RESEARCH ARTICLE | *Sensory Processing*

Spatiotopic coding during dynamic head tilt

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Mikellidou K, Turi M, Burr DC. Spatiotopic coding during dynamic head tilt. *J Neurophysiol* 117: 808–817, 2017. First published November 30, 2016; doi:10.1152/jn.00508.2016.—Humans maintain a stable representation of the visual world effortlessly, despite constant movements of the eyes, head, and body, across multiple planes. Whereas visual stability in the face of saccadic eye movements has been intensely researched, fewer studies have investigated retinal image transformations induced by head movements, especially in the frontal plane. Unlike head rotations in the horizontal and sagittal planes, tilting the head in the frontal plane is only partially counteracted by torsional eye movements and consequently induces a distortion of the retinal image to which we seem to be completely oblivious. One possible mechanism aiding perceptual stability is an active reconstruction of a spatiotopic map of the visual world, anchored in allocentric coordinates. To explore this possibility, we measured the positional motion aftereffect (PMAE; the apparent change in position after adaptation to motion) with head tilts of ~42° between adaptation and test (to dissociate retinal from allocentric coordinates). The aftereffect was shown to have both a retinotopic and spatiotopic component. When tested with unpatterned Gaussian blobs rather than sinusoidal grating stimuli, the retinotopic component was greatly reduced, whereas the spatiotopic component remained. The results suggest that perceptual stability may be maintained at least partially through mechanisms involving spatiotopic coding.

NEW & NOTEWORTHY Given that spatiotopic coding could play a key role in maintaining visual stability, we look for evidence of spatiotopic coding after retinal image transformations caused by head tilt. To this end, we measure the strength of the positional motion aftereffect (PMAE; previously shown to be largely spatiotopic after saccades) after large head tilts. We find that, as with eye movements, the spatial selectivity of the PMAE has a large spatiotopic component after head rotation.

head tilt; PMAE; retinotopic; spatiotopic coding; visual stability

AS WE MOVE THROUGH THE WORLD, our eyes, head, and body are in continual motion, yet the world appears absolutely stable, and we are able to interact with it effortlessly. One possible mechanism aiding visual stability could be the construction of a map anchored in real-world, allocentric coordinates, which would work in conjunction with retinotopic maps. The existence of such a map would not necessarily substitute a retinotopic-based coordinate system into which all images are ini-

tially encoded, but rather help maintain stability in the face of prominent image transformations induced by eye and head movements (see Burr and Morrone 2012 for review). However, despite solid evidence from psychophysical and imaging studies in humans as well as electrophysiological studies of non-human primates, the notion of spatiotopy has been highly controversial.

Adaptation, a widely used psychophysical technique, has been proven invaluable in the study of spatiotopy because it allows adaptation of one retinal region and testing of another by interspersing an eye movement between the two periods. Adaptation has shown that position, orientation, event time, and numerosity are at least partially encoded in allocentric coordinates (Arrighi et al. 2014; Burr and Morrone 2011; Burr et al. 2007; Demeyer et al. 2010; Fornaciai et al. 2016; Melcher 2005; Morrone et al. 2010; Turi and Burr 2012; Zimmermann et al. 2011, 2013). In addition, adaptation to color also seems to be head-centered (Wittenberg et al. 2008), whereas contrast, thought to be processed primarily in V1, seems to be purely retinotopic (Melcher 2005).

Spatiotopic coding has also been demonstrated using other psychophysical techniques. Howe et al. (2011) showed that attention is allocated in spatiotopic coordinates by evaluating visual tracking performance of multiple targets. Pertzov et al. (2010) showed that inhibition of return (inferior performance for stimuli positioned at recently cued locations) is compromised when the target and cue share the same screen (not retinal) coordinates. This evidence, however, has been disputed, because others have argued that the native coordinate system of spatial attention is retinotopic (Golomb et al. 2008). In addition, we have recently shown that the oblique effect, superior performance for stimuli at cardinal orientations (0° and 90°) compared with oblique orientations (45°), remains anchored in allocentric coordinates, irrespective of head position (Mikellidou et al. 2015). Melcher and Morrone (2003) showed that motion signals can be integrated across saccades, provided they are spatially coincident, and Ong et al. (2009) have shown that short-term memory for motion is encoded in spatiotopic coordinates, providing further evidence for functional spatiotopy in motion areas such as MT. Again, this work has been challenged (Morris et al. 2010).

Motion aftereffects (MAE) have been proven to be a particularly useful tool to demonstrate spatiotopy. Whereas the standard motion aftereffect is entirely retinotopic, as originally

reported by Addams (1834) and subsequently confirmed by others (Knapen et al. 2009; Wenderoth and Wiese 2008; Wohlgemuth 1911), the positional motion aftereffect (PMAE) turns out to be spatiotopic (Turi and Burr 2012). In the PMAE, adaptation to motion within a window causes a subsequent presentation of the windowed grating to appear displaced in the direction opposite to the direction of adapting motion (Nishida and Johnston 1999; Snowden 1998). The effect is spatially selective, and if a saccadic eye-movement is interspersed between the adaptation and test, the selectivity is in spatiotopic coordinates (Turi and Burr 2012). Despite both effects being motion induced, they appear to be distinct; whereas the classical MAE exhibits very high dependence on the spatiotemporal characteristics of the adapting and test stimuli (Cameron et al. 1992; Thompson 1981), the PMAE appears to be impervious to any stimulus alterations (McGraw et al. 2002). This lack of stimulus specificity suggests that the PMAE occurs at a "higher level" visual brain area, in contrast to the classical MAE that most likely occurs at a "low-level" area.

