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Tilt representation beyond the retinotopic level

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We perceive a stable visual world, which enables successful interaction with our environment, despite movements of the eyes, head, and body. How are such perceptions formed? One possibility is that retino-centric visual input is transformed into representations at higher levels, such as head-, body-, or world-centered representations. We investigated this hypothesis using the tilt aftereffect in a balanced adaptation paradigm designed to isolate head-, body-, and world-centered aftereffects. Observers adapted to two oppositely tilted stimuli, each contingent on one of two different gaze, head, or body directions. We found aftereffects contingent on gaze direction, but not head or body direction. This demonstrates that adaptable tilt representations exist in a head-centric frame but not in higher reference frames. These aftereffects may be attributed to adaptation of retinotopic tilt-sensitive neurons whose responses are modulated by gaze direction (gain fields). Such neurons could support functionally head-centric tilt representations and are found as early as V1. On the basis of our results we would not expect activity in tilt-sensitive neurons to be modulated by head or body direction. The balanced adaptation paradigm is a useful tool for examining properties of the process responsible for gaze modulation of activity in visual neurons.

Introduction

Maintaining a stable impression of the visual world despite movements of the eyes, head, and body requires that retinotopic visual input is interpreted taking these movements into account. How our spatial constancy is achieved is a topic of debate (Galletti, Battaglini, & Fattori, 1993; Duhamel, Bremmer, BenHamed, & Graf, 1997; O'Regan & Noë, 2001; Cavanagh, Hunt, Afraz & Rolfs, 2010; Burr & Morrone, 2011; Land, 2012; Turi & Burr, 2012). In principle, by registering the positions of the eyes in the head, the head on the body, and the body in the world, representations may be generated by transforming visual information in retinotopic coordinates into head, body, and world coordinates. However, which visual information is transformed, and how it may be represented within higher level reference frames, is not yet clear.

At the lowest level in the hierarchy, retinotopic representations of the visual world are formed by detailed analysis of visual information that encodes low-level properties such as tilt and contrast. Transformation to a higher level reference frame may not preserve all of these properties. For example, at a high level, the locations of objects relative to the body are encoded in an egocentric memory representation, but these representations are more limited than those that form our perceptual experience (Tatler & Land, 2011). Thus, some features represented at lower levels may not be represented at higher levels, or may be encoded differently.

Evidence for transformation of visual feature representations from the retinotopic level to a head-centric or higher level has been mixed. Some psychophysical studies have found various visual aftereffects (AEs) at an adapted spatial location following a saccade, suggesting certain details are represented beyond the retinotopic level (tilt, form, and face AEs: Melcher, 2005; motion AE: Ezzati, Golzar, & Afraz, 2008; positional motion AE: Turi & Burr, 2012). However, others have provided strong evidence for retinotopic, but not head-centric or higher representations of various low-level visual features (direction AE: Wenderoth & Wiese, 2008; motion AE: Knapen, Rolfs, & Cavanagh, 2009; tilt AE: Rieser & Banks, 1981; Knapen, Rolfs, Wexler, & Cavanagh, 2010; Mathôt &

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Theeuwes, 2013). Evidence from imaging studies investigating the types of reference frames found in visual areas is also mixed. Some functional magnetic resonance imaging (fMRI) evidence has indicated that spatial maps in early visual areas are strongly retinotopic, not head-centric or higher (Gardner, Merriam, Movshon, & Heeger, 2008), while others have reported fMRI evidence of mapping beyond the retinotopic level, which is dependent on attention (Crespi, Biagi, d'Avossa, Burr, Tosetti, & Morrone, 2011). It is not yet clear how visual information might be represented beyond the retinotopic level.

However, a well-established key finding from electrophysiological studies has given an important insight into how coordinate transformations may be performed in the cortex. Sensitivities of many retinotopic neurons are modulated by two-dimensional (2-D) gaze direction, and networks of such neurons may be important in solving problems of spatial constancy. Andersen and Mountcastle (1983) found retinotopic neurons in macaque posterior parietal cortex whose activity was modulated by 2-D gaze direction during visual attention. This retinotopic gain field behavior can, in principle, allow the encoding of visual stimuli in a functionally head-centric way by combining retinotopic location with gaze direction extracted from the population activity (Andersen, Essick, & Siegel, 1985; Weyland & Malpeli, 1993; Bremmer, Schlack, Duhamel, Graf, & Fink, 2001; Merriam, Gardner, Movshon, & Heeger, 2013). Electrophysiological studies have also found parietal gain-field behavior for changes in eye-in-head, head-on-body, and body-in-world direction (Brotchie, Andersen, Snyder, & Goodman, 1995; Snyder, Grieve, Brotchie, & Andersen, 1998), suggesting possible head-, body-, and world-centered representations mediated by parietal cortex. In occipital cortex, gaze gain field behavior is found in visual neurons even in the earliest visual cortical areas. It has been found in primary visual cortex in cats (Weyland & Malpeli, 1993), in several early visual areas in macaques (Galletti & Battaglini, 1989; Trotter & Celebrini, 1999; Rosenbluth & Allman, 2002), and has been observed using fMRI in human retinotopic visual cortical areas (Merriam et al., 2013).

