The reference frame of the tilt aftereffect

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Perceptual aftereffects provide a sensitive tool to investigate the influence of eye and head position on visual processing. There have been recent indications that the TAE is remapped around the time of a saccade to remain aligned to the adapting location in the world. Here, we investigate the spatial frame of reference of the TAE by independently manipulating retinal position, gaze orientation, and head orientation between adaptation and test. The results show that the critical factor in the TAE is the correspondence between the adaptation and test locations in a retinotopic frame of reference, whereas world- and head-centric frames of reference do not play a significant role. Our results confirm that adaptation to orientation takes place at retinotopic levels of visual processing. We suggest that the remapping process that plays a role in visual stability does not transfer feature gain information around the time of eye (or head) movements.

Keywords: active vision, eye movements, receptive fields, spatial version, visual cortex

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Introduction

We have the impression of stable visual perception of the world around us despite our eye, head, and body movements that drastically change the images landing on our retinas. For perception of the world to be stable, movements of eyes and head have to be taken into account and recent neurophysiology has provided several indications of possible mechanisms. Visual perception takes as its initial input the signals from the retina, so the original visual signals are based in retinotopic coordinates. This frame of reference rotates and translates relative to world and head coordinates whenever the eyes rotate in their sockets and it rotates and translates relative to the world whenever the eyes or head rotate or translate. This leads to the interdependence of several different reference frames, namely those based on retinal, head (also called craniotopic), and body (or world) coordinates. These three reference frames are the principal coordinate systems that, when the appropriate extra-retinal signals are taken into account, could support behavior and representations in world-centric coordinates.

There is evidence at various levels of the visual system for signals selective to gaze and head orientation. For example, the visual sensitivity of many retinotopic neurons in parietal cortex is modulated by gaze direction and head orientation relative to body and world (Andersen, Essick, & Siegel, 1985; Andersen, Snyder, Li, & Stricanne, 1993), enabling at least theoretically, a recovery of locations in world coordinates (Snyder, Grieve, Brotchie, & Andersen, 1998). There is also an influence of gaze direction on single cell responses in areas V1, V2, V3A, and V4 (Galletti & Battaglini, 1989; Rosenbluth & Allman, 2002; Trotter & Celebrini, 1999). In line with these physiological reports, the strength of visual aftereffects, such as those for motion and tilt, decreases by about 10% if gaze shifts by more than 60 degrees between adaptation and test even when the test stimulus is at the same retinal location as the adaptation stimulus (Nishida, Motoyoshi, Andersen, & Shimojo, 2003).

Although cells modulated by eye, head, and body positions could underlie a recovery of world coordinates, the findings of Duhamel, Colby, and Goldberg (1992) and others (Batista, Buneo, Snyder, & Andersen, 1999; Colby, Duhamel, & Goldberg, 1996; Heiser & Colby, 2006) in parietal areas have offered an alternative mechanism. Specifically, these authors report cells that become active before a saccade brings a stimulus into their receptive field (remapping). Thus, prior to an eye movement these cells are activated by stimuli presented in two regions: locations in their classical receptive field and locations in the world that will fall inside their receptive field only after the saccade. This means that these neurons have

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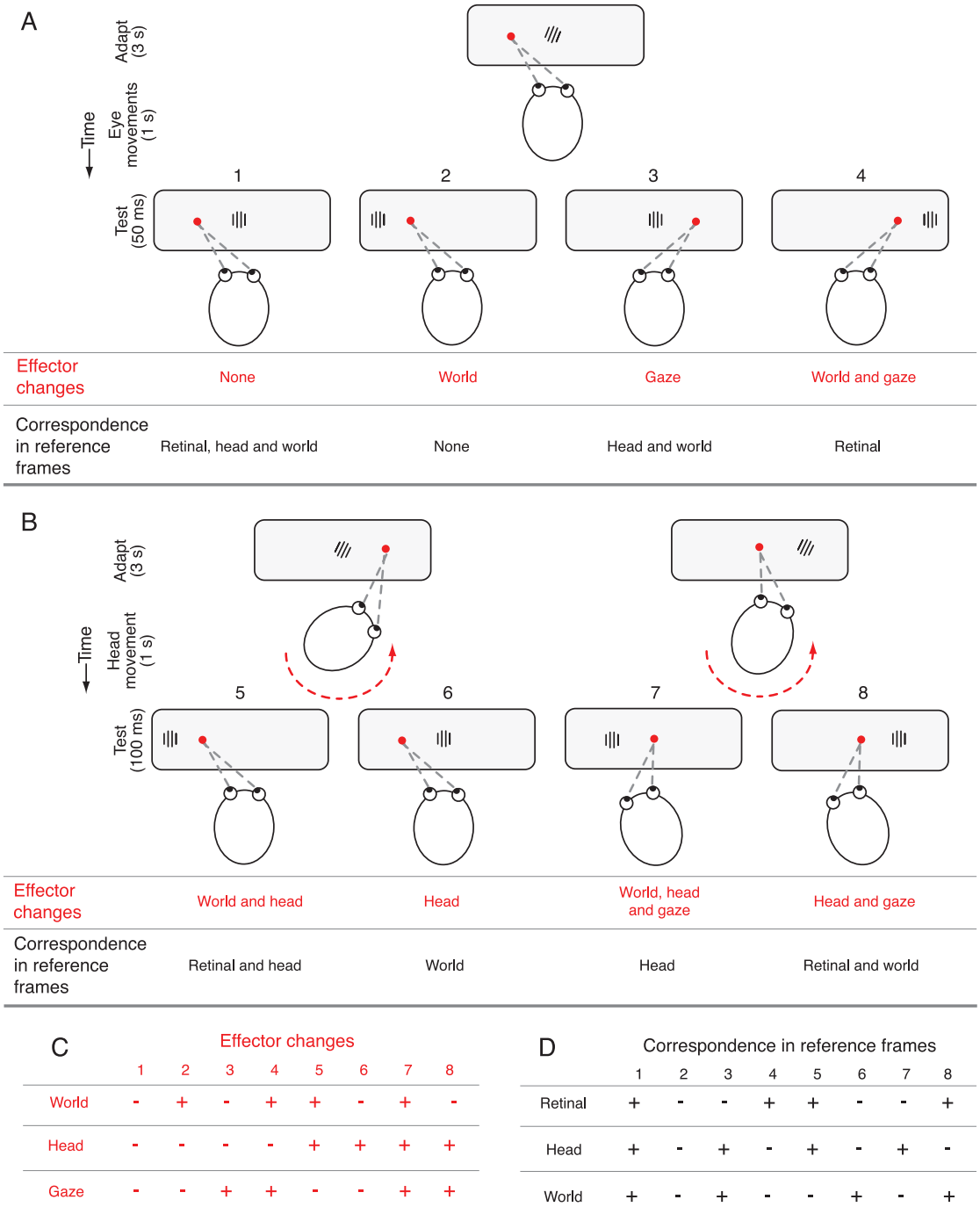