Spatiotopic coding has also been observed at the neural level in both single-cell recordings in primates and imaging studies in humans. In fact, the first evidence for spatiotopic coding came from single-cell recoding in the monkey, showing that neurons in V6 have spatial tuning invariant with gaze position (Galletti et al. 1993), later also reported in the ventral intraparietal cortex (VIP) by Duhamel et al. (1997). Subsequently, the same group showed that V6 is organized in a retinotopic fashion, with individual cells showing a sensitivity to the real motion of objects in allocentric coordinates (Gamberini et al. 2015). Even in the primary visual cortex, V1, the selectivity has been shown to modulate to some extent with gaze (Celebrini et al. 2009; Durand et al. 2010). Vestibular input modulates the activity of single units in the mammalian visual cortex (Jung et al. 1963), and in nonhuman primates, a subpopulation of V1 neurons have head-centered receptive fields that use eye position information to shift their receptive field location and their retinal orientation tuning, partly compensating for the ocular counter-roll reflex (OCR) (Daddaoua et al. 2014). Similarly, in the cat visual cortex, a minority of cortical units change receptive field orientation following the spatial rather than the retinal orientation of the stimulus (Denney and Adorjani 1972; Horn and Hill 1969). Imaging studies have reported that the blood oxygen level-dependent (BOLD) response of the human MT+ complex, and much of parietal cortex, varies with gaze position in a way that is consistent with spatiotopic coding (Crespi et al. 2011; d'Avossa et al. 2006), but like most evidence for spatiotopy, this result has been contested (Gardner et al. 2008). Subsequent studies showed that spatiotopy is attention dependent: when attention was directed toward the stimuli, as occurs in normal viewing, the selectivity was in external coordinates; however, when attention was directed to the fovea (Gardner et al. 2008), a large retinotopic component emerged (Crespi et al. 2011).

Most studies of spatiotopy have investigated the consequences of saccadic eye movements on spatial selectivity. However, head movements can also provide major challenges to visual stability. Whereas rotations in the horizontal and sagittal planes can be compensated by eye movements, tilting the head in the frontal plane causes retinal image distortions that are only partially counteracted by torsional eye rotation. Variations of head tilt in the frontal plane activate the OCR by rotating slightly both eyes in the opposite direction of head tilt to partially counteract the resulting image distortion. The OCR is a response of the otolith organs, which detect changes in the direction of gravitational force during static head tilt. These compensatory eye movements correct only about 10% of the total amount of tilt for head tilts up to 45° (Bockisch and Halswanter 2001) with a small drift during sustained head tilt (Palla et al. 2006). However, Medendorp et al. (2002) observed no systematic directional errors when participants were asked to look to remembered targets following intervening torsional head movements. Similar results were also observed with passive head movements (Klier and Angelaki 2008; Klier et al. 2008). These results suggest that visual stability is maintained during head tilt by active neural mechanisms. Spatiotopic coding could play a part in maintaining stability.

Given the emerging evidence from diverse methodologies suggesting that spatiotopic coding occurs in several visual areas and that this coding could play a key role in maintaining visual stability, in this study we looked for evidence of spatiotopic coding after retinal image transformations caused by head tilt, using a similar methodology to Turi and Burr (2012). We measured the strength of the PMAE after large head tilts and found that, as with saccadic eye movements, the spatial selectivity of the PMAE has a large spatiotopic component after head rotations along the frontal plane.

METHODS

Participants. Nine observers (1 female; age range 18–35 yr) participated in the first experiment, and six of them also participated in the second experiment (all males; age range 18–35 yr). All observers were naive to the objective of the experiments, except authors M. Turi (sinusoidal grating and unpatterned Gaussian blob experiment) and K. Mikellidou (sinusoidal grating experiment only). All had normal or corrected-to-normal vision. Experimental procedures were approved by the regional ethics committee (Comitato Etico Pediatrico Regionale-Azienda Ospedaliero-Universitaria Meyer, Florence) and are in line with the Declaration of Helsinki. All participants gave informed written consent.

Stimuli and apparatus. Stimuli were generated under MATLAB version 7.6 using Psychtoolbox routines (Brainard 1997; Kleiner et al. 2007) and presented on a linearized, gamma-corrected, 19-in. Barco CRT monitor with $1,024 \times 768$ resolution at a refresh rate of 60 Hz and mean luminance of 38 cd/m^2. Subjects viewed the stimuli binocularly from a distance of 57 cm. We eliminated all visual references by running the experiment in total darkness throughout the study. In *experiment 2*, we carried out an additional step to eliminate any remaining visual references that could potentially be used as spatiotopic points of reference; stimuli were viewed through a dark circular tube, making the visible screen circular instead.

Adaptation stimuli were two Gaussian-windowed sinusoidal gratings, modulated in luminance on a gray background [carrier frequency was 1 cycle/deg, drift velocity 3 deg/s (3 Hz), Gaussian space constant 1°, contrast 0.9]. The two gratings were horizontally aligned and separated by 3.8° from each other and placed at 1.9° above the center of the screen. In *experiment 1*, the test stimuli were identical to the adaptation stimuli, except that the former were stationary. In *experiment 2*, test stimuli were unpatterned Gaussian-windowed patches with Gaussian space constant 1° and contrast 0.9. To regulate the angle of the head tilt, a special V-shaped headrest was constructed comprising two resting wooden plates each deviating 30° from the vertical midline (as shown in Figs. 1).

Before the main experiments, the range of retinal cyclotorsion across a 60° headrest was measured for each individual separately. To determine the exact degree of image displacement as each participant

Fig. 1. Timeline of the pre-retinotopic experiment. After 30 s of adaptation with the head resting against the right plate, subjects tilted the head to the left resting plate and adjusted the 2 bright circles to match the position of the perceived afterimage. The 2 bright circles rotate together around the fixation point, and α corresponds to the matched angle for each participant.

tilted their head from one side of the headrest to the other, we employed the iconic afterimage technique shown in Fig. 1 (Afraz and Cavanagh 2009). Participants placed their head on the right plate of the headrest and fixated a white fixation point on the screen while two horizontally aligned bright circles of 1° diameter, separated by 3.8° from each other and 1.9° above the screen center, were presented for 30 s. After extinction of the white circles, participants moved their head to the left plate of the headrest while keeping fixation and were asked to adjust, using key arrows, the angle of two bright circles on the screen to match the afterimage created on their retina. The two gratings rotated together as a single object around the fixation point, and α corresponds to the matched angle for each participant individually (see Fig. 1). This process was repeated three times to obtain an average value, which was subsequently used as the position of the adapting stimuli in the retinotopic condition of *experiments 1* and *2*. These measurements allowed us to compensate for individual differences in head size, which would affect the size of the head rotation, and also to discount any corrective torsional eye movements. Table 1 shows the average stimulus displacement for each participant ($n = 9$). As expected, there is considerable intersubject variability of the image displacement.

