The gender-specific face aftereffect is based in retinotopic not spatiotopic coordinates across several natural image transformations

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In four experiments, we measured the gender-specific face-aftereffect following subject's eye movement, head rotation, or head movement toward the display and following movement of the adapting stimulus itself to a new test location. In all experiments, the face aftereffect was strongest at the retinal position, orientation, and size of the adaptor. There was no advantage for the spatiotopic location in any experiment nor was there an advantage for the location newly occupied by the adapting face after it moved in the final experiment. Nevertheless, the aftereffect showed a broad gradient of transfer across location, orientation and size that, although centered on the retinotopic values of the adapting stimulus, covered ranges far exceeding the tuning bandwidths of neurons in early visual cortices. These results are consistent with a high-level site of adaptation (e.g. FFA) where units of face analysis have modest coverage of visual field, centered in retinotopic coordinates, but relatively broad tolerance for variations in size and orientation.

Introduction

David Marr (Marr, 1982) characterized vision as "*knowing what is where*." For much of the visual cortex, "knowing where" appears to be based in a *retinotopic coordinate system*. With each eye, head and body movement, the image of the world shifts on the retina and across the retinotopic cortical areas. Despite these displacements, our perception of the world is for the most part reassuringly stationary and stable. Evidently, these displacements in retinal coordinates are corrected at some higher level to generate world-based coordinates. Whether these coordinates are explicitly represented in a spatiotopic map (d'Avossa, Shulman, Snyder, & Corbetta, 2006; Melcher & Morrone, 2003) or are only derived for individual objects when needed (Colby, 1998; Klier & Angelaki, 2008; Wolbers, Hegarty, Buchel, & Loomis, 2008) is a topic of intense debate. Clearly, a retinotopic map can be made to track object locations in the world if retinotopic target positions are shifted to compensate for eye movements (Colby & Duhamel, 1996; Goldberg & Colby, 1992; Wurtz, 2008). One approach to examine the coordinate frame of visual coding is to test for aftereffects of adaptation when an eye movement intervenes between adaptation and test.

There have been reports of spatiotopic aftereffects—the presence of an aftereffect at the same spatial location as the adaptation but different retinal location—for tilt, shape and face adaptation (Melcher, 2005) as well as for motion (Ezzati, Golzar, & Afraz, 2008). As pointed out by Melcher (2005), faces are among the stimuli thought to require the highest level of visual analysis (Afraz, Kiani, & Esteky, 2006; Kanwisher & Yovel, 2006; Leopold, O'Toole, Vetter, & Blanz, 2001; Leopold, Rhodes, Muller, & Jeffery, 2005; Moradi, Koch, & Shimojo, 2005) and therefore more likely to tap spatiotopic representations. For that reason, we focus here on several types of retinotopic versus spatiotopic coordinate frames (head centered and body centered) for the face aftereffect (FAE). There are a number of different face aftereffects in the literature (identity, gender, race and general shape distortion, etc). We chose the gender-specific aftereffect as it is well documented (Ng, Boynton, & Fine, 2008; Rhodes et al., 2004; Webster, Kaping, Mizokami, & Duhamel, 2004) (also (Melcher, 2005)—gender adapt but identity test) and more robust in the periphery where we must test in order to compare retinotopy versus translational spatiotopy. Martelli et al, for example, has shown that face identification drops dramatically once fixation is outside the face itself (for frontal face views) (Martelli, Majaj, & Pelli, 2005).