C

Effector changes

	1	2	3	4	5	6	7	8
World	-	+	-	+	+	-	+	-
Head	-	-	-	-	+	+	+	+
Gaze	-	-	+	+	-	-	+	+

D

Correspondence in reference frames

	1	2	3	4	5	6	7	8
Retinal	+	-	-	+	+	-	-	+
Head	+	-	+	-	+	-	+	-
World	+	-	+	-	-	+	-	+

Figure 1. Design of experiments. (A) Experiment 1. The time course of trials in the different conditions of Experiment 1. Three seconds of adaptation were followed by 1 s for eye movements, after which a test stimulus of 50 ms was presented. Changes: With the head remaining in the same orientation one can change gaze and retinal position between adaptation and test, in a 2 by 2 design. Between adaptation and test there were always two saccades to equate the number of eye movements across trials. Reference frames: Using these different conditions, we can differentiate between head/world reference frames on the one hand, and the retinal reference frame on the other, but this design conflates head and world reference frames. To differentiate between the two, we need head movements. (B) Experiment 2. The design with changes of head orientation between adaptation and test and the trial time course. Again, in two conditions gaze is changed and in two conditions retinal position is changed, but now these changes are combined with the changes in head orientation. (C) Effector changes: Design matrix for the changes using different effectors, i.e., world, head, and gaze. (D) Reference frames: Design matrix that shows the factors of the different reference frames. Vectors from this matrix were used for the generation of refactored data in Figures 3C and 3D. For example, the factor of the head-centric reference frame is (1 + 3 − 2 − 4) / 2 in Experiment 1 and (5 + 7 − 6 − 8) / 2 in Experiment 2, whereas the factor of the world-centric frame of reference is (1 + 3 − 2 − 4) / 2 in Experiment 1 and (6 + 8 − 5 − 7) / 2 in Experiment 2.

access to the amplitude and direction of the impending saccade and can use this information to pre-activate even before visual information reaches their classical receptive field. The same process has also been found in the frontal eye fields (Sommer & Wurtz, 2006; Umeno & Goldberg, 1997, 2001) and visual cortex (Nakamura & Colby, 2002) using single-cell physiology, and similar responses have been demonstrated in humans in both parietal (Medendorp, Goltz, Vilis, & Crawford, 2003; Merriam, Genovese, & Colby, 2003) and visual cortices (Merriam, Genovese, & Colby, 2007) using functional imaging. Remapping has been suggested as a solution to visual stability (Melcher & Colby, 2008; Wurtz, 2008) because it could be used to keep track of where targets are in the world as the eyes move even though it is based on a retinotopic representation.

Psychophysical investigation of the feature content of remapping activity is possible using negative aftereffects, a prominent example of which is the tilt aftereffect (TAE). In this illusion, prolonged exposure to a tilted stimulus causes changes in the sensitivity of the visual system such that a subsequently presented vertical pattern will appear to be tilted in the direction opposite to the adapting pattern. This illusion lasts several seconds, so that the subject may make a saccade between adaptation and test. This allows researchers to investigate whether feature-specific information embodied as adaptation is remapped. If adaptation is remapped when we make a saccade, we should be able to find a TAE by testing in retinal locations that have not been stimulated but correspond to the world- or head-centric location of the adapting stimulus.

There have been reports that form and motion after-effects may also be remapped around the time of a saccade (Ezzati, Golzar, & Afraz, 2008; Melcher, 2007) in order to be aligned in a spatiotopic frame of reference (Melcher, 2005). The results for motion adaptation are controversial, however, as other studies find no evidence of spatiotopy, but report instead that the reference frame of motion adaptation is robustly retinotopic (Knapen, Rolfs, & Cavanagh, 2009; Wenderoth & Wiese, 2008).

In order to investigate the different reference frames involved in vision, it is necessary to separate the presentation of adaptation and test stimuli with an effector movement, such as a change in position of the stimulus on the screen (change in world location), or movement of the observer's gaze or head orientation. In our study here, changes in world position, gaze direction, and head orientation combine to provide coincidence, or lack thereof, between adaptation and test stimulus presentation in three different reference frames. This adaptation-test coincidence in different reference frames allows us to dissociate the importance of neural processing in retina-, head- and world-centric coordinate systems. Because the inclusion of head rotations requires special precautions, we separated our study into two experiments, one in which the head was held fixed and one in which the head was rotated between adaptation and test on every trial. The conditions in this experimental design are depicted in Figure 1. This design allows us to compare all relevant reference frames and the additional and independent effect of gaze direction (but not head direction) of the retinotopic TAE within experiments.

As we see from left to right in Figure 1A, in Experiment 1 there are conditions with correspondence of stimulus position between adaptation and test in (1) all three, (2) none, (3) head and world, and (4) retinal reference frames, respectively. In Experiment 2 (Figure 1B), head orientation is always changed between adaptation and test. This allows us to examine the difference between world- and head-centric reference frames. In the conditions of Experiment 2, there is correspondence between adaptation and test in (5) head and retinal, (6) world, (7) head, and (8) world and retinal, when seen from left to right. So, in total, all 8 possible combinations of the three reference frames are investigated.

In previous research that used only an eye movement to dissociate retinal and spatial positions (Ezzati et al., 2008; Knapen et al., 2009; Melcher, 2005, 2007, 2008a, 2008b; Wenderoth & Wiese, 2008), spatiotopic tests are at the same location in space but also at the same location in head-centered and body-centered coordinates. In these experiments, the eyes move to a new fixation spot following adaptation and the test is presented at the same spatial location as the adapting stimulus. Since the eyes have moved but the head has not, the locations that are considered spatiotopic (same in world coordinates) are also the same in head-based coordinates. Our present design enables us to disentangle eye, head, and world-spatial coordinates by separating the adapting and test stimulus by a change in world position, a change in gaze, and/or a change in head orientation.

Materials and methods

Experiments 1 and 2

Six participants (3 naive) took part in Experiment 1 and 6 in Experiment 2 (4 naive), age 20–42. Observers were seated in a silent and dimly lit room with the head positioned on a chin rest, 63 cm (Experiment 1) or 57 cm (Experiment 2) in front of a computer screen.