Psychophysical evidence for gaze modulation of visual responses has been found using adaptation paradigms (Nishida, Motoyoshi, Andersen, & Shimojo, 2003; Knapen et al., 2010). Nishida et al. (2003) found that motion, tilt, and size aftereffects were all reduced by approximately 15% when the test was presented at the same retinal location as the adaptor, but at a different gaze angle, 62°, away. Mayhew (1973) used a balanced adaptation paradigm in which observers alternated their gaze every few seconds between two oppositely rotating adaptation stimuli: one rotating clockwise at 20° to the left of the midline and the other rotating counterclockwise at 20° to the right. In this paradigm, adaptation to the retinotopic information alone should balance out and produce no net aftereffect. Instead, opposite aftereffects were found which had co-developed, contingent on the gaze direction of the stimuli. Gaze-contingent effects produced by balanced adaptation have since been found for depth and color (Nieman, Hayashi, Andersen, & Shimojo, 2005). These opposing gaze-contingent aftereffects provide psychophysical evidence for joint encoding of visual features and gaze direction. These aftereffects cannot be ascribed to a purely retinotopic reference frame; however, it has not been established which higher reference frame(s)—head-centric, body-centric, world-centric, or some combination of these—may be used in representing visual features. Identifying the frames of reference used in perceptual representations and examining how such representations may be produced is fundamental to the understanding of spatial constancy. We address these questions in the present study.

We used a balanced adaptation paradigm to investigate the use of gaze, head, and body direction information in the construction of visual representations. By balancing adaptation across specific reference frames (retino-centric, head-centric, and body-centric) we can factor them out and therefore potentially expose aftereffects occurring in remaining unbalanced reference frames. We examined the tilt aftereffect since orientation is a fundamental visual attribute, and we examined gaze, head, and body direction contingent tilt adaptation conditions, which have not been investigated previously.

Methods

Apparatus and stimuli

Stimuli were presented on each of two 19-in. CRT monitors (Mitsubishi Diamond Pro 920, 1024 × 768 pixels, 100-Hz vertical refresh rate). The two monitors' luminance profiles were linearized and their luminance range and chromaticity were matched as closely as possible using a CRS Colorcal colorimeter (Cambridge, UK) to rule out aftereffects contingent on these properties (Mayhew & Anstis, 1972). White-level luminance was 40.78 versus 40.63 cd/m^2 and CIE1931 coordinates were [0.302, 0.325] versus [0.300, 0.328]. The monitors were placed one to the left (–30°) and one to the right (30°) of the observer's head at a distance of 114 cm in the arrangement shown in Figure 1. Observers placed their head on a sturdy chinrest and performed the experiments standing, except Experiment 3 where they were seated. Head and body orientation was monitored using a Polhemus FASTRAK device (Colchester, VT). Head orientation was

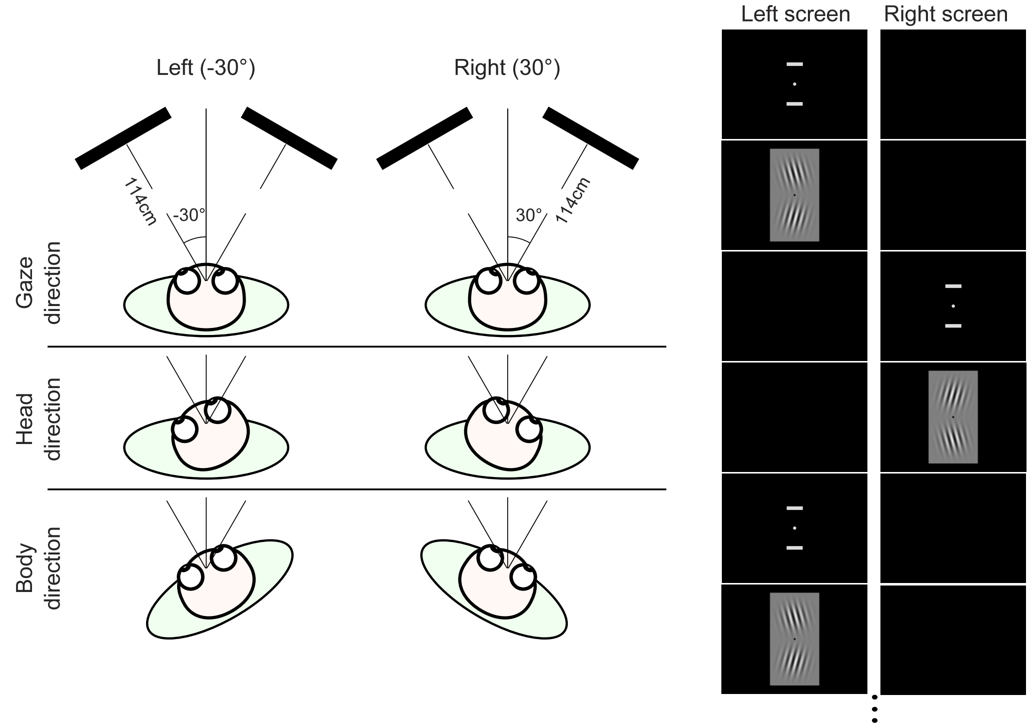

Figure 1. Left panel: Arrangement of the monitors and viewing conditions used in the experiments (not to scale). Observers viewed stimuli presented alternately on the left and right monitors, either alternating their gaze direction, head direction, or body direction. Right panel: During adaptation, observers adapted to oppositely tilted stimuli alternately on the two monitors. Before a stimulus was presented, realtime feedback on head and body direction was presented via icons above and below fixation, respectively, to ensure correct alignment. A horizontal bar indicated correct alignment; otherwise an arrow indicated the direction of head or body adjustment required. The tilted Gabor configuration on the left screen in this Figure (top counterclockwise from vertical, bottom clockwise) is coded negative and predicts a negative contingent tilt aftereffect. The signs are reversed for the stimuli on the right screen.

measured with a sensor fixed to a baseball cap. Body orientation was measured with a sensor fixed to a small plinth held tightly against the sternum with a four-point harness. The experiments were performed in a lightproof room and nothing other than the stimuli was visible. This ruled out the possibility of aftereffects contingent on other contextual visual properties (e.g., Potts & Harris, 1975). Stimuli were generated using MATLAB with PsychToolbox (Brainard, 1997).