Moreover, to verify that the angle measured in the pre-retinotopic experiment using the iconic afterimage technique (Afraz and Ca-

vanagh 2009) was reasonable, at the end of the experiments we additionally recorded kinematics data about the head rotation from two subjects (S2 and S7) using a mobile device placed on the back of the subjects' head. The head orientation position signal was sampled at 30 Hz using an Android phone application (Sensor Kinetics by RotoView; Innoventions, Houston, TX) and then calculated by the app integrating the signal from the built-in accelerometer and gyroscope, expressed as angles of deviation from the horizontal axis.

In Fig. 2, *A* and *B*, we plotted the head tilt angle from the two subjects for the entire duration of the experiment, and as can be seen, the total amount of head rotation for both subjects was similar to those measured by the iconic afterimage technique (S2: 44.4° vs. 42.6°; S5: 37.3° vs. 38.1°; using the afterimage technique and Android app, respectively). In Fig. 2, *C* and *D*, we plotted subsampled kinematics recording data ranging from 35 to 70 s to show the dynamic of the head movements.

Design and procedure. We measured the strength of the PMAE with an alignment paradigm in the first and second experiments. Each session commenced with an initial adaptation period of 30 s followed by a further "top-up" adaptation of 3 s before each test trial . During adaptation, the two adaptor grating patches, one left and one right, drifted in opposite directions at 3 deg/s. Subjects maintained fixation on a spot at the center of the screen throughout the course of the experiment. After extinction of the adaptor, there was a 1,150-ms interstimulus interval that allowed sufficient time for a head movement to be performed. Subsequently, the stationary test gratings were presented for 500 ms and participants reported by key press whether the left test patch appeared higher or lower than the right test patch. After each trial there was a 3-s pause.

The size of the positional shift induced by the PMAE was measured using an annulment technique, by shifting the position of the left grating patch up or down. The amount of shift was determined online by the adaptive QUEST algorithm (Watson and Pelli 1983), homing in on the point where the two patches appeared aligned. To ensure a spread of shifts around the point of subjective alignment (PSA), the QUEST estimate was jittered by adding to the best estimate a random number drawn from a Gaussian distribution of standard deviation 0.15°.

Table 1. *Average stimulus displacement*

Subject	Retinal Image Displacement, °	SE
S1	47.0	0.8
S2	44.4	1.8
S3	52.2	0.3
S4	36.5	1.3
S5	31.7	0.2
S6	55.7	0.4
S7	37.3	1.2
S8	33.2	1.6
S9	43.3	0.8
Average	42.4	1.0

Data are average stimulus displacement calculated for each participant ($n = 9$) in the preretinotopic experiment.
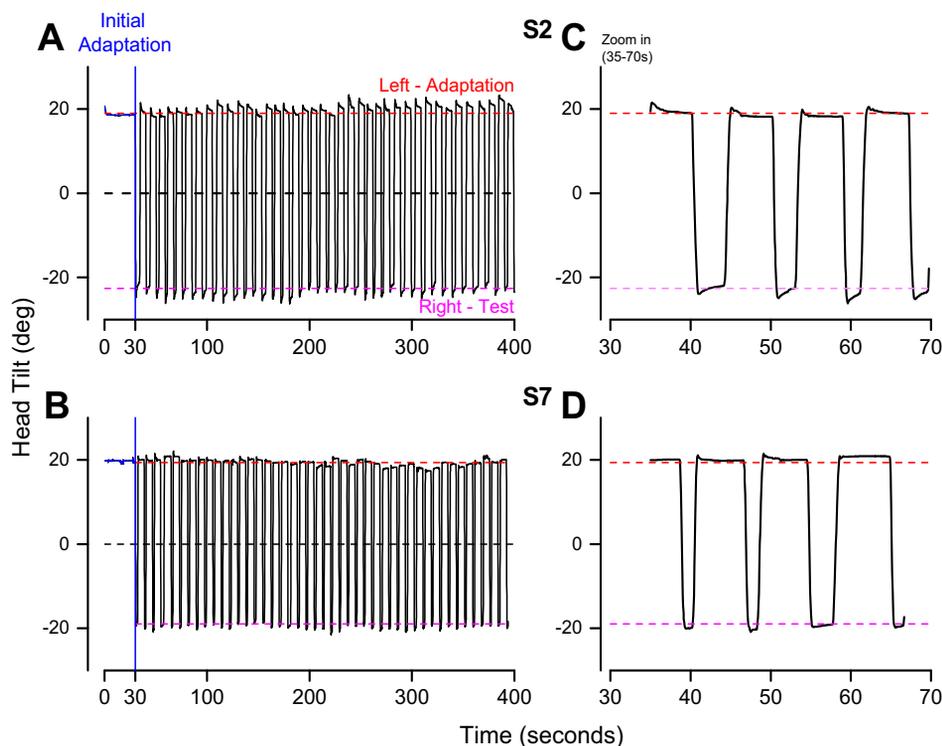
Fig. 2. *A* and *B:* head-tilt kinematics data across 1 session of the experiment for 2 representative subjects S2 (*A*) and S7 (*B*). Red and pink dashed lines indicated the mean of head tilt when the head was placed respectively on the left and on the right. *C* and *D:* subsamples of the entire kinematics data recording ranging from 35 to 70 s for the 2 representative subjects S2 (*C*) and S7 (*D*).