Experiment 1

Stimuli were presented on a gamma-linearized 22″ Formac ProNitron 22800 screen with a spatial resolution of 1440 by 1050 pixels and a vertical refresh rate of 100 Hz. Gaze position of the right eye was measured using an EyeLink 1000 Desktop Mount (SR Research, Osgoode, Ontario, Canada) with an average spatial resolution of

0.25 to 0.5 degrees of visual angle, sampling at 1 kHz. Saccades were detected using a two-dimensional velocity space algorithm (Engbert & Mergenthaler, 2006). The experiment was controlled by an Apple MacPro Xeon computer running custom software. Manual responses were recorded via a standard keyboard.

Stimulus presentation

The location of the fixation mark was 5 degrees left or right of the center of the screen. Stimuli were presented at −10, 0, or 10 degrees eccentricity on the horizontal midline of the screen. Thus, the distance from fixation to the adaptation or test stimulus was always 5 degrees, and the distance between adaptation and test stimuli was either 0 or 10 degrees in retinal or spatial coordinates. This stimulus layout is shown in Figure 2. Between adaptation and fixation, observers were required to make 2 saccades, one to an intermediate position above or below the center of the screen. The location (above, below) of this intermediate fixation mark alternated from trial to trial. This dual saccade approach serves to equate the number of saccadic transients (Nishida et al., 2003) that may influence perceptual adaptation (Ross & Ma-Wyatt, 2004).

Stimulus properties

Both adapting and test stimuli were Gabor patterns, with an envelope σ of 1.3 degrees of visual angle and a spatial frequency of 1.44 cycles per degree. Adaptation contrast was 100% to maximize the magnitude of the TAE (Parker, 1972), and the grating was cycled for one full period during the adaptation presentation. The direction of this cycling motion was drawn randomly for each trial. Test contrast was 50% in Experiment 1, to increase the magnitude of the TAE (Parker, 1972). Adaptation tilt in both experiments was ±15 degrees. The fixation stimulus consisted of a black circle, 14′ across, within which a 6′ colored disk was drawn. The color of the fixation mark indicated the phase of the trial to the observer. The fixation mark was red during adaptation and refixation phases, green during and before test stimulus presentation, and blue when the observers was to answer.

Adaptation duration was 3000 ms, observers were given 500 ms to fixate at the eccentric intermediate fixation position (see Figure 1), and 750 ms for reaching the fixation mark used during test stimulus presentation. Test presentation duration was 50 ms. After test stimulus presentation, observers responded using the arrow keys on the keyboard, indicating the perceived orientation of the test stimulus (tilted to the left or to the right).

Test stimulus orientation ranged from −4 to 4 degrees with 1-degree steps. Adaptation tilt, experimental conditions, test stimulus orientation, fixation position, and head orientation (in Experiment 2) were interleaved randomly. In Experiment 1, five sessions in which each condition was sampled 4 times were run for each observer, leading to a maximal total of 20 judgments per data point. Gaze position was recorded in all trials, and trials in which gaze position was outside a 2.5-degree radius around the intended fixation position at any single time point during the trial's adaptation or fixation phases, the trial was excluded from further analysis. This strict exclusion rule resulted in the deletion of 4.5 ± 1.5% of the trials. Saccade latencies for the first saccade were 123.3 ± 5.7 ms, and for the second saccade to the fixation location for testing it was 98.9 ± 7.6 ms.

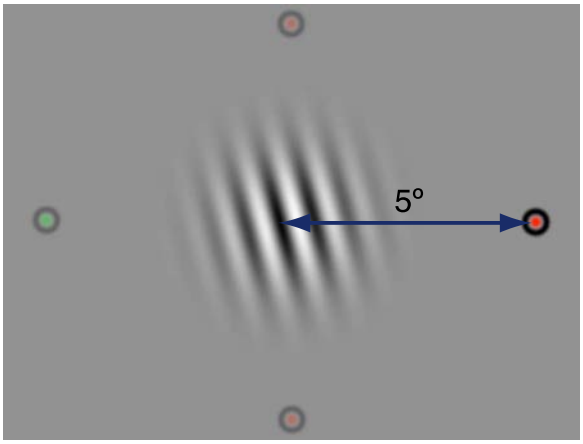

Figure 2. Stimulus image and fixation locations layout for Experiment 1. Intermediate fixation stimulus locations and possible test fixation location are shown using diminished opacity.

The remaining data were combined across adaptation tilt and fixation position for fitting of two parameters, standard deviation and mean (σ and μ) of a single cumulative Gaussian function, of which the mean represents the TAE. As expected, this resulted in almost identical results when compared to the difference between μ parameters of fits to data for both adaptation orientations separately. We chose to fit one function instead of two to improve fit reliability. This also enables bootstrapping of single fit results in order to calculate standard errors.

Experiment 2

All experimental parameters were identical to Experiment 1, except the following. Stimuli were presented on a 20″ Dell screen with a spatial resolution of 1024 by 768 pixels and a vertical refresh rate of 120 Hz. Gaze position of both eyes was measured using an EyeLink2 Head-mounted system (SR Research, Osgoode, Ontario, Canada). Three-dimensional head orientation was recorded using an optical motion tracker (LaserBird, Ascension), with the lightweight sensor worn on the EyeLink2 helmet that held it fixed to the head. The experiment was controlled by a Dell computer running custom software. Manual responses were recorded via a standard keyboard.

Stimulus presentation

Gaze angle and head angle were varied according to the design depicted in Figure 1. Head orientations were measured with respect to a near-vertical axis of rotation, calculated in a preliminary calibration procedure in which the subjects performed natural sideways head rotations. Orientation 0 corresponds to the subject directly facing the monitor, and positive orientations correspond to head turns to the right. Head orientations during adaptation and test were ±7 and ±7, or ±14 and 0 degrees, depending on conditions (see Figure 1). Thus, the change in head orientation was equal across conditions in this second experiment. Gaze orientation and retinal stimulus eccentricity was always ±7 degrees. During the 1-s interval between adaptation and test, observers were required to rotate their head to a designated angle. They were guided in their head rotation by a tone, whose frequency and spatial origin indicated the desired direction of head rotation, and which would attenuate as the observer's head approached the desired orientation, and which would stop altogether when the observer's head orientation was within 1 degree of the desired head orientation, indicating that the desired head orientation had been reached.

Test stimulus contrast was 100% and the adapting grating was not cycled in this second experiment. The fixation mark was a 6′ colored disk. The color of the fixation mark indicated, conjointly with the auditory signals provided, whether the observer's head orientation was within set limits (green when in range, red when further head rotation was required).