Adaptation stimuli

Adaptation stimuli comprised a pair of Gabors, one above the other, on a gray background, as in Figure 1 (right panel). Upper and lower Gabors were tilted in opposite directions within an image. Stimuli presented on the right monitor had opposite tilts to those presented on the left. The tilt of each Gabor was either +15° (clockwise) or −15° (counterclockwise), chosen since the tilt aftereffect typically peaks for adaptor tilts between 10° and 20° (Howard & Templeton, 1966). Grating spatial frequency was 1.44 cpd, gaussian standard deviation was 1° and center-to-center separation between the two Gabors was 5.5°. The Gabors were shown on a gray rectangular background ($20.2 cd/m^2$, 6 × 11.6°). The phases of the two gratings were modulated sinusoidally in opposite directions at 1 Hz to prevent build-up of negative afterimages. The duration of each adaptation stimulus was 10 s (which is sufficient to produce a conventional tilt aftereffect; Gibson & Radner, 1937) and contrast was 100% in all experiments except Experiment 4, which included a contrast-change detection task during adaptation.

Test stimuli

Test stimuli had the same configuration as the adaptation stimuli. Upper and lower test Gabors were tilted in opposite directions by equal amounts. Their relative tilt varied between trials according to a staircase procedure. The background was presented 500 ms before Gabor onset. The test Gabors were shown at 50% contrast since larger tilt aftereffects are produced with lower contrast test stimuli (Parker, 1972). The test Gabors had a relatively short duration of 100 ms because previous studies have found such short durations produce larger tilt aftereffects (Wolfe, 1984; Harris & Calvert, 1989).

Procedure

An experimental session had three phases: preadaptation test, adaptation, and postadaptation test phases.

Preadaptation test phase

In the preadaptation test phase, a trial began with a fixation marker presented on one of the two monitors. Icons above and below the fixation marker provided feedback on whether the head and body were correctly oriented as per instructions specific to the experimental session. After 3 s, if the head and body were correctly oriented to within 2°, then a test stimulus was presented on the same monitor. Pilot work established that 3 s was sufficient time for participants to correctly orient themselves in all the conditions tested here, so 3-s intervals were used in gaze, head, and body direction conditions to ensure the same timing of presentation across conditions. The observers' task was to identify, for each test image, the relative tilt direction between upper and lower Gabors and respond via a joypad. After the response the next trial began on the other monitor, thus test stimuli were presented on each monitor in alternation. The relative tilt between the Gabors in a test image was varied using a staircase procedure to estimate apparent collinearity for test stimuli presented on left and right monitors (i.e., one staircase for the left monitor and another for the right monitor). Test stimuli were presented on alternate monitors until at least eight reversals (six in Experiment 2) had been obtained in both the left monitor staircase and the right monitor staircase. Apparent collinearity estimates for left and right monitors were calculated from each final pair of reversals in each staircase.

Adaptation and postadaptation test phases

The adaptation phase followed immediately from the preadaptation test phase. In the adaptation phase, stimuli were presented alternately, and with opposite tilt, on the left and right monitors as shown in Figure 1 (right panel). Observers viewed each in turn, either alternating their gaze, head, or body direction according to the instructions for the particular session. Only one of the three conditions—gaze, head, or body direction—was tested in a given session. Fourteen adaptation stimuli were presented in total during the adaptation phase: seven on one monitor and seven oppositely tilted counterparts on the other. Before each stimulus, accurate head and body orientation was established before presenting the adaptation stimuli, in the same way as described for the preadaptation stimuli.

After the adaptation phase, postadaptation tilt estimates were obtained as described for the preadaptation test phase. Again, a separate staircase was run for left and right monitors and just as before, this phase continued until eight reversals (six in Experiment 2) had been obtained in both left and right staircases. To prevent dissipation of aftereffects, each test stimulus was preceded by two top-up adaptation stimuli, one on each monitor beginning on the left or right (e.g., top-up-left, top-up-right, test-left). This allowed us to distinguish whether aftereffects were in fact contingent on the monitor direction (i.e., aftereffect sign predicted by top-up-left in this example), or merely based on the adaptation stimulus immediately preceding the test (i.e., aftereffect sign predicted by top-up-right in this example) since the two possibilities predict different signs. The order of the two top-up stimuli alternated between each test stimulus to maintain balanced adaptation. Each session tested one condition and lasted approximately 30 min. Observers only ever performed one session in a 24-hr period. The number of sessions differed for each experiment (see below).

Aftereffects were calculated separately for left and right monitors as the change between pre- and postadaptation collinearity estimates (i.e., the preadaptation data served as a baseline). Preadaptation values were close to 0° on average so we only show the aftereffects here. Pre- and postadaptation data are shown in Supplementary Figures S1 and S2.

Experiment 1: Tilt adaptation contingent on gaze direction

In Experiment 1 we sought initially to establish whether visual tilt adaptation is contingent on gaze direction, as has been found with aftereffects of motion, depth, and color. Gaze-contingent tilt aftereffects would implicate tilt representations at head-centric or higher levels of representation.

Method

Participants

Ten observers (eight males) aged 18–60 years ($M = 25.1$, $SD = 12.7$) participated in Experiment 1. All had normal or corrected vision.

Procedure

Observers performed one experimental session, testing the gaze direction condition in which tilt adaptation was balanced across gaze direction using stimuli shown in Figure 1 (right panel).