The proportion of trials where the left test patch appeared higher than the right test patch was plotted against the physical offset between the test patches stimuli and fitted with a cumulative Gaussian function (like those of Fig. 3). The median of the functions estimated the PSA, the position where the proportion of responses was at 0.5, and the strength of the position aftereffect was taken as the difference in PSAs measured with upward and downward adaptation (distance between the dashed lines of Fig. 3). The subtraction between the two conditions was designed to eliminate systematic biases that may have resulted from head tilt or any other factors. Note that the subtraction technique leads to estimates that are twice as large as would have been obtained by using other techniques, such as subtracting a baseline, nonadapted condition. The standard deviation of the cumulative Gaussian functions yields an estimate of the precision threshold (just-noticeable difference, JND).

We tested four experimental conditions. In all conditions, the test stimuli were presented at the same screen position, whereas the position of the adaptor gratings varied between conditions (see Supplemental Material, Supplemental Movies S1 and S2, available on line at the Journal website). In the "full" adaptation condition, participants held their head straight between the two resting plates (Fig. 3*A*, *left*) throughout the course of the session, and the test gratings were presented at the same screen location as during adaptation. The two adaptor grating patches matched the exact screen position of the stationary test grating patches (one centered 1.9° left of screen center and the other 1.9° right of center).

For the spatiotopic and retinotopic conditions, the subjects were trained to hold their head on the left plate during adaptation and then to tilt their head to the right during the 1,150-ms following extinction of the adaptor and remain still for the test phase (Fig. 3, *B* and *C*, *left*). After reporting by key press whether the left test patch appeared higher or lower than the right test patch, the subjects returned their head to the left plate (intertrial pause) and repeated the same process for each trial. In the spatiotopic condition, the adaptation and test stimuli were displayed on the same part of the screen (i.e., 1.9° to the left and right of the central fixation point), as in the "full" condition. However, because the position of the head varied from the left resting plate during adaptation phase to the right during test phase, the adaptation and test stimuli were projected on different retinal positions, with no overlap between them (checked by using the afterimage procedure described above).

In the retinotopic condition, the head position was identical to that of the spatiotopic condition, but the positions of the adapting stimuli were rotated counterclockwise around the fixation point to ensure stimulation of the same retinal area where the test stimuli were subsequently displayed. The stationary test gratings were presented in the same screen position as in all other experimental conditions. The exact amount of adapting stimuli rotation varied across participants and was determined in the pre-retinotopic experiment by using an afterimage technique described previously.

In the final "unmatched" condition, the adaptor stimuli were rotated 60° counterclockwise from the vertical axis, similar to the retinotopic condition, but with no intervening head movement. Consequently, the adaptation and test stimuli coincided in neither retinotopic nor spatiotopic coordinates. This was used as a baseline condition.

All experimental conditions were tested in blocks, with a pseudo-randomized order counterbalanced between subjects. Forty-five trials were run for each session, with two sessions per subject, leading to 90 trials in total for each subject for each one of the four experimental conditions.

ANOVA, t-tests and bootstrapping. To determine whether there was a significant main effect of experimental condition on the size of the PMAE, we performed a one-way repeated-measures ANOVA with four levels. For the statistical comparison between experimental conditions, we carried out six one-tailed paired *t*-tests, applying a Holms-Bonferroni correction for multiple comparisons. We also performed two-tailed bootstrap sign tests (Efron and Tibshirani 1994), a technique that takes into account the error associated with each individual threshold (for both directions of adapting motion) as well as the between-subject variance. A total of 10,000 iterations were run separately for each paired comparison. On each iteration, the data for each subject were independently sampled (with replacement), with 90 independent samples drawn from the 90 trials for that specific subject and condition, and the PSA was calculated by fitting that sample with a cumulative Gaussian. The PSAs were then averaged over all subjects and compared across conditions. The *P* value was taken as
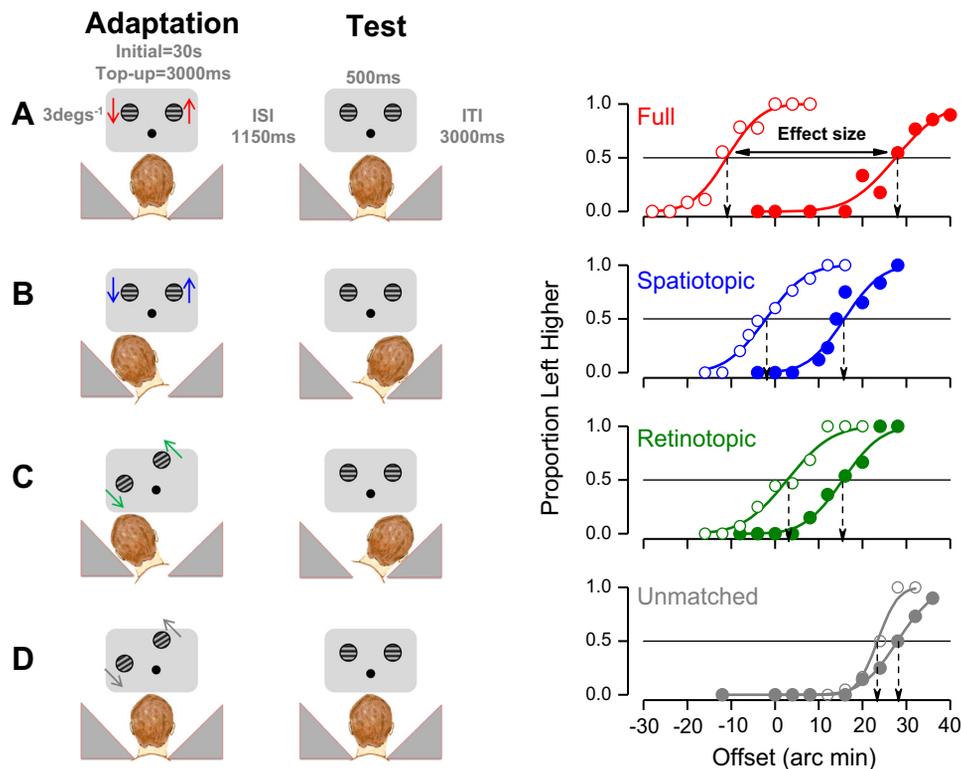
Fig. 3. *Left*: schematic representation of stimuli and head position in each of the 4 experimental conditions. Position of test gratings is identical in all conditions. *Right*: psychometric functions from a typical participant. Open circles indicate positional motion aftereffects (PMAE) following adaptation to upward motion in the left grating and downward motion in the right grating; filled circles indicate the opposite. Dashed arrows indicate the point of subjective alignment (PSA) for each condition; the size of the adaptation effect is given by the difference of the PSAs in the 2 adaptation conditions (horizontal arrow). *A*: full adaptation (red); adaptor and test grating patches coincide in both spatiotopic (screen) and retinal coordinates with the head remaining upright throughout. *B*: spatiotopic adaptation (blue); position of adaptor and test gratings is identical to that in *A*, but a head tilt is performed between the 2 phases, preserving the spatiotopic, but not retinal, component of the PMAE. *C*: retinotopic adaptation (green); a head tilt is performed between presentation of adaptor and test grating patches, preserving the retinal, but not spatiotopic, component of the PMAE. Position of adaptor gratings is determined for each individual in a pre-retinotopic session (see METHODS). *D*: unmatched (gray); adaptor and test grating patches do not coincide in spatiotopic or in retinal coordinates. Note that adaptor gratings were moving at 3 deg/s as indicated by example arrows (see METHODS), whereas test gratings were stationary.