Adaptation duration was 3000 ms, 1 s was allotted to reach the desired head orientation for test stimulus presentation. Test presentation duration was 100 ms.

Both gaze and head orientations were recorded at the screen refresh rate for offline analysis. In conditions 5 and 6, observers made saccades to the second fixation point (latency 182 ± 2.4 ms), followed by a slower head movement; in the two other conditions, observers maintained fixation and moved their heads. Trials in which the observer failed to rotate the head into the desired range within the 1-s interval appropriated for the head rotation or in which gaze and head orientation deviation during adaptation and test was greater than the 95% confidence interval across all trials in that session were discarded from further data analysis.

Results

Experiment 1: Head fixed

Adaptation to tilt causes a subsequent vertical test pattern to appear to be tilted in the opposite direction: the TAE. Figure 3A shows the data for the first experiment, in which the head was fixed in all conditions. Clearly, strong TAEs occur only when the adapting and test stimuli coincide on the retina. This is confirmed by the significance of the retina effect in a repeated measures ANOVA ($F(1, 5) = 23.8$, $p < 0.01$). Although the difference between first and fourth bars could be interpreted as a replication of previous results (Nishida et al., 2003), in our model the factor of gaze does not reach significance ($F(1, 5) = 5.2$, $p = 0.07$), nor is there a significant interaction ($F(1, 5) = 1.4$, $p = 0.29$). After statistical analysis, these results can be further visualized by plotting the factors of the different reference frames and the effect of gaze by multiplying the data for each subject with the design vector of that factor as given in Figure 1D. For instance, to generate the value for the head-centric frame of reference this becomes the multiplication of data in conditions $(1 + 3 - 2 - 4) / 2$ and for retinal it is $(1 + 4 - 2 - 3) / 2$. The gaze dependency effect is recovered from the retinotopic TAEs, that is, from conditions 1 and 4. Replotting the data in this manner emphasizes visually what was clear from the statistics: the TAEs found in Experiment 1 are solely retinotopic.

Experiment 2: Head shifted

The data for the second, head-moving experiment is depicted in Figure 3B. Again, by far the largest values for the TAE occur in situations where the adapting and testing stimulus coincide in terms of retinal position (5 and 8). There is a slight difference between conditions 6 (correspondence in world coordinates) and 7 (correspondence in head coordinates), which differ in terms of the factor of gaze, albeit in conditions where there is no retinal overlap between adaptation and test. This factor of gaze does not reach significance in a repeated measures ANOVA ($F(1, 5) = 1.4$, $p = 0.28$). As in Experiment 1, the retinal factor is significant ($F(1, 5) = 13.6$, $p = 0.01$) and the interaction between factors is not ($F(1, 5) = 1.7$, $p = 0.25$). As in Figure 3C, in Figure 3D we replot the data by multiplying the vector of the design for all head-shifted conditions for visual emphasis. The gaze dependency factor is computed from conditions 5 and 8, and by means of example, the world reference frame factor is computed as follows: $(6 + 8 - 5 - 7) / 2$, as can be gleaned from Figure 1D. Again, the results of this computation show that the retinotopic frame of reference is the only significant factor.

Discussion

We have conducted two experiments that determine the coordinate frame of the tilt aftereffect. Specifically, we differentiate between the retinotopic and head- and world-centric frames of reference. The data from our

