggested that, without changes in the visual context (whether the stimulus was the figure or the ground), this type of remapping (transfer of adaptation during an eye movement) might be based on bottom-up processing in which the figure and the ground

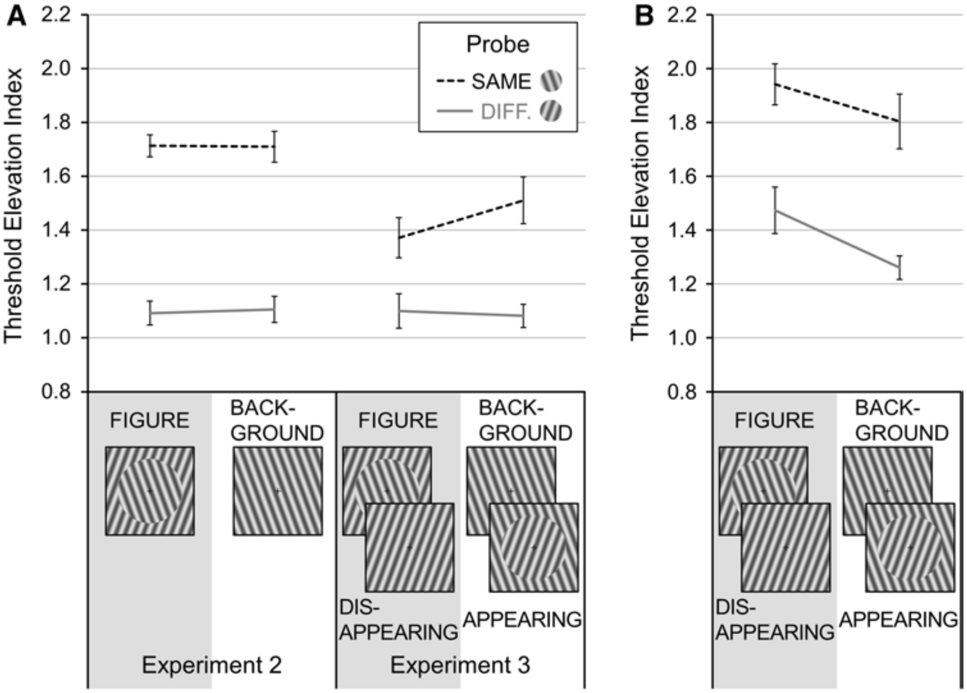


Fig. 5 **a** TEIs from Experiments 2 and 3. Elevated thresholds for the same orientation probe (*dashed line*) indicate the amount of transferred aftereffects. Significant differences between TEIs from the same orientation probe and the different orientation probe (*solid line*) showed that the orientation-specific adaptation remained at the postsaccadic RF during the saccades (both Experiments 2 and 3). There was a significant interaction between the type of manipulation and the orientation of the probe (Experiment 3), showing that modulation effects were more pronounced with disappearing manipulation. **b** TEIs from a control experiment. The participants did not move their eyes in the control experiment. Note that the figure shows the pure amount of adaptation caused by the adapter, as was the case in Experiment 3 without eye movements

were processed in similar ways. Note that this orientation-specific adaption is location-specific and barely affected by conscious perception (He and MacLeod 2001). Along with the results of Experiment 1, these results support the idea that neurons with shifting RFs process the same stimuli over a saccade. Another important finding of Experiment 2 is that the transfer of aftereffects can be generalized to orientation-specific adaptation. Thus far, only tilt aftereffects (Melcher 2007, 2008, 2009; Knapen et al. 2010) and motion aftereffects (Biber and Ilg 2011) have been used to study transfers of aftereffects in retinotopic brain regions.

Experiment 3

In Experiment 3, we investigated the effects of top-down signals on the transfer of aftereffects by manipulating the representational strength of the adapting stimuli in a saliency map (the visual context). We changed the adapter status of the figure and the ground within 1 s following the same adaptation period used in Experiment 2. After adapting to the figure adapter, the figure disappeared toward a fixation cross, changing the status of the adapter from the figure to the background in the saliency map. After adapting to the background adapter, the figure appeared from the fixation cross, thus changing the status from the background to the figure. This manipulation only altered the representational strength in the saliency map, while maintaining the same amount of adaptation used in Experiment 2, as we used the same adapting stimuli for the same period before this manipulation. We predicted that this manipulation would influence the remapping of the disappearing figure more than it would influence that of the background (the figure appearing in the background), because remapping via a saliency map plays a role in maintaining attention toward the location of important objects (Cavanagh et al. 2010).

Methods

The participants, experimental settings, stimuli, and procedures were identical to those of Experiment 2. The only difference was a 1-s manipulation period following the adaptation period (Fig. 2). In the disappearing manipulation, the radius of the disk decreased to zero within 1 s. A cosine function scaled to have a maximum value of 1 and minimum value of 0 was used to determine the radius of the circle. The cosine function had a cycle of 2 s, and a half-cycle, declining from 1 to 0, was used in the manipulation period of 1 s.