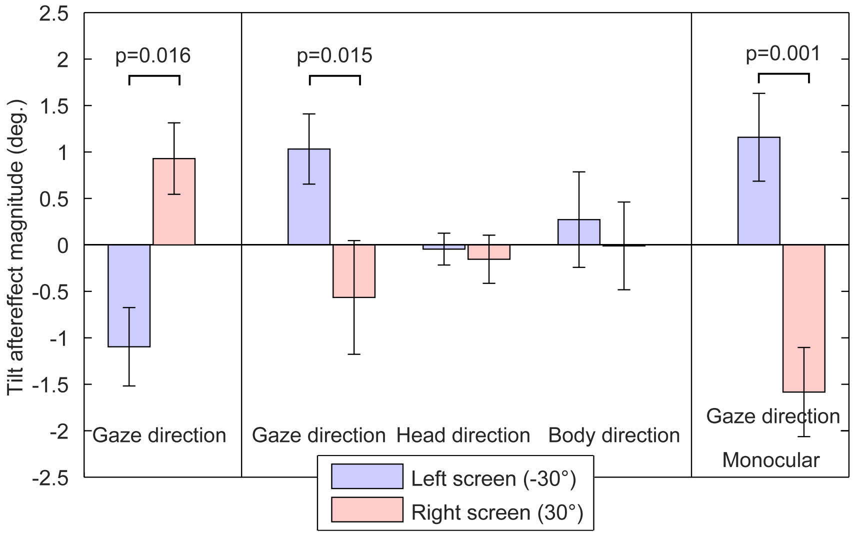

Figure 2. Left panel: Tilt aftereffect results from Experiment 1 ($N = 10$). Middle panel: Results from Experiment 2 ($N = 11$). Right panel: Results from Experiment 3 ($N = 7$). Error bars indicate ±1 *SEM*.

Results

Results of Experiment 1 are shown in the left panel of Figure 2. These results show that tilt adaptation balanced across two viewing directions elicited opposing tilt aftereffects contingent on viewing direction, $t(9) = -2.952$, $p = 0.016$. The aftereffects on left and right monitors have the same signs as the adaptors on left and right monitors, as predicted by contingent adaptation. Had we found effects with opposite signs, this would have indicated conventional aftereffects (i.e., ones simply based on the adaptation stimulus immediately preceding the test). These findings of aftereffects contingent on viewing direction are consistent with those found by Mayhew (1973) for a motion aftereffect and Nieman et al. (2005) for depth and color aftereffects. The results are not predicted on the basis of purely retinotopic adaptation alone since purely retinotopic aftereffects would cancel out. The results indicate that information about the visual direction of the stimuli is used in the encoding of visual tilt. In this experiment, the most reliable source of this information would be extraretinal eye position signals (Rogers & Bradshaw, 1995; Backus, Banks, van Ee, & Crowell, 1999).

Experiment 2: Tilt adaptation contingent on gaze, head, and body direction

The gaze-contingent tilt aftereffects found in Experiment 1 cannot result from a purely retinotopic representation, but could result from adaptation of a head-centric or body- or world-centric representation. In Experiment 2 we sought to determine at which of these levels visual tilt representations are encoded. We examined whether the tilt aftereffect is, in addition to being contingent on gaze direction, contingent on head and body directions. A positive result in the head direction condition would implicate a body- or world-centered representation. A positive result in the body direction condition would implicate a world-centered representation. The possible reference frames implicated by positive results in gaze, head, and body direction conditions are summarized in Table 1.

Method

Participants

Eleven observers (two males) aged 19–41 years ($M = 22.6$, $SD = 6.3$) participated in Experiment 2. All

	Possible reference frame			
Aftereffect contingent on:	Retino-centric	Head-centric	Body-centric	World-centric
Gaze direction	No	Yes	Yes	Yes
Head direction	No	No	Yes	Yes
Body direction	No	No	No	Yes

Table 1. Interpretations of contingent tilt aftereffects in gaze, head, and body direction conditions.

had normal vision. None had participated in Experiment 1.

Procedure

Participants performed three experimental sessions, one for each of the gaze, head, and body direction conditions. Sessions were performed in pseudorandom order to closely balance conditions across sessions. We reversed the tilt directions of the adaptation stimuli from those in Experiment 1; therefore, aftereffects should have reversed signs. This provided a check that observers' data indicated aftereffects of the tilted adaptation stimuli and not spurious biases perhaps related to the direction of the monitors.

Results

Results of Experiment 2 are shown in the middle panel of Figure 2. As in Experiment 1, aftereffects were found to be contingent on gaze direction. The signs of the aftereffects were reversed from Experiment 1, demonstrating that the aftereffects depend on the adaptation stimulus tilt and do not reflect biases related to monitor direction. A two-factor analysis of variance (ANOVA) revealed an effect of viewing condition in interaction with monitor direction, $F(2, 20) = 4.023$, $p = 0.034$. Paired sample t tests revealed that aftereffects were significantly different across the two directions in the gaze direction condition only, $t(10) = 2.917$, $p = 0.015$. There were no significant aftereffects in the head, $t(10) = 0.326$, $p = 0.751$, n.s., or body conditions, $t(10) = 0.345$, $p = 0.737$, n.s.

To test whether aftereffects varied with session number we performed a two-factor ANOVA on the aftereffect data ordered by session number. This revealed no effect of session order in interaction with direction, $F(2, 20) = 0.212$, $p = 0.811$, n.s.; therefore, the pattern of results is not due to session order, which was closely balanced across participants.

These results support the conclusion that visually perceived tilt is represented in a head-centric reference frame, but not in a body- or world-centered frame.