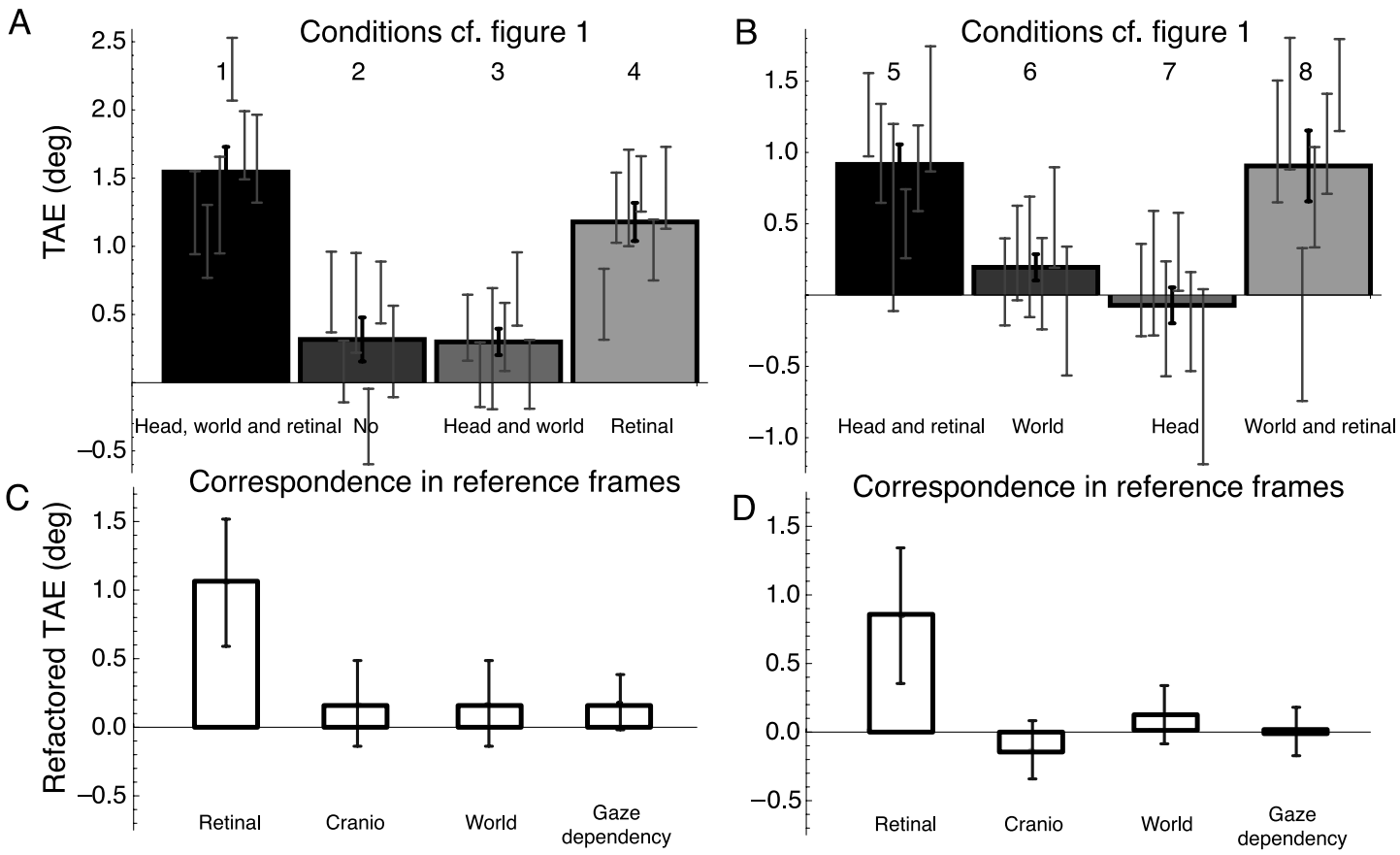

Figure 3. (A) Results of Experiment 1. TAE magnitude in the four different conditions depicted in Figure 1A. TAE magnitude is greatest in the conditions in which the test stimulus coincided with the adapting stimulus on the retina. There is hardly any TAE when the test stimulus and adapting stimulus do not coincide on the retina (second and third bars). (B) Results of Experiment 2. TAE magnitude in the four different conditions depicted in Figure 1B. As in Experiment 1, TAE magnitude is greatest in those conditions in which test and adapting stimuli coincided on the retina (first and fourth bars). Black error bars indicate the standard error across subjects. The light gray error bars indicate the mean and the standard error on the fitted mean (1000-fold bootstrap) for each subject separately. (C, D) Refactored TAEs for Experiments 1 and 2, respectively. We multiply the design vector for each of the reference frames of interest (see Figure 1D), including the gaze correspondence, with the data on a per-subject bases. This distilled data we plot with error bars that signify 95% confidence intervals, allowing direct visual assessment of the different reference frames' roles. Clearly, only the retinal frame of reference is of importance.

two experiments show unequivocally that the coordinate frame for the tilt aftereffect is principally retinotopic. We find no evidence of adaptation in the reference frames of head or world. Thus, our results point strongly to a dominant role of mechanisms in lower, retinotopically organized visual areas as the neural substrate for adaptation to orientation.

Our experimental design was intended to investigate the role of different reference frames in the generation of the TAE. Independently of the question of reference frame, a related question is whether a change using an effector such as the eye, the head, or the world has an impact on the TAE. Full investigation of the effect of effector changes would require a different set of experiments that would be outside the scope of the present paper. However, in our experimental design, we can investigate the effect of gaze on the retinotopic TAE. In both our experiments, there is a trend toward larger TAE when gaze direction remains the same in both adaptation and test. This effect could be mediated by the known dependence of neural activity on gaze direction even in the lowest levels of visual cortex (Galletti & Battaglini, 1989; Rosenbluth & Allman, 2002; Trotter & Celebrini, 1999). This trend is in accordance with previous psychophysical results showing gaze dependence of the TAE (Nishida et al., 2003). This effect of gaze difference on the magnitude of the TAE reaches borderline significance at the gaze difference used in our main experiment. To more directly compare Nishida et al.'s (2003) study with our own present study, we conducted a control experiment to investigate the influence of gaze difference between adaptation and test (details of the experiment are described in Appendix A).

In our control experiment, we increase the gaze angle difference parametrically and replicate Nishida et al.'s results by finding a significant dependence of TAE on gaze difference between adapt and test.

Rieser and Banks (1981) found that the TAE occurs in a retinal frame of reference under conditions of head rotations about the line of sight. In their study, the TAE was fully retinotopic, and any world-referenced results were due to extravisual head orientation adaptation. The threshold elevation aftereffect also occurs in a retinal frame of reference when rotations of the head about the line of sight are used to distinguish reference frames (Findlay & Parker, 1972; Mitchell & Blakemore, 1972).

We investigate the importance of the separate frames of reference that play a role in our TAE experiments. In our results, there is a very dominant influence of the retinal reference frame in the TAE (see Figure 3). Using head movements, we can distinguish whether the computations underlying the tilt aftereffect extend beyond retinotopic processing in a head-centered or a body- or world-centered (spatiotopic) frame of reference, if any.

These results are most readily understood from the visualization shown in Figures 3C and 3D. This figure shows the weights of the factors for the three reference frames in question and indicates that there is no role for head-centric nor world-centric processing in the generation of the TAE: only the retinal frame of reference is of importance.

The absence of a spatiotopic effect in both our experiments differs from previous results (Melcher, 2005, 2007, 2008a, 2008b). Based on these earlier results, Melcher (2005, 2007, 2008a, 2008b) and his colleagues proposed that information regarding visual features, such as the gain control settings for those features (their adaptation), is remapped on retinotopic representations around the time of each saccade to remain aligned with their locations in space (Melcher, 2007; Melcher & Colby, 2008). We explored these empirical claims and the possible sources of differences between the earlier results and our own by replicating the experimental conditions of Melcher's experiments. Using code and details of experimental procedures provided by Dr. Melcher, in several experiments we were unable to replicate the reported pattern of results. We are therefore at a loss concerning the source of the difference between Melcher's results and our own. Detailed methods and results for this set of experiments are presented in Appendix A.

Information intimately linked to navigation and perception of space for motor behaviors is known to be analyzed in higher level areas (Colby & Goldberg, 1999; Snyder et al., 1998), and it is thus not surprising that these areas take into account not only visual information but also different forms of proprioceptive information to create a role for other than retinal reference frames (Bradley, Maxwell, Andersen, Banks, & Shenoy, 1996; Crowell, Banks, Shenoy, & Andersen, 1998). For visual feature information, which is analyzed in a frame of reference bound to the retina, the situation is likely very different. For instance, eye movements can be made to any target in the visual field, and it is known that adaptation to orientation takes place in primary visual cortex (Dragoi, Rivadulla, & Sur, 2001; Dragoi, Sharma, & Sur, 2000; Jin, Dragoi, Sur, & Seung, 2005). This means that remapping of adaptation would require that the modified, adapted state of neurons that is thought to be the substrate of perceptual aftereffects (Clifford et al., 2007; Jin et al., 2005; Kohn & Movshon, 2003, 2004; Schwartz, Hsu, & Dayan, 2007) be transmitted horizontally through the brain in any direction and amplitude depending on the impending eye movement, necessitating a very dense connectivity in lower level visual cortex for which there seems to be no neurophysiological evidence.