The current study contains four experiments, investigating various types of retinotopy and spatiotopy for the FAE. The first experiment studies FAE across eye movements. This is similar to Melcher's (Melcher, 2005) original study with a simpler design. The second and third experiments of the current study are concerned with FAE across head movements. Following a translatory head movement, a complementary eye movement can maintain the position of a target on the retina (Kirschfeld, 1997) but no such correction is possible following a large head tilt. Nevertheless, despite the rotation of the image on the retina, our impression is still one of a stable world. If there is a spatiotopic representation, it needs to deal with rotations caused by head tilts as well as simple displacements caused by eye movements or translatory head movements. The second experiment examines this possibility, comparing the size of the FAE for test stimuli that match the adapting orientation in space versus stimuli with orientations matched on the retina. The retinal size of the visual objects can also change without any physical change in the actual size of objects as the head moves toward or away from them. No eye movements can correct for this transformation either. The third experiment contrasts the transfer of FAE across different retinal sizes for two conditions; when the change in retinal size is induced by head movement and when the size change is the result of an actual size change in the physical stimulus. Again, we compare the size of the FAE for test stimuli that match the adapting size in space versus stimuli with sizes matched on the retina.

A critical goal of the visual system is to encode where objects are. In this regard, a spatiotopic representation that explicitly codes object location in world coordinates might be only a special case. A more general solution is to keep the track of selected objects and their properties, including location, as they move (Gordon & Irwin, 1996; Kahneman, Treisman, & Gibbs, 1992). One paper has reported that the tilt aftereffect can be found at the end location of an object's trajectory when that object (that has an oriented texture) shifts position between adaptation and test (Melcher, 2008). In the paper, Melcher suggests that the spatiotopic aftereffects that he has reported are the consequence of object-specific effects that rely on the attentive tracking of visual objects. The fourth experiment investigates the question of a FAE that follows the adapting object as it shifts to new locations.

Experiment 1

Introduction

In the first experiment the spatial arrangement of the FAE is examined across eye movements. The main goal of this experiment is to examine the extent of retinotopoty versus spatiotopy of the FAE.

Methods

Subjects and procedure

Subjects were trained to identify the gender of faces that were chosen randomly from a morphing spectrum between male and female prototypes generated by a computer graphics program (FaceGen) based on 3D scans of real faces. The face stimuli were made with Singular Inversion's FaceGen which produces facial prototypes based on 3D scans of numerous faces (similar to the methods used by O'Toole AJ et al. (O'Toole, Vetter, & Blanz, 1999)). The facial structure varied across morphing level but the identical texture was mapped onto the structure for all faces. Experimental sessions started after subjects reached 85% performance level on the gender identification task. The initial training task included the whole range of morphing values to familiarize subjects with the main task. Subjects were given feedback for their correct and incorrect key presses at this stage. They could never reach 100% performance because there were difficult (near average face) stimuli in the set as well as faces with strong gender signal (far from the average).

Experiments were conducted in a dim lit room with the subjects' head resting on a chin and forehead rest 57 cm away from the screen. Stimulus presentation procedures were controlled by a PC processor using MATLAB psychtoolbox (version 2.54) and displayed on a 60 Hz 17 in. monitor. Face stimuli used for the test phase spanned seven levels of morphing (including the average face and four levels in each direction) between 75% male and 75% female prototypes. The female prototype (100% female face) was used as the adapting stimulus. The size of the face stimuli was 6° of visual angle (the average of the vertical and horizontal diameters of the face) and they were displayed on a uniform gray background.