Experiment 3: Monocular tilt adaptation contingent on gaze direction

It is known that conventional tilt aftereffects, obtained by adapting to a single tilt, are strongly retinotopic. In contrast, our gaze-contingent tilt aftereffects cannot be attributed to a purely retinotopic mechanism and may involve different mechanisms from those probed by conventional tilt aftereffects. The conventional tilt aftereffect can be produced by either binocular or monocular adaptation (Wolfe & Held, 1981; Burke & Wenderoth, 1989), but it is not known whether the same is true of our gaze-contingent aftereffects. In Experiments 1 and 2 we demonstrated gaze-contingent tilt aftereffects under binocular viewing. In Experiment 3 we examined whether monocular viewing is sufficient to produce these aftereffects. Monocular aftereffects would rule out the possibility that the aftereffects are contingent on binocular disparities and thus establish that the aftereffects are contingent on gaze eye position.

Method

Participants

Seven observers (two males) aged 22–35 years ($M = 25.4$, $SD = 4.6$) participated in Experiment 3. All had normal or corrected vision. None had participated in the other experiments.

Procedure

Observers performed a single experimental session, testing the gaze direction condition. They viewed the stimuli with their preferred eye while wearing a patch over the other eye. Observers were seated. To make the test stimuli easier to judge, the gray background remained on the screen after the Gabors had disappeared, until a response was made. This avoided any masking effect on the Gabors due to background offset. Adaptation stimuli were the same as in Experiment 2.

Results

Results of Experiment 3 are shown in the right panel of Figure 2. As in Experiments 1 and 2, aftereffects were contingent on monitor direction, $t(6) = 6.505$, $p = 0.001$. This shows that once again, and in a different group of subjects, the aftereffects are reliable. These results demonstrate that monocular viewing is sufficient to produce gaze-contingent aftereffects and therefore binocular processes are not required to account for the results of our experiments. The finding of monocular gaze-contingent tilt aftereffects indicates that our gaze-specific tilt aftereffects involve eye position signals rather than binocular information. However, this conclusion does not preclude the possibility that tilt aftereffects could be contingent on binocular information in other situations. For example, vertical size disparities can provide information about gaze direc-

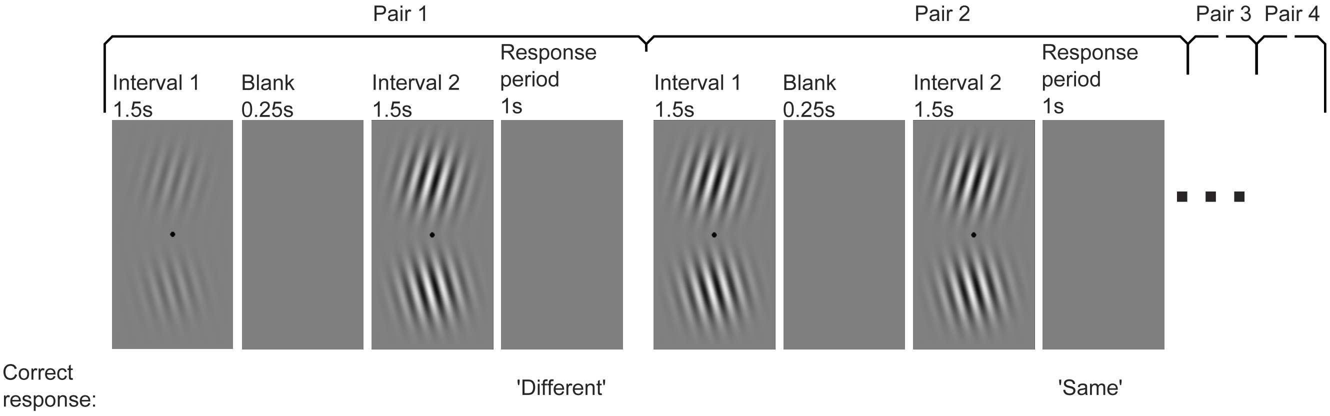

Figure 3. Example of the adaptation stimuli used in Experiment 4. The contrast difference in the first pair is exaggerated here for exposition.

tion and head-centric stimulus direction (Gillam & Lawergren, 1982; Mayhew & Longuet-Higgins, 1982), which could be used to support representations beyond the retinotopic level. Stimuli much larger than those used here would be required to test this possibility because vertical disparities are unreliable in small displays (Rogers & Bradshaw, 1995; Backus et al., 1999), are largest in the periphery, and are pooled by the visual system within fairly large regions of the visual field (Kaneko & Howard, 1997; Howard & Rogers, 2012).

Experiment 4: Tilt adaptation contingent on gaze and head direction, with attention to adaptors

Experiment 2 found no evidence for representations of visually perceived tilt beyond the head-centric level. One possibility is that such representations do exist, but the effect of adaptation is smaller at these higher levels, making the aftereffects difficult to measure. Previous studies have found that attention to tilted adaptation stimuli enhances the tilt aftereffect (Spivey & Spirn, 2000; Festman & Ahissar, 2004; Liu, Larsson, & Carrasco, 2007); therefore, we used an attention task in Experiment 4 to try and enhance the aftereffects and look again for adaptation beyond the head-centric level. A further reason for using an attention task is that attention may be necessary to engage higher level representations. Consistent with this argument is the report that spatiotopic (i.e., at least head-centric) responses observed via fMRI in several brain regions are only found under conditions of attention (Crespi et al., 2011).

Method

Participants

Nine observers (seven males) aged 19–60 years ($M = 28.8$, $SD = 13.5$) participated in Experiment 4. Most had experience of performing the tilt judgment task (five had participated in Experiment 1; two others had participated in Experiment 2). All had normal or corrected vision.