Our results indicate that adaptation to stimulus features occurs only at the retinotopic levels of the visual hierarchy that are known to be involved in analysis of features such as orientation (Hubel & Wiesel, 1959). In this regard, our results dovetail very well with other recent results in face adaptation (Afraz & Cavanagh, 2008, 2009) and motion adaptation (Knapen et al., 2009; Wenderoth & Wiese, 2008). Lastly, our results suggest that the remapping process that plays a role in visual stability (Duhamel et al., 1992) is unlikely to involve a remapping of feature gain control settings that underlie the perceptual effects of adaptation.

Appendix A

Additional experiments

Spatiotopicity of the TAE?

We also performed several additional experiments to investigate the origin of the difference between our results and those reported previously (Melcher, 2005, 2007, 2008a, 2008b).

Additional conditions

Figure A1 shows the design we used based as closely as possible on Melcher's original experiment (Melcher, 2005), and the resulting data after 5 s of adaptation in 4 subjects. Stimulus parameters were identical to our Experiment 1. These results fail to show any significant spatiotopic TAE. Dr. Melcher kindly showed us a new procedure that he felt was even more successful and sent us experimental code as well. Using this second design, observers adapted in the periphery and then saccaded to the adapting stimulus' location on the screen, where they judged the tilt of the test, now presented at the fovea (rather than the original adaptation at the fovea with test in the periphery; Melcher, 2005). We randomly interleaved

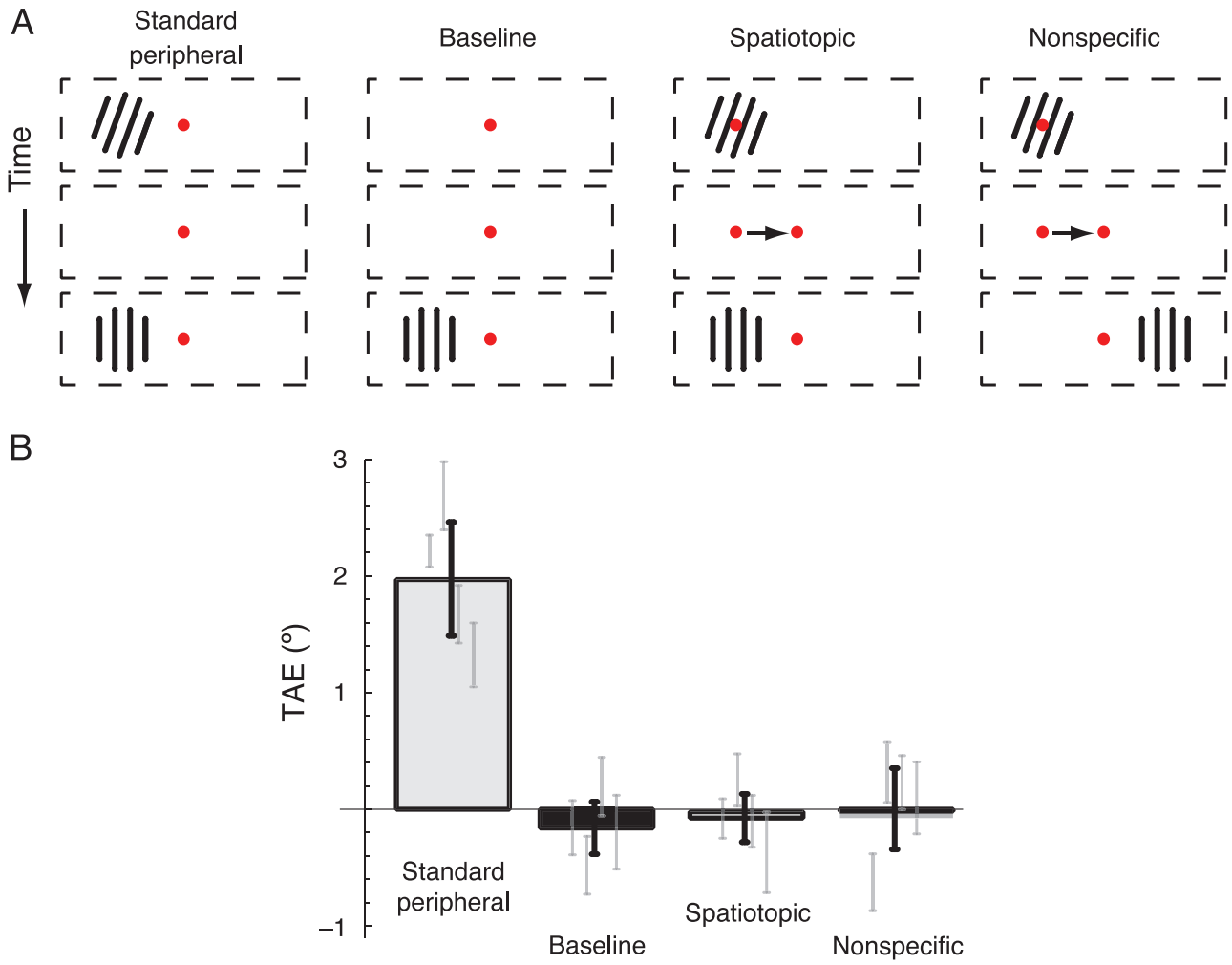

Figure A1. Spatiotopic TAE experiment following Melcher's original design: Conditions and results. (A) Experimental design as used by Melcher and duplicated here. (B) As in our Experiment 1, the retinotopic condition produces a strong TAE. None of the baseline, spatiotopic, and opposite conditions show any TAE. Black error bars indicate the standard error across subjects. The light gray error bars indicate the mean and the standard error on the fitted mean (1000-fold bootstrap) for each subject separately.

these conditions, the original and this new procedure as depicted in the top row of Figure A2A. That is, in half of the trials, adaptation was peripheral (left column) and test foveal, whereas in the other half of the trials, adaptation was foveal and test peripheral (right column, original design; Melcher, 2005).

Whereas strong retinotopic TAEs were found using both paradigms, neither experimental paradigm yielded significant spatiotopic TAEs. For adaptation in the periphery and test at the spatiotopic location (the new design), there is a significant TAE, but when corrected for the non-specific TAE this result disappears (*t*-test left column, $p = 0.08$), indicating that, as in the second experiment, the effect can be accounted for by spatially general non-specific adaptation. The original design (Melcher, 2005) yields a spatiotopic TAE in neither corrected nor uncorrected form (shaded right column, Figure A2A). The bottom row shows the true spatiotopic TAE, corrected by subtracting the non-specific TAE for each observer, identified by their initials, separately.