Five subjects including one of the authors participated in Experiment 1. All subjects had normal or corrected-to-normal vision. There were four conditions in this experiment: spatiotopic test, control test (test was at neither the spatiotopic nor retinotopic location), retinotopic test and non-adapted test. In the first two conditions (spatiotopic and control) a small red fixation target appeared randomly at one of the two left and right lateral positions on the monitor, 10° away from the center of the display. Subjects were instructed to keep their gaze on the red target throughout the trial. Then the female prototype face was presented for 5 adaptation seconds at the lateral fixation spot. Then the adapting face disappeared and the fixation target moved to the center of the display (subjects had to follow that with their gaze). After 800 ms, the test stimulus was presented for 100 ms at either the same spatial location as the adaptor (spatiotopic test) or the opposite location on the screen (control location test) (Figure 1). The fixation point turned green then and subjects had to report the gender of the test face by pressing one of the two keyboard buttons. In the retinotopic adaptation condition, subjects maintained their
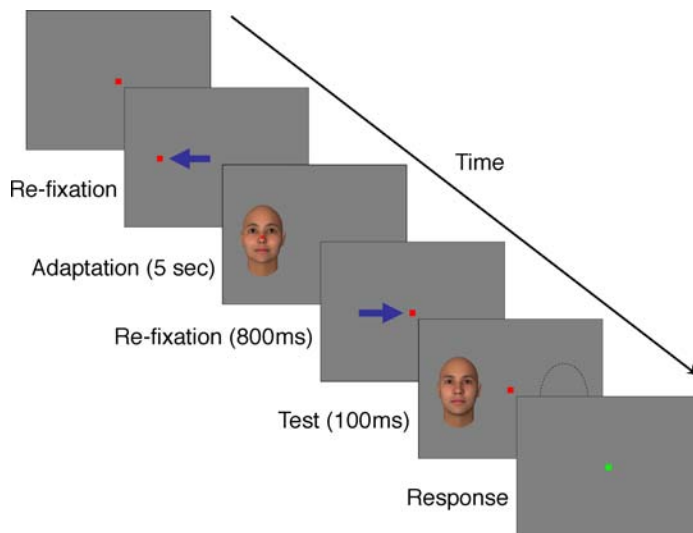
Figure 1. Experiment 1. Subjects started the trial by changing their fixation to a lateral fixation point (presented randomly to the left or right of the center of the display at 10° eccentricity). The adapting face was presented at the lateral fixation point for 5 seconds. Then the fixation point moved back to the center of the screen and a test stimulus was shown for 100 ms following a 800 ms blank period. The test stimulus was shown either at the same location as the adaptor (spatiotopic test, shown here) or at the opposite location on the screen with respect to the central fixation point (the control test condition which is neither spatiotopic nor retinotopic test). In the retinotopic test (not shown here) subjects maintained their fixation at the central target throughout the trial and both adaptor and test stimuli were shown at the same lateral location.

fixation on a central fixation point during the trial while the adapting face (the same as the other two conditions) was presented for 5 seconds at one of the lateral positions randomly. The test stimulus was presented at the same location following a 800 ms blank period. The non-adapted condition was the same as the retinotopic condition with the exception that there was no adapting stimulus. Eye-movement conditions (spatiotopic and control) were blocked together and no-eye-movement conditions (retinotopic and non-retinotopic) were run in separate blocks. The order of trial types within each block was randomized. There was a mandatory resting period of at least 2 minutes after each 28 trials. 280 trials were collected from each of the subjects. Eye movements were monitored at 250 Hz from the right eye using an *EyeLink I* infrared eye tracker (SR research).