In the appearing manipulation, the sequence of the disappearing manipulation was played in reverse order. Thus, the disappearing and appearing manipulations had the same stimuli with different sequences over time. In this reversed sequence, a disk containing a sine-wave grating appeared from the center of the background adapter and grew to the size of the disk of the figure adapter.

Results

The right part of Fig. 5a depicts the TEIs for the four conditions (two types of adapters × two types of probes). A repeated-measures ANOVA revealed that the aftereffects from the figure adapter were influenced more by the manipulation introduced in Experiment 3 compared to the aftereffects from the background adapter (interaction between the adapter and the probe: $F(1, 4) = 8.591$, $p < .05$).

Discussion

As we expected, manipulation of the saliency map influenced the remapping of the figure more than it influenced that of the background. When a figure disappeared and the representational strength was reduced in the saliency map, top-down signals suppressed the remapping of the location where there had been a figure. However, the remapping of the background was modulated less because the saliency map had a weaker representation for the location of the background (Gottlieb 2007).

A control experiment was run to test the possibility that the manipulation itself had different effects on the figure and ground adapters in the initial adaptation. We measured the threshold elevations of the five participants, including one of the authors, for the probe presented at the location of the adapter after the participants adapted to the same adapter used in Experiment 3. Participants were instructed to maintain their gaze on the initial fixation point throughout the trial instead of making a saccade. TEIs from the control experiment were plotted in Fig. 5b. The only significant difference was found on the types of the probes [$F(1, 4) = 26.021$, $p < .05$]. The interaction between the types of manipulations and the types of the probes was not significant, unlike in the main experiment [$F(1, 4) = 0.384$, $p = .569$]. These results suggest that the interaction found in Experiment 3 does not occur due to the different influence of the manipulation on the amount of adaptation, but because it influences adaptation in the remapping process.

The amount of transfer was similar in Experiments 1 and 2, and the amount differed when the visual context was changed by manipulating representations in the saliency map (Experiment 3). Consistently, Melcher (2008) found that the remapping could be object-based if enough visual contexts were given. A novel finding here was that the object-based effects were due to different representational strengths in a saliency map.

General discussion

We found that aftereffects from both the figure and the ground were transferred to the post-saccadic RF location similarly, unless their representational strength in the saliency map (the visual context) was unchanged. Differences between the remapping of the figure and the ground arose from the manipulation of the representations in the saliency map. When participants adapted to the figure or the ground adapter and the representational strength then changed, the amount of transfer was modulated depending on whether the adapter was the figure or the ground during the adaptation period. These results are consistent with the previous findings in that the aftereffects from the figure adapter were transferred to the post-saccadic RF locations (Melcher 2007) and that the aftereffects from the figure adapter were influenced by a similar form of the object-hood manipulation (Melcher 2008). Joiner et al. (2011) found that FEF neurons' anticipatory responses to the stimuli presented in the post-saccadic RFs were reduced when distractors were added outside of the RFs, and thereby, the saliency of a stimulus inside of the RF was reduced. They also found that distractors did not affect responses to the stimuli presented in the current RFs of FEF neurons. These physiological results corresponded nicely with our finding that the saliency of the stimuli only influenced the process of remapping. Our findings suggest that the background, or less salient stimuli, is included in the remapping process. More importantly, top-down signals from a saliency map influence the remapping of figures more than that of the background. In addition, we found that orientation-specific adaptation was transferred to the post-saccadic RF locations, as were the tilt and motion aftereffects, further extending the previous findings (Biber and Ilg 2011; Knapen et al. 2010; Melcher 2007, 2008, 2009; Zirnsak et al. 2011).

Studies that measured the transfer of aftereffects, including our own, support the idea of a shifting RF as a mechanism. In those studies, aftereffects were transferred to the post-saccadic RF locations, where neurons would process them after an impending saccade. Physiological studies have found consistent evidence supporting the idea of a shifting RF. For example, FEF neurons were shown to respond to a stimulus presented at the location of the post-saccadic RF before saccadic onset (Sommer and Wurtz 2006). In that study, the shifting of RFs was mediated by corollary discharge signals from the SC. Since the SC receives signals from retinal ganglion cells, this mechanism may work during the feed-forward sweep of visual processing. Given that figure and ground modulation originates from top-down signals (Hupé et al. 1998), there would be no differences between the processing of the figure and that of the ground in this feed-forward sweep. In accordance with the results from physiological research, our findings in Experiments 1 and 2 behaviorally showed that aftereffects were transferred during feed-forward processing, which handled the figure and the ground similarly.