Presentation sequence

Another difference between our experimental approach and that of Melcher is that in our experiments all conditions were interleaved, whereas in his they were blocked per session. We therefore repeated our experiment blocking conditions in a single session. A finding of a spatiotopic TAE in the blocked design, but not in the interleaved design, would indicate that expectancy regarding the location of stimulus reappearance plays a role in the spatiotopic TAE. Figure A2B shows that there is no spatiotopic TAE when employing the blocked presentation sequence, either. This indicates that differences in results are not due to a difference in presentation sequence. Again, the spatiotopic TAE corrected for the non-specific TAE is shown in the bottom row for individual subjects.

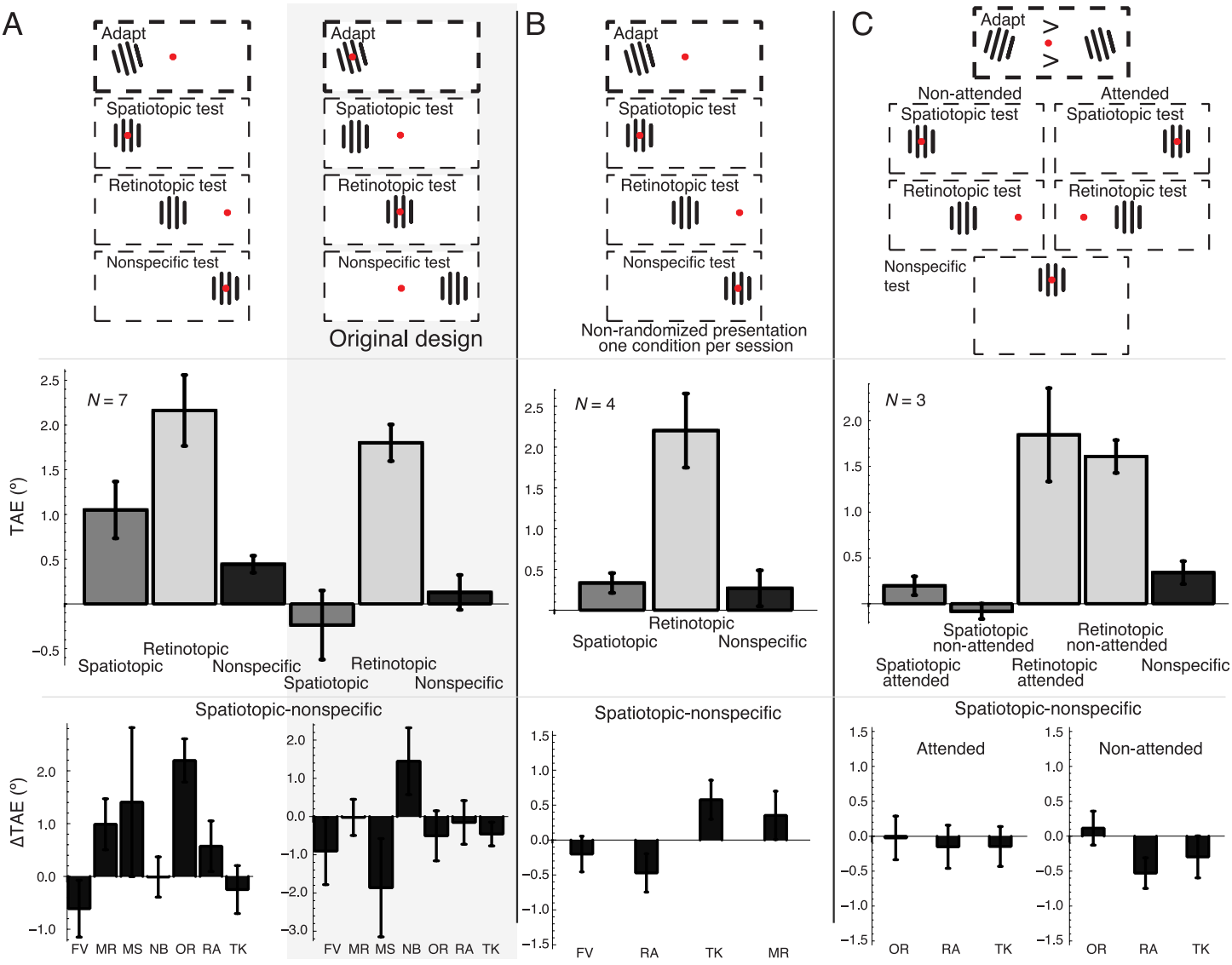

Figure A2. Extra experiments: Conditions and results. (A) Original and inverted experimental design of the spatiotopic TAE experiment. Adaptations in the periphery (left column) and in the fovea (right column, original design) yield similar results. The "spatiotopic" TAE does not reach significance in either case, when corrected for the non-specific TAE. Corrected spatiotopic TAEs are shown on a per-subject basis in the bottom row. (B) When using a blocked design, presenting only stimuli from a single condition in one session, the results are similar to those found when using a randomized presentation sequence (A, left column, and Figure 1, top row). (C) Control experiment: attention. Attention was directed at one of two oppositely tilted gratings at either side of fixation, as indicated by two arrow signs above and below fixation. Observers were instructed to count the number of contrast decrements (4 or 5) in the attended stimulus. After this peripheral adaptation, a saccade was made to either the attended or non-attended stimulus, and a test stimulus would be presented at either a spatiotopically or retinotopically corresponding location. Again, a strong retinotopic TAE is evident, and its magnitude is not greatly dependent on attention. In addition, whether or not attention was directed to the adapting stimulus location, no significant spatiotopic TAE is found.

Attentional control

As suggested by Melcher (2008b), the spatiotopic TAE may rely on remapping processes that are known to be specific to task-relevant (attended) targets (Goldberg, Bisley, Powell, & Gottlieb, 2006; Gottlieb, Kusunoki, & Goldberg, 1998). To investigate whether we can find a spatiotopic TAE when attention is explicitly directed to a stimulus, we conducted the experiment depicted in Figure A2C (top row). With two adapting stimuli at equal distance from fixation, a central cue indicated to the observer to which of the two stimuli should be attended. During the adaptation interval 4 or 5 Gaussian-enveloped contrast decrements (σ = 100 ms, contrast decrement = 0.75) occurred in this stimulus, which the observer had to count. After adaptation, the observer made a saccade to either the screen location where the attended stimulus had been, or the opposite side, where an opposite-orientation