Data analysis

The behavioral performance was plotted separately for each of the four conditions (for each subject) as the proportion of 'female' choices against the stimulus which varied from male to female (Figure 2). Data points were fitted with the following logistic function to calculate the
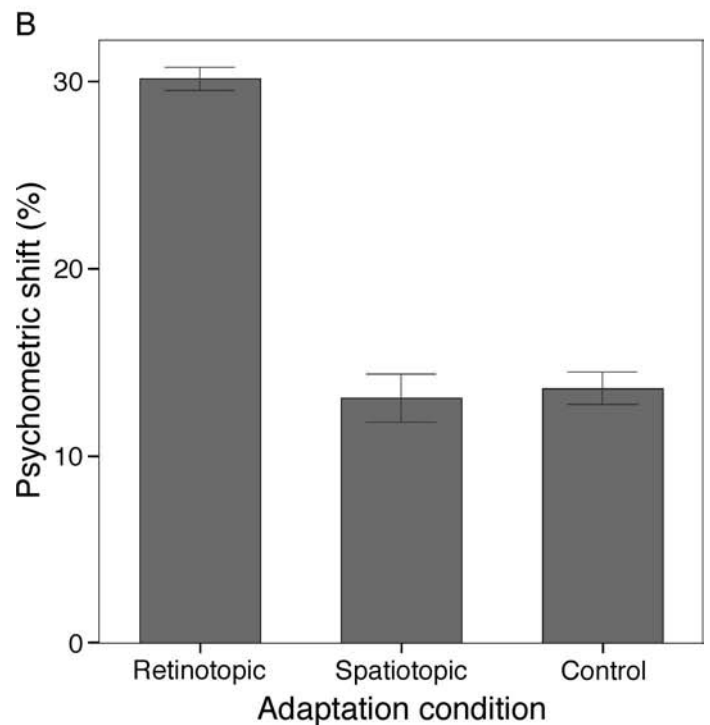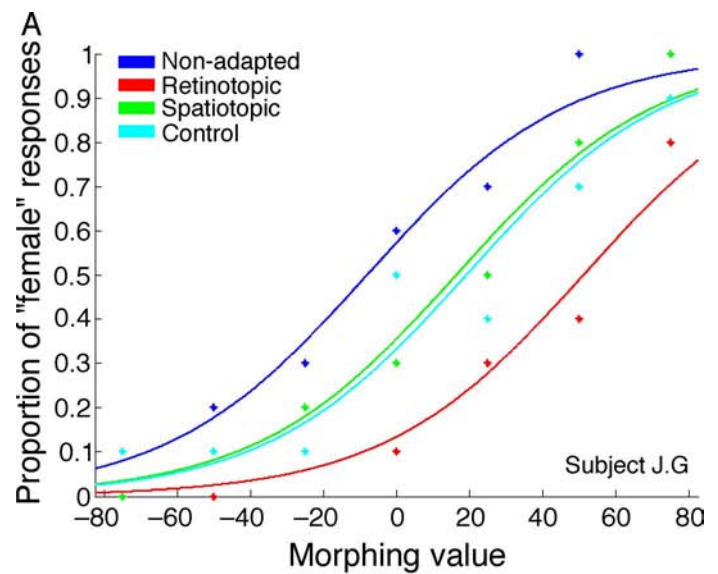

Figure 2. FAE as a function of test location. A) Psychometric functions for one of the subjects. The horizontal axis shows the face morphing level. Positive values indicate female faces and negative values stand for male. The vertical axis indicates the proportion of female responses. Colored curves show the logistic fits to the psychometric results for the four experimental conditions. The rightward shift of each psychometric curve from the non-adapted curve (shown in blue) indicates the magnitude of the face aftereffect for that condition. B) Face aftereffect strength for the three experimental conditions. The vertical axis shows the magnitude of the face aftereffect (the shift of the psychometric function from the baseline condition) on a scale of 0–100 (spanning the entire range between the male and the female prototype). The bars indicate the average FAE across subjects for the three experimental conditions. Error bars show ±1 *SE* of mean.

PSE (point of subject equality) where the face looked equally male and female for each curve.

$$p(x) = \frac{1}{1 + e^{-(\alpha + \beta x + \lambda_1 I_1 + \lambda_2 I_2 + \lambda_3 I_3)}}, \qquad (1)$$

where x is the morphing percent and $P(x)$ is the probability of female response. I is a binary variable, set to either 1 or 0 to indicate the presence or absence of each adaptation condition. α, β and λ are free parameters that were fit using the maximum likelihood fitting procedure (Meeker & Escobar, 1995).

The shift of the PSE for each of the adaptation conditions from the non-adapted condition was defined as the FAE magnitude.