the proportion of iterations where *condition A* had a higher PSA than *condition B*. The bootstrap test is powerful because it considers both intra- and intersubject variability.

RESULTS

Experiment 1: PMAE with head tilt. We measured the magnitude of the positional motion aftereffect (PMAE) under four conditions (full, spatiotopic, retinotopic, and unmatched), some involving a head tilt between adaptation and test periods. The full adaptation condition is the simplest, with no head tilt between adaptation and test, resulting in both spatiotopic and retinotopic adaptation. For all conditions, we measured the effect with both upward motion in the left window and downward in the right, and vice versa, to create two different psychometric functions for each observer, as shown in Fig. 3.

Adaptation to upward motion on the left and downward on the right causes opposite displacements of the positions of the patch. These effects were nulled by adding a displacement to the position of the left grating, resulting in a leftward shift of the psychometric function along the abscissa. Similarly, adaptation in the opposite manner (i.e., upward motion on the right and downward on the left) causes a rightward shift of the psychometric functions. The difference in the PSAs of the two functions (vertical arrows)

gives an estimate of the strength of adaptation, which is 39 arc min for the full condition, 18 arc min for the spatiotopic, 18 arc min for the retinotopic, and 4 arc min for the unmatched (Fig. 3, *A–D*, *right*). We note that there is a bias in all conditions, including the unmatched. However, this bias was also evident in the absence of head tilt in Turi and Burr (2012). To remove any such bias, we subtract the two conditions with opposite motion induction.

The bars of Fig. 4*A* show the mean magnitude of the PMAE in all four conditions (with symbols indicating effect magnitudes for individual subjects). The effect was clearly largest in the full condition, but also quite substantial, and significantly greater than the baseline (unmatched) condition, in both the spatiotopic and the retinotopic conditions. A repeated-measures ANOVA revealed a main effect of condition [$F(3, 24) = 58.3$, $P < 0.0001$].

We then carried out six pairwise Holms-Bonferroni-corrected *t*-tests. The most prominent PMAE occurred with the full adaptation condition (mean 27.6, SD 8.6 arc min) and was significantly greater than for the spatiotopic (mean 12.9, SD 8.6 arc min; $P < 0.0001$), retinotopic (mean 10.1, SD 7.0 arc min; $P < 0.0001$), and unmatched (baseline) conditions (mean 2.1, SD 3.9 arc min; $P < 0.0001$). The PMAE for both the spatiotopic and retinotopic conditions was significantly greater than for the baseline condition ($P <$
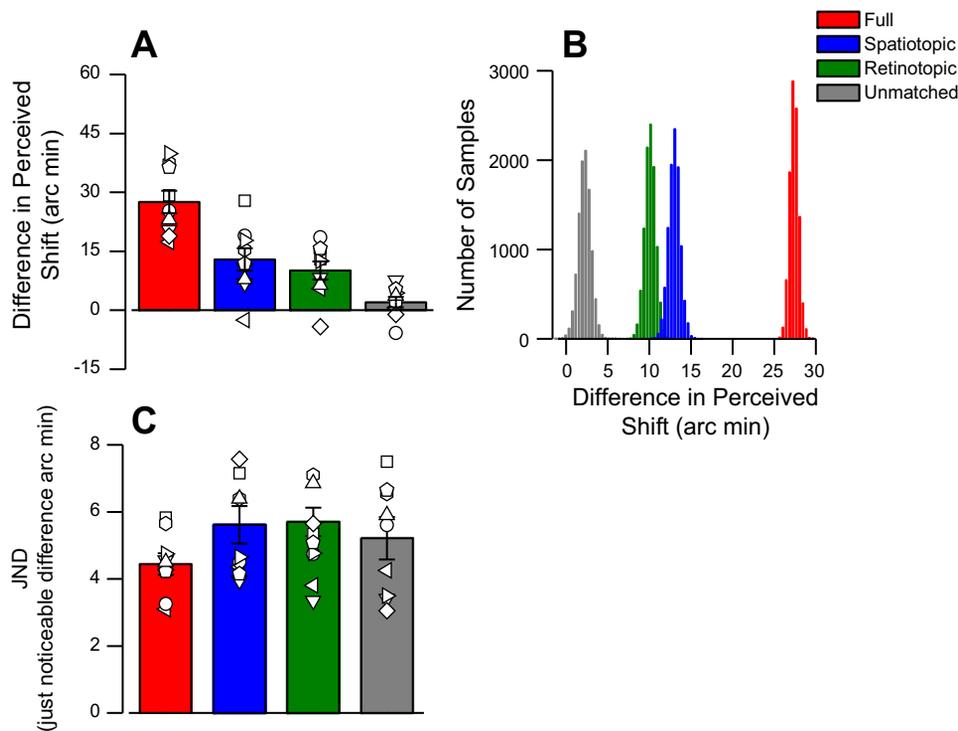
Fig. 4. *A*: mean magnitude of the PMAE for all subjects (*n* = 9) across the 4 experimental conditions (error bars show ±SE): full (mean 27.6°; red), spatiotopic (mean 12.9°; blue), retinotopic (mean 10.1°; green), and unmatched (mean 2.1°; gray). *B*: bootstrap distribution (10,000) of the PSA difference in each experimental condition. *C*: mean and individual JNDs across the 4 experimental conditions in *experiment 1* (error bars show ±SE).