adaptation stimulus had been presented. After this saccade, a test was presented either at the spatiotopically corresponding location of the attended or non-attended stimulus, or at a retinotopically corresponding location. An additional condition tested, as in the other experiments, the non-specific TAE. The fixation mark changed position to a location on the screen with the same distance to the initial fixation position, but above or below the center of the screen. The observer saccaded to that location and the test stimulus was presented there, as was the case in the spatiotopic conditions. Results are shown in the middle row of Figure A2C. In the retinotopically corresponding locations, there are strong TAEs in both the attended and non-attended conditions. In the spatiotopically corresponding locations, there was no TAE, whether attention had been explicitly directed to the adapting stimulus or not: in both cases the TAE was not significantly different from that found using the non-specific test. In all these additional experiments, parameters were identical to those stated for the main Experiments 1 and 2 with the exception of two parameters that were changed to match exactly those in the experimental code furnished by Dr. Melcher. Size of the stimuli was changed to $\sigma = 0.8$ degrees of visual angle and spatial frequency was changed to 2.16 cycles per degree. Adaptation duration was 4 s in all additional experiments. In all experiments, eye movements were recorded and analyzed. As in the first experiment, gaze position was recorded in all trials, and trials in which gaze position was outside a 2.5-degree radius around the intended fixation position at any single time point during the trial's adaptation or fixation phases, the trial was excluded from further analysis. Note that subjects showing a spatiotopic TAE in the experiment in Figure A2A in the peripheral-adaptation, changed experimental paradigm fail to show the same pattern of results upon retesting (Figures A2B and A2C). This variability was typical for spatiotopic TAEs indicating that the results that did reach significance for some subjects in some sessions were due to chance variations. In contrast, retinotopic TAEs were all significant, all the time, showing that the tilt aftereffect is robustly retinotopic and shows no evidence of spatiotopy.

Gaze dependency of the TAE

We performed two control experiments to investigate whether the difference in gaze angle between adaptation and test influences the size of the retinotopic TAE in a parametric way. We used a pair of oppositely oriented stimuli, above and below fixation, as both adapting and test stimuli replicating the stimulus arrangement by Nishida et al. (2003). We used custom software on a

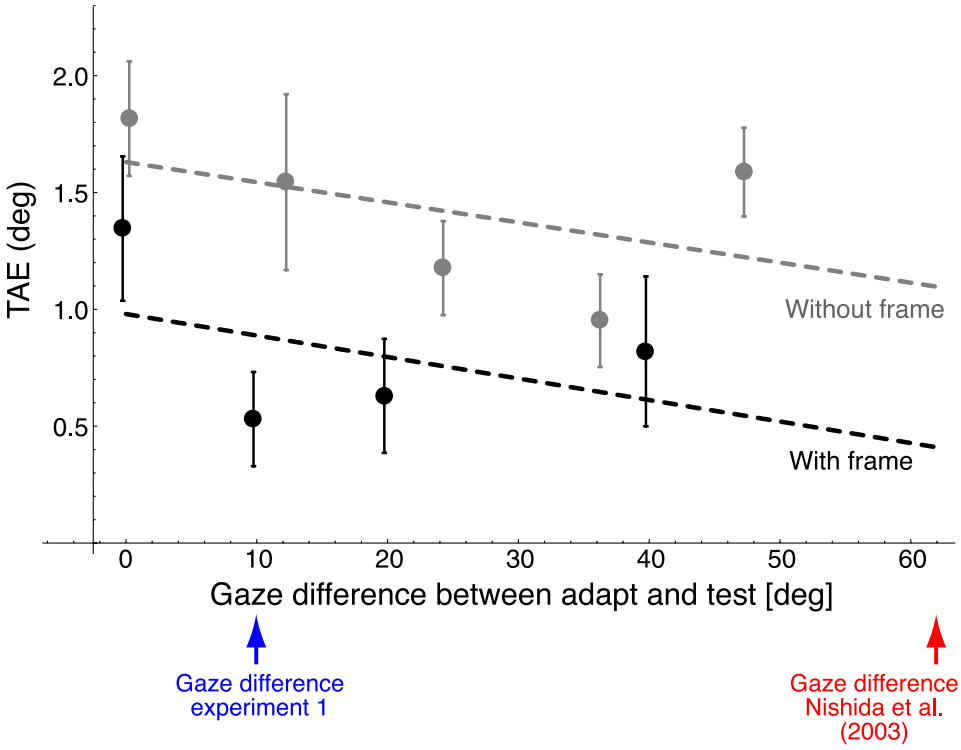

Figure A3. Gaze dependency of the TAE in our experiment. As difference in gaze angle between adaptation and test increases, the strength of the TAE decreases. Dashed lines result from the statistics as described in the text, for both experiments separately. Note that both slope and offset were fitted in both experiments: there is highly similar change with gaze angle difference both with and without the addition of a surrounding frame. The blue vertical arrow at 10 degrees difference indicates the gaze difference used in our Experiment 1, the gaze difference value used by Nishida et al. (2003) is depicted by the red arrow.

Macbook Pro displaying stimuli on a single Dell 20″ LCD screen running at a resolution of 1600 × 1200 and a refresh rate of 60 Hz, placed at 31-cm distance, subtending 62 degrees in width. This allowed us to parametrically increase the gaze difference between adaptation and test over a range large enough to investigate the difference between our main results and the results by Nishida et al. (2003), who used a difference in gaze of 62 degrees. We ran two experiments; one in which the full screen was of mean luminance as in all our experiments, the other in which the two stimuli were surrounded by a frame of mean luminance, with the screen at the lowest luminance setting (black), as in Nishida et al. (2003). In both control experiments, adaptation and test were separated by two saccades, as in our Experiment 1. The adaptation stimulus was presented on one side of the screen and the test stimulus was presented at distances of 0, 12, 24, 36, or 47 degrees away (no frame experiment), or 0, 10, 20, or 40 degrees away (frame experiment). Stimulus size, spatial frequency, contrast, adaptation tilt, test stimulus tilt range, and distance between fixation and stimuli were identical to our previous experiments. Adaptation duration was 5 s. The width of the surrounding frame was 4.5 times the standard deviation of the Gabors, and the height was 9 times the standard deviation. Four subjects ran in both experiments; 3 were naive in each (Figure A3).

Both with and without a frame around the stimulus, our data show that the retinotopic TAE decreases with the increase in gaze away from the direction held during adaptation (without frame linear regression slope = −0.0086 deg TAE per deg gaze difference, $t = -2.94$, $p = 0.03$ with frame slope = −0.0092 deg TAE per deg gaze difference, $t = -2.90$, $p = 0.03$). This set of experiments replicates the gaze dependency of the TAE found by Nishida et al. (2003) and supports our claim that our gaze contingent TAE was smaller because the gaze change in our experiment was smaller.

Additional information

The authors declare no conflict of interest. Observers gave informed consent for their participation.

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