Results

Figure 2A shows the results of Experiment 1 for one of the subjects. The largest shift of the psychometric function was observed for the retinotopic condition in all of the subjects. FAE was also significant for both spatiotopic and control conditions (logistic regression, $p < 0.05$ for all subjects). FAE was significantly larger for the retinotopic condition in contrast to both spatiotopic and control conditions (logistic regression, $p < 0.05$ for all subjects). No significant difference was observed between the spatiotopic and control conditions (logistic regression, $p > 0.6$ for all subjects). Figure 2B demonstrates the average shift of the psychometric function (from the non-adapted curve) for all of the subjects across different experimental conditions. Repeated measures ANOVA revealed the significant effect of experimental condition on the FAE magnitude ($F(2, 8) = 370.9$, $p < 0.001$). FAE was significantly smaller for both spatiotopic tests (paired sample t-test, $t(4) = 24.35$, $p < 0.01$, Bonferroni corrected) and the neither spatiotopic nor retinotopic control tests (paired sample t-test, $t(4) = 28.33$, $p < 0.01$, Bonferroni corrected) conditions in contrast to the retinotopic tests. No significant difference was observed between the shift values of the spatiotopic location and the neither spatiotopic nor retinotopic control test locations (paired sample t-test, $t(4) = -0.64$, $p = 0.56$).

Discussion

The FAE was strongest when the test and adapting locations matched in retinotopic coordinates. The FAE was smaller but still significant for both the spatiotopic and the control location with no privileged adaptation for the spatiotopic location. The results clearly show that adaptable face analyses units are based in a retinotopic coordinate frame. No evidence was found in support of

spatiotopy for the FAE. Our results show that spatiotopy is not a general property of face aftereffect. In the experiments that follow this one, we will expand the range of image transforms over which we test spatiotopy versus retinotopy to see if this first result is a general one or limited to translational changes in viewpoint.

Although we did not find spatiotopy, two other experiments have (Melcher, 2005; van Boxtel, Alais, & van Ee, 2008). Our experiment is most closely related to the FAE experiment of Melcher (2005). He showed a significant face aftereffect following a change of fixation when the test stimulus was presented at the same spatial location as the adapting stimulus. He also showed that the magnitude of the FAE for the spatiotopic location was approximately equal to a retinotopic FAE measured when adaptation and test stimuli were both presented at the same peripheral location on the retina and there were no eye movements. In contrast, we find that the FAE at the spatiotopic location is no different in strength from the control FAE seen at a location equally distant from the adapting site but which does not correspond to the adapted location in spatiotopic (or retinotopic) coordinates. In other words, we do not find any additional adaptation at the spatiotopic location that cannot be explained by general transfer of the FAE over distance.

How did Melcher's (2005) study differ from ours? First, his procedure did not correspond to the classic paradigm that we used (Fang & He, 2005; Jiang, Blanz, & O'Toole, 2006, 2009). Specifically, his subjects were adapted to a female face. They then had to identify a test face as one of three target male faces. The test face was chosen from one of three morphs, each of which varied from one of the three target male faces along a morphing path to the adapting female face. The percentage of correct discrimination naturally increased as the percentage of male target increased in the test morph. In Melcher's procedure, the percentage of correct decisions at a given level of morph was taken as the measure the strength of adaptation. In other words, adapting to the female face is taken as equivalent to adding more male face (or less female) in the test morph and so should increase performance. However, this "percent correct" measure suffers from a general performance confound as anything that improves performance (such as higher level factors like attention) will be taken as an increase in the FAE strength. For instance, depending on the task instructions or the subject's natural strategy for attention allocation, if the spatiotopic location drew more attention (in contrast to the control condition location), it would have higher performance and this would be considered an aftereffect in Melcher's analysis. To avoid this possible confound, other studies that used "percent correct" to determine the FAE always measured the percent correct for a non-adapted face as well (Anderson & Wilson, 2005; Leopold et al., 2001). This crucial non-adapted face control condition for the general performance is absent in Melcher's paradigm,

leaving open the possibility that general performance factors affected the results.

In our experiment, by measuring the shift of the psychometric function along the male–female morph dimension in a classical paradigm, we avoided possible general confounds and found no significant spatiotopic FAE, at least for the case of gender-specific FAE. In an earlier study, we investigated retinotopy vs. spatiotopy for the identity-specific FAE (Afraz, S-R., & Cavanagh, P. (2006). Is the "face aftereffect" retinotopic or spatiotopic? [Abstract]. *Journal of Vision,* http://journalofvision.org/6/6/882/). There we found no evidence to support the spatiotopy of the FAE although there were still methodological differences between our procedure and Melcher's (2005) that might explain the difference in outcome.