0.001). The PMAE for the spatiotopic condition was not significantly different from that for the retinotopic condition (*P* = 0.33).

We also bootstrapped the data (as described in METHODS) as a further set of significance. The results of 10,000 bootstraps are shown in Fig. 4*B*, confirming that the strongest effect is evident with the full adaptation condition, which is significantly greater than for the other three conditions (bootstrap sign-test, *P* < 0.0001). The PMAE for both the spatiotopic and retinotopic conditions was significantly greater than for the baseline condition (bootstrap sign-test, *P* < 0.0001 and *P* = 0.0006, respectively). The bootstrapped distribution for the spatiotopic condition was also higher than the retinotopic distribution (bootstrap sign-test, *P* = 0.006), which was not significant with the pairwise Holms-Bonferroni-corrected *t*-test, probably because the bootstrap is more sensitive since it considers both intra- and intersubject variability.

Figure 4*C* also shows the precision of the subjects in the alignment task, expressed as the precision thresholds, or JND, in each psychometric function. We measured thresholds separately for upward and downward motion and then averaged the two values across the four experimental conditions. As can be seen from the graph, the precision of the subjects in the task was quite similar across the different conditions, confirmed by a repeated-measures ANOVA that did not reveal a main effect of condition [*F*(3, 24) = 1.66, *P* > 0.05].

Experiment 2: PMAE tested with unpatterned Gaussian blobs. In the previous experiment, the test stimuli were stationary sinusoidal gratings, allowing the PMAE to be strengthened by a traditional MAE, resulting from the direct motion stimulation, which in turn leads to an apparent displacement of the grating patches (Nishida and Johnston 1999; Turi and Burr 2012). Given that the traditional MAE is spatial frequency selective, in this experiment we re-

peated the same procedure using unpatterned Gaussian blobs as test stimuli instead, to minimize the indirect effect of the traditional MAE. In addition, in this experiment participants viewed the stimuli through a dark circular tube through to ensure the edges of the screen and other parts of the room that could potentially serve as spatiotopic points of reference were not visible. Consequently, the visible screen was circular. All other experimental details were identical to those of the previous experiment.

Figure 5*A* shows the mean magnitude of the PMAE in all four conditions (with symbols indicating effect magnitudes for individual subjects). As before, the effect was largest in the full condition, but also quite substantial, and significantly greater than in the baseline (unmatched) condition, in the spatiotopic condition. The size of the adaptation effect in the spatiotopic condition was very similar to that observed with grating test stimuli. However, the effect increased in the full condition and decreased in the retinotopic condition. A repeated-measures ANOVA revealed a main effect of condition [*F*(3, 15) = 59.8, *P* < 0.0001].

We then carried out six pairwise Holms-Bonferroni-corrected *t*-tests. The largest PMAE occurred with the full adaptation condition (mean 43.0, SD 9.4 arc min), which was significantly greater than for the spatiotopic (mean 15.2, SD 7.0 arc min; *P* < 0.0001), retinotopic (mean 6.0, SD 7.4 arc min; *P* < 0.0001), and unmatched baseline conditions (mean 1.0, SD 3.5 arc min; *P* < 0.0001). The PMAE for the spatiotopic condition was significantly different from that for the unmatched condition (*P* < 0.001), whereas the effect for the retinotopic condition was not significantly different from that for the unmatched condition (*P* = 0.16). Finally, the effect for the spatiotopic condition was significantly greater than that for the retinotopic condition (*P* = 0.02).

Figure 5*B* shows the precision of the subjects in the alignment task, clearly similar across the different conditions. This