Adaptation stimuli and task

To engage attention on the adaptation stimuli, we incorporated a contrast-change detection task into the adaptation stimulus presentation. This was similar to the contrast-change detection task used by Festman and Ahissar (2004) who found that this attention task enhanced the tilt aftereffect. We replaced the 10-s duration adaptation stimuli used in Experiments 1, 2, and 3 with 17-s sequences of eight adaptation stimuli lasting 1.5 s each, as shown in Figure 3. All of the eight stimuli in a sequence were shown on the same monitor. The eight stimuli were presented as four pairs. Each pair of stimuli could have the same or different contrast (either 90% or 100%). After each pair, observers had 1 s to respond whether the pair had the same or different contrast. Thus, participants made four responses within a single sequence. Auditory feedback indicated whether the response was correct or not. Headphones were used so the sounds did not provide useful cues to head direction (Stricanne, Andersen, & Mazzoni, 1996). Adaptors were present for 12 s in total during each 17-s sequence (adaptation stimulus duration was 1.5 s and four pairs of adaptation stimuli were presented in a sequence: $1.5 \times 2 \times 4 = 12$ s. The remaining time consisted of blank intervals: $4 \times (0.25 + 1) = 5$ s. A complete sequence of eight adaptation stimuli was presented on one monitor, then another sequence of eight adaptation stimuli were presented on the other

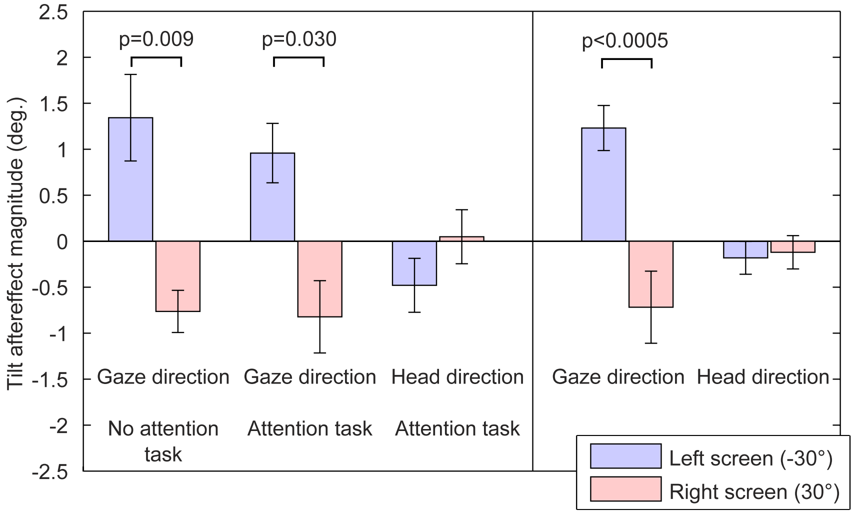

Figure 4. Left panel: Tilt aftereffect results from Experiment 4 ($N = 9$). Right panel: Results from gaze and head direction conditions from Experiments 2 and 4 combined ($N = 18$). Error bars indicate ±1 *SEM*.

monitor, but with opposite tilt. Thus, opposite adaptor tilts were presented in alternation on left and right monitors as before. Adaptor tilt directions were the same as Experiments 2 and 3. As in Experiment 3, the gray background of the test stimuli remained on until a response was made to avoid any masking effects of background offset.

Procedure

Observers performed three experimental sessions, each testing a different experimental condition. Two sessions were performed with the attention task: one testing gaze direction and the other head direction conditions. A third session tested the gaze direction condition with the same changing-contrast adaptation stimuli used in the attention task conditions, but without performing the attention task (gaze direction, no-attention task condition). This no-attention task condition was included for comparison to test whether the gaze-contingent tilt aftereffect is enhanced by attention to the adaptors. Session order was pseudorandomly balanced across participants.

Results

Data for the contrast-change detection task (percent correct) and the tilt judgment task (aftereffect in degrees) were analyzed separately.

Attention task

On average, observers scored 74.2% correct on the attention-to-adaptors task, indicating that the task was appropriately demanding of attention. There was no significant difference in performance between conditions: 72.0% in the gaze condition versus 76.4% in the head condition, $t(8) = -1.946$, $p = 0.089$, n.s.

Aftereffects

Aftereffect results are shown in the left panel of Figure 4. Aftereffect magnitude varied significantly with viewing condition (two-factor ANOVA, viewing condition × monitor direction, $F[2, 16] = 9.284$, $p = 0.019$). Both of the gaze direction conditions, but not the head direction condition, produced significant aftereffects: Paired sample t tests revealed a significant effect of monitor direction in the gaze conditions with no attention task, $t(8) = 3.445$, $p = 0.009$, and with the attention task, $t(8) = 2.630$, $p = 0.030$, but not the head direction condition with attention task, $t(8) = -1.041$, $p = 0.328$. n.s.

The attention-to-adaptors task engaged attention on the adaptors effectively but it did not produce an aftereffect in the head direction condition, nor did it enhance the gaze-contingent tilt aftereffects (two-factor ANOVA, attention task × direction, $F[1, 8] = 0.145$, $p = 0.713$). There was no session order effect (two-factor ANOVA, session × direction, $F[2, 16] = 3.435$, $p = 0.286$, n.s.).

These results further support the conclusion that visually perceived tilt is represented at a head-centric level and not at a higher level. The use of an attention task during adaptation was intended to increase the possibility of finding head direction contingent aftereffects; however, none were found. The finding that attention did not enhance the gaze-contingent tilt aftereffect suggests that it is qualitatively different from the conventional tilt aftereffect. One possibility is that attention exerts its effect within retinotopic tilt mechanisms and not the nonretinotopic mechanism exposed here by the gaze-contingent adaptation paradigm.