Another possible explanation of our results is the distortion of RFs toward a saccadic target (Zirnsak et al. 2011). As the RFs of neurons were drawn toward the saccadic target, the location of adaptation was also drawn toward the saccadic target. Since we measured the adaptation around the saccadic target throughout our experiment, this hypothesis can certainly explain our results. However, we found a different amount of modulation, depending on the status of the adapter (figure or ground), although the location of the measurements was the same. Physiological evidence also showed that neurons with RFs in the periphery could shift their RFs at the time of saccade (Joiner at el. 2010), suggesting that the visual system had an ability to remap stimuli in the periphery.

Cavanagh et al. (2010) proposed another mechanism, which accounted for the remapping of attention. According to their findings, activation from a stimulus is transferred to the neurons processing the post-saccadic retinotopic location of the stimulus via the saliency map. This transferred activation then trickles down to the visual cortices to facilitate the processing of the stimulus, which would be located at the post-saccadic retinotopic location after the completion of a saccade. Since signals from a saliency map contain location information about objects of interest (Gottlieb 2007), their proposed mechanism predicts that the remapping of the figure is more sensitive to the attentional modulation. We found consistent results in that the remapping of the figure was sensitive to the manipulation of representations in the saliency map. Studies supporting this idea found remapping to be most effective after saccadic onset, as it was happening after the signals from the saliency map reached the visual cortices. Behaviorally, attention to a specific location was remapped after the completion of a saccade (Golomb et al. 2008, 2010). Physiologically, anticipatory responses were observed after saccadic onset in V1 (Nakamura and Colby 2002).

This study proposes that there are different aspects of remapping that represent the different underlying neural mechanisms. One type of remapping occurring at the feed-forward sweep of visual processing processes figures and the ground similarly. In Experiments 1 and 2, we showed that the background was remapped and maintained similarly to the figure. These results were supported well by neurons with shifting RFs working in the earlier visual cortices. Since the RFs of neurons were shifted, almost all of the information, including the visual features, pertaining to figures and the ground was preserved during this stage of remapping. This type of remapping might be needed to check whether the visual scene was the same as expected just after the completion of a saccade. In order to make sure that nothing had changed over an eye movement, the visual system should monitor features over the whole visual field as well as the locations of objects (Crapse and Sommer 2012). Another type of remapping takes modulatory roles, based on activation transfer, via a saliency map. Since a saliency map represents the objects of interest on a locational map (Gottlieb 2007), a remapping mechanism based on a saliency map would have a greater impact on the remapping of a figure. Experiment 3 showed that the transfer of aftereffects was modulated by changes in the saliency map and that the modulation was stronger when the figure representation in the saliency map changed. Given that top-down signals from a saliency map take time to arrive at the visual cortices, this stage of remapping could later modulate the remapping based on the feed-forward sweep of visual processing. Consistent with this idea, people lose their ability to localize stimuli during the early period of a saccade, whereas they have an intact ability to report visual features such as color and size (Lappe et al. 2006; Luo et al. 2010). This type of remapping might support the human ability to maintain a seamless perception between fixations, as it helps our visual system to maintain locational maps of important (attended) objects and to process those objects as soon as the gaze stabilizes.

In conclusion, this study proposes that there are different remapping mechanisms working together to maintain visual stability. In the feed-forward sweep of visual processing, bottom-up signals cause neurons in the early visual cortices to shift their RFs. Top-down signals from a saliency map, as Cavanagh et al. (2010) proposed, later modulate the remapping caused by the shifting RF. Our findings support the idea of a shifting RF as a basic factor of the remapping and integrate a mechanism based on a saliency map as a modulatory factor based on the visual context.

Acknowledgments This research was supported by the Basic Science Research Program through the National Research Foundation of Korea (NRF), funded by the Ministry of Education, Science and Technology (2009-0089090).

Conflict of interest The authors declare that they have no conflict of interest.

References

Batista AP, Buneo CA, Snyder LH, Andersen RA (1999) Reach plans in eye-centered coordinates. Science 285:257–260

Biber U, Ilg UJ (2011) Visual stability and the motion aftereffect: a psychophysical study revealing spatial updating. PLoS ONE 6:1–11

Brainard DH (1997) The psychophysics toolbox. Spat Vis 10:433–436

Castiello U, Umiltà C (1990) Size of the attentional focus and efficiency of processing. Acta Psychol 73:195–209

Cavanagh P, Hunt AR, Afraz A, Rolfs M (2010) Visual stability based on remapping of attention pointers. Trends Cogn Sci 14:147–153

Colby CL, Duhamel JR, Goldberg ME (1996) Visual, presaccadic, and cognitive activation of single neurons in monkey lateral intraparietal area. J Neurophysiol 76:2841–2852