Fig. 5. *A*: mean magnitude of the PMAE for all subjects (*n* = 6) across the 4 experimental conditions: full (mean 43.0°; red), spatiotopic (mean 15.2°; blue), retinotopic (mean 6.0°; green), and unmatched (mean 1.0°; gray). *B*: mean and individual JNDs across the 4 experimental conditions in *experiment 2*. *C*: psychometric functions from a typical participant. Open circles indicate PMAE following adaptation to upward motion in the left grating and downward motion in the right grating; filled circles indicate the opposite. Difference between dashed arrows indicates the size of the PMAE in each case.
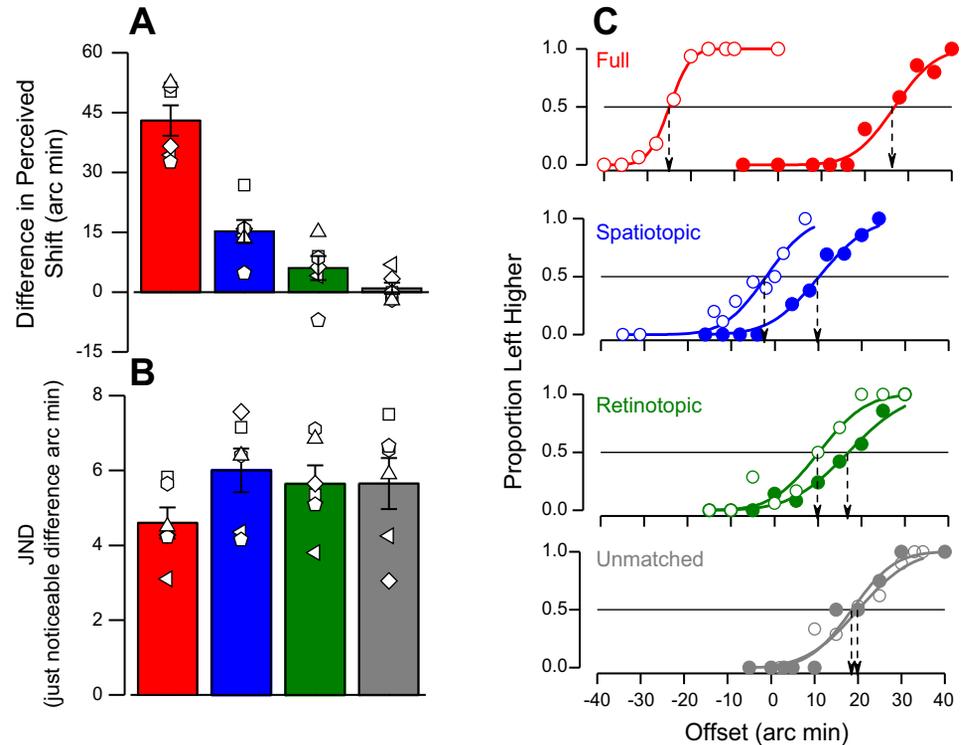
is confirmed by a repeated-measures ANOVA that revealed no main effect of condition [$F(3, 15)$ = 2.98, $P > 0.05$]. Finally, to compare precision across the first and second experiments, a two-way repeated-measures ANOVA was performed. The ANOVA revealed a main effect of the condition [$F(3,15)$ = 3.41, $P = 0.045$ (full: mean 4.45, SE 0.34; spatiotopic: mean 6.35, SE 0.51; retinotopic: mean 6.25, SE 0.56; and unmatched: mean 5.7, SE 0.47)] but no significant effect of the experiment [$F(1,5)$ = 1.29, $P = 0.30$] and no significant condition-by-experiment interaction [$F(3,15)$ = 1.053, $P = 0.39$]. This suggests that the precision of adjustment was very similar for the two types of stimuli used in the two experiments. Figure 5*C* plots the psychometric functions from a typical participant.

Finally, because the amount of image displacement caused by head tilt varied between individuals, we considered the possibility that the amplitude of the PMAE in the spatiotopic and retinotopic conditions could depend on the amount of afterimage displacement, as measured by the afterimage displacement in the pre-retinotopic experiment. As shown in Fig. 6, *A* and *B*, there were no significant correlations between the amplitude of afterimage displacement and perceived positional shift in either of the two conditions in both experiments (all *P* values >0.05). On the other hand, we found a good correlation [$r_{(22)}$ = 0.77, $P < 0.05$] between perceived shift after motion adaptation in the first and second experiment across all the experimental conditions for the six participants who carried out both experiments, as shown in Fig. 6*C*.

DISCUSSION

The aim of our study was to investigate whether the positional motion aftereffect (PMAE), where objects appear to be displaced after adaptation to motion, was spatially selective in spatiotopic or retinotopic coordinates after head tilt in the

frontal plane. We observed both spatiotopic and retinotopic components of the aftereffect. In the condition where local motion adaptation aftereffects were minimized by using unpatterned Gaussian blob test stimuli, the spatiotopic component was much larger than the retinotopic component, which did not reach statistical significance. The clear spatiotopic component in the illusion provides strong evidence for spatiotopic coding during head tilt.