To obtain more precise tilt aftereffect estimates for gaze direction and head direction conditions from the data in the current study, we combined data from Experiments 2 and 4, which tested both conditions as repeated measures. We established that there were no significant differences between the results of the two experiments in either condition. Two participants had performed both experiments, so we omitted their data from Experiment 2 to give two independent groups of nine participants per experiment. There was no difference between the head conditions of Experiments 2 and 4 (two-factor ANOVA, Experiment 2 vs. 4 × direction, $F[1, 16] = 3.737$, $p = 0.071$, n.s.). There was no effect of attention task in the gaze direction conditions of Experiment 4 (two-factor ANOVA, attention task × direction, $F[1, 8] = 0.239$, $p = 0.713$, n.s.), so we averaged these data. These averaged data were no different from the gaze direction data in Experiment 2 (two-factor ANOVA, Experiment 2 vs. 4 × direction, $F[1, 16] = 0.175$, $p = 0.681$, n.s.). The combined group ($N = 18$) mean tilt aftereffects from gaze and head direction conditions are shown in the right-hand panel of Figure 4. The gaze direction data show a clear effect of direction, $t(17) = 4.979$, $p < 0.0005$, but there is no evidence of an effect of direction in the head condition, $t(17) = -0.203$, $p = 0.842$, n.s. We can more confidently conclude that the tilt aftereffect is contingent on gaze direction but not head direction.

Discussion

The present experiments used a balanced tilt adaptation paradigm to investigate the possible existence of head-, body-, and world-centered representations of oriented visual features. The logic of this paradigm was that by adapting to two equal and oppositely tilted stimuli across two equal and opposite directions in a given reference frame, no net aftereffect should occur in that reference frame. Therefore, systematic aftereffects would indicate the existence of representations in one or more reference frames not balanced in the experiment. By examining whether balanced tilt adaptation produces aftereffects contingent on gaze, body, and head direction, we were able to factor out purely retino-centric, head-centric, and body-centric tilt adaptation respectively to identify which frame(s) of reference are used in representations of tilt. In all of our experiments we found that tilt aftereffects were contingent on gaze direction. We confirmed that these aftereffects arise from the use of eye position signals in a monocular experiment, which ruled out binocular disparities as an alternative source of contingent information. Our gaze-contingent aftereffects cannot be attributed to purely retino-centric tilt adaptation and instead implicated at least a head-centric frame of reference.

To examine the possibility that visually perceived tilt is represented beyond the head-centric level (i.e., at body- or world-centered levels), we balanced tilt adaptation across both retino- and head-centric frames together, but we found no systematic aftereffects, even when ensuring attention was engaged on the adaptors. A further condition, which balanced adaptation across retino-, head-, and body-centric frames of reference, also failed to find evidence for world-centered representations.

Overall, we found that the tilt aftereffect is contingent on gaze direction, but not head or body direction. We conclude from this that tilt is encoded at the head-centric level, and we have found no evidence of adaptive tilt representations at higher levels.

An alternative possibility is that the failure to find aftereffects in the head- and body-contingent conditions might indicate that observers had problems fixating the stimuli in those conditions. This is unlikely because (a) the central marker was the same in all conditions and always clearly visible. (b) Shifting fixation away from the marker as a deliberate strategy in any of the conditions is unlikely as it would make the tilt judgment task more difficult. (c) If any condition was a challenge to fixation it was the gaze direction condition, as gaze was held alternately at + and −30° for 10-s periods, whereas gaze was not eccentric in the head and body conditions. However, the gaze direction condition produced aftereffects, so fixation must have been successful in arguably the most challenging of the conditions. (d) Contrast-change detection task performance did not differ between gaze or head direction conditions, suggesting no difference in the ability to fixate the stimuli between conditions. We conclude that the results are not due to a problem with fixation.

Another suggestion, provided by a review of this paper, is that perhaps a reason for not finding aftereffects in the head direction condition is if head direction is not encoded as accurately as gaze direction. However, Rossetti, Tadary, and Prablanc (1994) found, using an open-loop pointing task to assess the accuracy of gaze and head direction signals, that variability due to head direction was substantially less than that due to gaze. Also, constant errors increased with increasing gaze, but not head direction. These behavioral results suggest that registration of head direction is not worse than gaze direction. Also, electrophysiological results show that gaze and head direction produce equivalent gain field modulations in the same cells in parietal cortex (Brotchie et al., 1995), so head direction information in the cortex, at least as used in these mechanisms relevant to spatial constancy, does not seem to be worse than that for gaze direction. Further, it is not likely that head motion per se abolished the tilt aftereffect. Knapen et al. (2010) found reliable tilt aftereffects when presenting adaptation and test stimuli at the same retinotopic location, but changing head direction.

Relationship to studies on the reference frame of the tilt aftereffect

In apparent contradiction to our findings, several recent studies examining the reference frame of the tilt aftereffect (Knapen et al., 2010; Mathôt & Theeuwes, 2013; Morgan, 2014) have concluded no evidence for tilt adaptation beyond the retinotopic level. In these studies, after adaptation observers shifted their gaze to a fixation point away from the adaptor. Aftereffects were found when a test was presented at the adapted retinal location but not when presented at a different retinal location but at the same spatial location as the adaptor. Therefore, these studies concluded evidence for adaptive tilt representations at the retino-centric level, but no evidence of adaptation at a higher level. How can this be reconciled with our findings of tilt adaptation at the head-centric level?

One answer is that truly head-centric representations of oriented features do not exist, but instead the visual system constructs functionally head-centric representations by combining retinotopic tilt signals with gaze signals. Strong candidates for this are networks of retinotopic tilt-sensitive neurons in early visual cortical areas whose gain is modulated by gaze direction, such as the type of V1 neurons reported by Trotter and Celebrini (1999). In this way, retinotopic tilt aftereffects arise from the retinotopic organization of V1, and our gaze-contingent tilt aftereffects could arise from adaptation of those retinotopic tilt-sensitive neurons, which are strongly activated by the particular combination of tilt and gaze direction during adaptation.