Crapse TB, Sommer MA (2012) Frontal eye field neurons assess visual stability across saccades. J Neurosci 32:2835–2845

Duhamel JR, Colby CL, Goldberg ME (1992) The updating of the representation of visual space in parietal cortex by intended eye movements. Science 255:90–92

Golomb JD, Chun MM, Mazer JA (2008) The native coordinate system of spatial attention is retinotopic. J Neurosci 28:10654–10662

Golomb JD, Nguyen-Phuc AY, Mazer JA, McCarthy G, Chun MM (2010) Attentional facilitation throughout human visual cortex lingers in retinotopic coordinates after eye movements. J Neurosci 30:10493–10506

Gottlieb J (2007) From thought to action: the parietal cortex as a bridge between perception, action, and cognition. Neuron 53:9–16

He S, MacLeod DIA (2001) Orientation-selective adaptation and tilt after-effect from invisible patterns. Nature 411:473–476

Heiser LM, Colby CL (2006) Spatial updating in area LIP is independent of saccade direction. J Neurophysiol 95:2751–2767

Hupé JM, James AC, Payne BR, Lomber SG, Girard P, Bullier J (1998) Cortical feedback improves discrimination between figure and background by V1, V2 and V3 neurons. Nature 394:784–787

Joiner WM, Cavanaugh J, Wurtz RH (2011) Modulation of shifting receptive field activity in frontal eye field by visual salience. J Neurophysiol 106:1179–1190

Knapen T, Rolfs M, Wexler M, Cavanagh P (2010) The reference frame of the tilt aftereffect. J Vis 10(1):1–13

Kusunoki M, Goldberg ME (2003) The time course of perisaccadic receptive field shifts in the lateral intraparietal area of the monkey. J Neurophysiol 89:1519–1527

Lappe M, Kuhlmann S, Oerke B, Kaiser M (2006) The fate of object features during perisaccadic mislocalization. J Vis 6:1282–1293

Luo G, Garaas T, Pomplun M, Peli E (2010) Inconsistency between peri-saccadic mislocalization and compression: evidence for separate “what” and “where” visual systems. J Vis 10:1–8

Melcher D (2007) Predictive remapping of visual features precedes saccadic eye movements. Nat Neurosci 10:903–907

Melcher D (2008) Dynamic, object-based remapping of visual features in trans-saccadic perception. J Vis 8:1–17

Melcher D (2009) Selective attention and the active remapping of object features in trans-saccadic perception. Vis Res 49:1249–1255

Michalewicz Z, Nazhiyath G, Michalewicz M (1996) A note on usefulness of geometrical crossover for numerical optimization problems. In: Proc of the 5th Ann Conf on Evolutionary Programming. MIT Press, Cambridge, pp 305–312

Nakamura K, Colby CL (2002) Updating of the visual representation in monkey striate and extrastriate cortex during saccades. Proc Natl Acad Sci USA 99:4026–4031

Pelli DG (1997) The VideoToolbox software for visual psychophysics: transforming numbers into movies. Spat Vis 10:437–442

Qiu FT, Sugihara T, von der Heydt R (2007) Figure-ground mechanisms provide structure for selective attention. Nat Neurosci 10:1492–1499

Rolfs M, Jonikaitis D, Deubel H, Cavanagh P (2011) Predictive remapping of attention across eye movements. Nat Neurosci 14:252–258

Sommer MA, Wurtz RH (2006) Influence of the thalamus on spatial visual processing in frontal cortex. Nature 444:374–377

Tolias AS, Moore T, Smirnakis SM, Tehovnik EJ, Siapas AG, Schiller PH (2001) Eye movements modulate visual receptive fields of V4 neurons. Neuron 29:757–767

Umeno MM, Goldberg ME (1997) Spatial processing in the monkey frontal eye field. I. Predictive visual responses. J Neurophysiol 78:1373–1383

Umeno MM, Goldberg ME (2001) Spatial processing in the monkey frontal eye field. II. Memory responses. J Neurophysiol 86:2344–2352

Walker MF, Fitzgibbon EJ, Goldberg ME (1995) Neurons in the monkey superior colliculus predict the visual result of impending saccadic eye movements. J Neurophysiol 73:1988–2003

Watson AB, Pelli DG (1983) QUEST: a Bayesian adaptive psychometric method. Percept Psychophys 33:114–120

Wichmann FA, Hill NJ (2001) The psychometric function: II. Bootstrap-based confidence intervals and sampling. Percept Psychophys 63(8):1314–1329

Wurtz RH (2008) Neuronal mechanisms of visual stability. Vis Res 48:2070–2089

Zirnsak M, Gerhards RG, Kiani R, Lappe M, Hamker FH (2011) Anticipatory saccade target processing and the presaccadic transfer of visual features. J Neurosci 31:17887–17891