The spatiotopic PMAE observed with intervening head rotations was never as large as that measured in the full adaptation condition. The reduction in effect size could result from an altered percept of the direction of gravity (Van Pelt et al. 2005). It may also suggest that at least part of the effect is generated by a retinotopic component, consistent with the retinotopic PMAE we observed, especially when gratings were used as test stimuli. These results are similar to our previous study on the PMAE, where we reported both retinotopic and spatiotopic effects after a saccade (Turi and Burr 2012). In that study we noted that the standard adaptation paradigm (like the one used in the present study) also causes a motion aftereffect, where the gratings within the windows appear to move after the real motion has stopped. This apparent motion could itself cause a displacement of apparent position, in the same way real motion does (De Valois and De Valois 1991). In that experiment (Turi and Burr 2012) we measured the PMAE with the apparent motion within the grating annulled by contrary motion, so the test gratings appeared stationary. Under those conditions, the retinotopic PMAE disappeared, leaving only the spatiotopic MAE. This points to two generators of the PMAE, one via the standard motion aftereffect, which is retinotopic and probably relatively low level, and another direct effect, which is spatiotopic and more high level (McKeefry et al. 2006). Both effects were present in *experiment 1*, with the use of stationary grat-
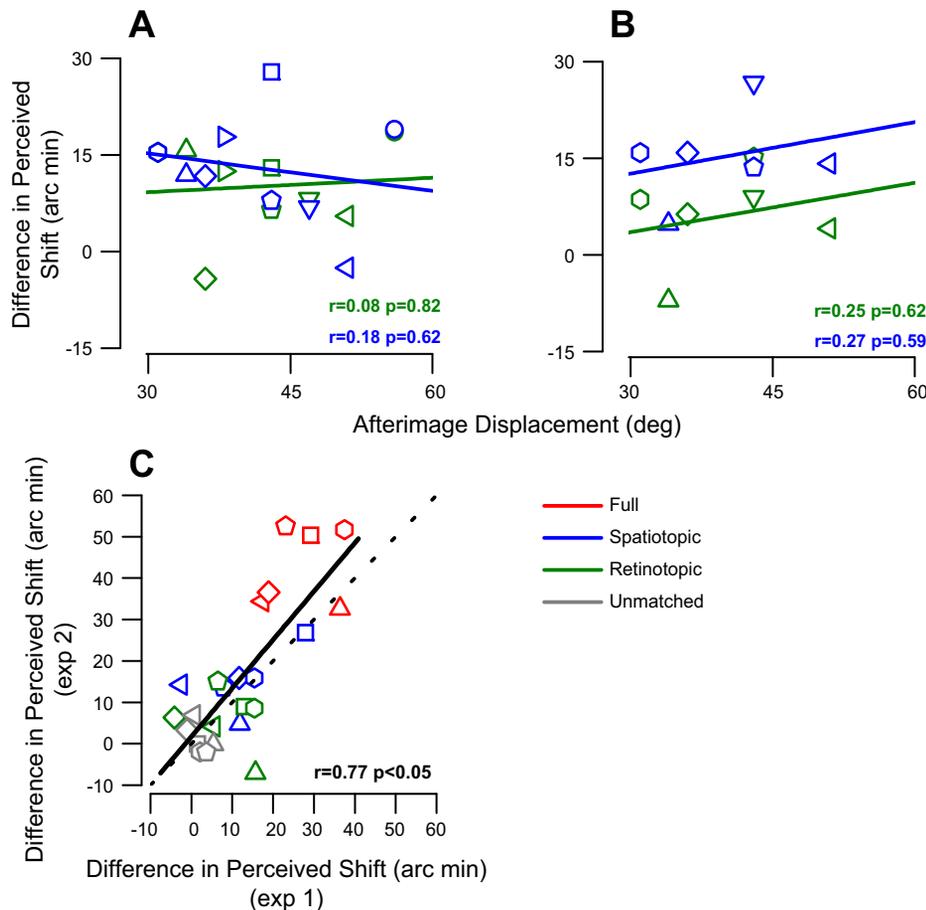
Fig. 6. Correlations between the amount of head tilt, in degrees measured by the afterimage displacement in the pre-retinotopic experiment, performed by each participant and the PMAE for the spatiotopic (blue) and retinotopic (green) conditions in the first (*A*) and second (*B*) experiment. *C*: correlation between perceived shift in the first (*exp 1*) and second experiment (*exp 2*) across all the experimental conditions ($N = 6$). Solid line represents the best linear fit to the data.

ings, where the spatiotopic and retinotopic effects were equally strong. To try and reduce this, we tested subjects with unpatterned test stimuli, simple Gaussian blobs. Under these conditions, the retinotopic effect was greatly reduced, to half that of the spatiotopic effect, and failed to reach significance compared with the unmatched baseline condition.

It could be argued that torsional eye movements (which we did not record) may have influenced our results during sustained head tilt (Palla et al. 2006). However, we do not believe that these small torsional movements of about 10% (Bockisch and Halswanter 2001) would have systematically affected our results, because in some blocks the adaptation was upward on the left stimulus and downward on the right, and in others, vice versa. Because head movements were always in the same direction, a drift in OCR would be in either the same or opposite direction of the illusion, and since our illusion index was the difference between the two conditions, the effect should cancel out.

Although controversial, there is now considerable evidence that adaptation and other effects can be selective in external coordinates after saccadic eye movements: that is, they are spatiotopic (see Burr and Morrone 2012 for review). However, no previous study has looked at spatiotopy after a head tilt. The present research shows that spatiotopy is preserved after head tilt, at least for the PMAE. This raises the question of what mechanisms may be responsible for spatiotopy, and how they function. Saccades cause simple shifts of the retinal image, which in principle can be corrected by simple subtraction of an "efference copy"

signal (van Holst and Mittelstaedt 1950). Head tilt, however, causes a rotation of the image, which requires a more complex correction. As mentioned earlier, a subpopulation of V1 neurons in the rhesus monkey has been shown to have head-centered receptive fields that use eye position information to shift their receptive field location and their retinal orientation tuning, partly compensating for OCR (Daddaoua et al. 2014). An equivalent subpopulation of neurons could exist in humans and could be part the neural substrate that deals with these kinds of distortions.

The present findings provide further support for the frequently contested notion that our visual system can utilize spatiotopic coding. They extend the previous research by showing that spatiotopic coding occurs not only after eye movement displacement of the retinal image but also after rotations of the retinal image caused by large head tilt along the frontal plane. Spatial maps can be modified by prolonged exposure to motion (McGraw et al. 2002; Nishida and Johnston 1999; Snowden 1998; Whitney and Cavanagh 2003), indicating a clear interaction between space and motion in the representation of our visual world. Results from the present study, as well as those from Turi and Burr (2012), show that the spatial maps that are affected by motion have a strong spatiotopic component. It is however important to note that although there is now very good evidence for the existence of spatiotopic mechanisms, it is extremely unlikely that they are the only mechanisms subserving visual stability: spatiotopic coding is likely to be too slow, and of too low resolution, for many aspects of per-

ception. As we have argued elsewhere (Burr and Morrone 2012), spatiotopic coding almost certainly play a role but are probably supplemented by more fast-acting mechanisms, such as transient remapping (Duhamel et al. 1997), which can create a transient spatiotopy that anticipates the action of saccades.

GRANTS

DISCLOSURES

The authors declare no competing interests that might be perceived to influence the results and/or discussion reported in this paper.

AUTHOR CONTRIBUTIONS

K.M., M.T., and D.C.B. conceived and designed research; K.M. and M.T. performed experiments; K.M. and M.T. analyzed data; K.M., M.T., and D.C.B. interpreted results of experiments; K.M. and M.T. prepared figures; K.M., M.T., and D.C.B. drafted manuscript; K.M., M.T., and D.C.B. edited and revised manuscript; K.M., M.T., and D.C.B. approved final version of manuscript.

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