Consider an example of balanced adaptation to −15° tilt at −30° gaze and +15° tilt at +30° gaze. If adaptation is greater in neurons responding to −15° tilt at −30° gaze (an adapted combination) than in neurons responding to +15° tilt at −30° gaze (not an adapted combination), then the overall response to a vertical test at −30° gaze would be skewed towards a positive tilt. This gaze-specific tilt adaptation would predict repulsive gaze-contingent aftereffects of opposite sign at the two gaze directions, as we have found.

Taken together, the results support the conclusion that tilt, encoded retinotopically, is jointly encoded with gaze direction, but not head or body direction, to form functionally head-centric, but not body- or world-centric, tilt representations.

Relationship to electrophysiological findings

The present results fit well with electrophysiological studies demonstrating gaze gain field modulation of activity in retinotopically organized networks. Early visual areas are particularly likely candidates; neurons in V1 are tilt sensitive (Hubel & Wiesel, 1959), adapt their tuning to tilt stimulation (Dragoi, Sharma, & Sur, 2000; Jin, Dragoi, Sur, & Seung, 2005), and their activity is modulated by gaze direction (Trotter & Celebrini, 1999). Parietal neurons exhibiting gain field behavior are less likely candidates for the tilt aftereffects reported here since parietal receptive fields are large and unsuited to detailed visual feature analysis. Instead, the gaze, head, and body direction gain field modulation found in parietal areas may support a form of spatial constancy based on attention (Cavanagh et al., 2010; Burr & Morrone, 2011) in which the locations of attended objects are updated in different frames of reference to support actions and navigation (Snyder et al., 1998). This process does not involve remapping of low-level visual features such as tilt (Knapen et al., 2009; Knapen et al., 2010; Mathôt & Theeuwes, 2013).

Gaze-contingent tilt aftereffects may be attributed to gaze modulation of activity in retinotopic tilt-sensitive mechanisms in early visual cortical areas. Since we found no head- or body-direction contingent aftereffects, we would expect that activity in retinotopic tilt-sensitive neurons is not modulated by head or body direction. We know of no electrophysiological studies that have examined this. While studies have found head and body direction gain field modulation in parietal cortex (Brotchie et al., 1995; Snyder et al., 1998), on the basis of our results we would not expect the same of early visual areas involved in feature analysis.

Visual perception and visual memory

Our results are consistent with the idea that the phenomenal visual world involves the coordination of two types of representation which together support perception and action (Land, 2012): (a) visual perceptual representations in a head-centric frame, which provides compensation for eye movements (but not head or body movements, consistent with the absence of aftereffects in these cases), and (b) visual memory representations that support spatial constancy through compensation for movements of the head and body relative to the world (e.g., Snyder et al., 1998). Under this scheme, our gaze-contingent aftereffects reflect adaptation of perceptual representations (i.e., of activity in low-level tilt-sensitive mechanisms associated with immediate visual awareness). Failure to find head- or body-contingent aftereffects suggests that representations beyond the head-centric level are not based on the adaptive low-level, tilt-sensitive mechanisms that underpin our perceptual representations. Instead, spatial constancy under head and body movements is supported by egocentric memory representations, which are qualitatively different from perceptual representations (Tatler & Land, 2011). Such representations are automatically updated according to our body movements (Farrell & Robertson, 1998) and support actions such as the ability to point to an object after body movements when vision is not available (e.g., Wang & Spelke, 2000; Burgess, 2006).

Attention and the tilt aftereffect

The balanced adaptation paradigm provides a potentially useful way to probe the properties of the process responsible for gain field modulation of cortical neurons. We can speculate here about the operation of attention in relation to this process. It is interesting that we found no effect of attention on gaze-contingent tilt aftereffects. It may be that an effect could be revealed with a more sensitive method, but alternately the lack of an attention effect may provide a clue to the operation of attentional processes in tilt-sensitive cortical regions. It is known that attention enhances conventional tilt aftereffects (Spivey & Spirn, 2000; Festman & Ahissar, 2004; Liu et al., 2007), and conventional tilt aftereffects are strongly retinotopic (Knapen et al., 2010). In contrast, our gaze-contingent tilt aftereffects isolate a nonretinotopic process that does not seem to be affected by attention. We therefore speculate that attention modulates retinotopic tilt-related activity, not gaze-related activity. Two possibilities are that attention modulates tilt responses before gaze modulation, not after, or attention modulates tilt responses in neural mechanisms that are not modulated by gaze. Further studies using balanced adaptation paradigms will be able to examine properties of the gain field modulation process in more detail.

Conclusions

We have found tilt aftereffects contingent on gaze, but not head or body direction, using a balanced tilt adaptation paradigm. These aftereffects cannot be attributed to purely retinotopic mechanisms. Instead, they may reflect adaptation of a functionally head-centric neural representation of tilt such as may be produced by networks in early, retinotopically organized visual areas sensitive to tilt whose activity is modulated by gaze direction. Such a representation may provide spatial constancy for visual perception across eye movements, but not head or body movements, which are likely supported by higher-level mechanisms in parietal cortex. While electrophysiological studies have investigated modulation of neural activity by gaze, head, and body direction in parietal cortex, studies examining modulation in tilt-sensitive neurons in occipital cortex have only investigated gaze direction. On the basis of our findings, we would not expect activity in tilt-sensitive neurons to be modulated by head or body direction. The balanced tilt-adaptation paradigm is a useful tool for exploring the properties of the process responsible for gain field modulation in early visual areas.

Keywords: tilt aftereffect, adaptation, constancy, gain field

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