The second relevant paper (van Boxtel et al., 2008) found a spatiotopic bias in binocular rivalry following face adaptation. In that study, prolonged exposure to face or house stimuli biased subsequent rivalry in favor of the opposite category at both retinotopic and spatiotopic adaptation loci. However, their results show that in contrast to the strong and immediate retinotopic effect, the spatiotopic bias does not appear until after the first 10 seconds of testing and is much smaller than the bias at the retinotopic location. It is not yet clear what might underlie their result but higher level factors like spatial working memory (Horaguchi & Sugino, 2006; Irwin, Zacks, & Brown, 1990; Prime, Tsotsos, Keith, & Crawford, 2007) and attention (Golomb, Chun, & Mazer, 2008) cannot be ruled out.

As mentioned above, our goal is not to track down the differences between these two studies and our own but to extend our tests of retinotopy vs. spatiotopy to a wider range of image transforms. We have found an absence of general spatiotopy for simple eye movements but we now want to see if spatiotopy might nevertheless be found with other natural image transforms such as head translation or rotation or object movements.

Experiment 2

Introduction

The human anatomy allows a relatively wide range of head tilt toward the shoulders (planar rotation). Planar rotation of the skull induces fronto-parallel rotation of the image on the retina that needs to be discriminated from actual rotation of visual scenes in the external world. This creates a different version of the problem of spatiotopy. Experiment 2 is designed to examine rotation spatiotopy for the FAE. FAE transfers across large degrees of rotation (Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003; Watson & Clifford, 2003). Here we want to know if there is any difference in FAE following a head tilt of 90° for tests whose orientation matches the adapting

orientation on the screen and whose orientation matches the original retinal orientation.

One challenge for appropriate measurement of the FAE across head tilts is to control the confounding effect of the retinal cyclotorsion. Muscles of the orbit rotate the eyes in the direction opposite to that of the head, trying to stabilize the retinal image across head tilts (Balliet & Nakayama, 1978; Morrison, 1984). Although retinal cyclotorsion is possible only in a limited range (about 10°), it can bias the results in favor of a spatiotopic effect. To avoid this confounding factor, we measured and corrected for the exact amount of the retinal cyclotorsion for each individual.

Methods

Subjects and procedure

Four subjects including one of the authors participated in Experiment 2. To control the angle of the head tilt effectively a special V-shaped head-rest was used (see Figure 3). The head-rest had two (left and right) resting plates, each deviated 45° from the vertical midline line. A head band held two rectangular plastic plates on the left and right temporal bones of the subjects' head tightly. Subjects held their head between the two resting plates. They were trained to tilt their head (to the left or right depending on the trial instruction) and hold the solid plastic surface of the head band attached to the resting plate of the head-rest. Head band plates helped the subjects to keep their head aligned with the resting plates throughout the trial.

90° tilt of the skull does not transfer to 90° planar rotation of the retina because retinal cyclotorsion compensates part of the head rotation. Prior to the main experiment, the range of the retinal cyclotorsion across a 90° head tilt was measured for each individual separately. To measure the retinal cyclotorsion we used iconic aftereffect (Balliet & Nakayama, 1978). Subjects tilted their head to the left or right and fixated a small red target. A vertical bright line was then presented on a dark background for 10 seconds. Then the line disappeared and subjects tilted their head 90° to the opposite direction and fixated the red target again. Holding their head tilted, they adjusted the angle of a fade gray test line to match the after image of the adapted line. Each subject performed 10 adjustments.

Similar to the previous experiment there were four conditions in Experiment 2: spatiotopic, control (neither spatiotopic nor retinotopic), retinotopic and non-adapted. In the first two conditions (spatiotopic and control) a small red fixation target appeared in the center of the screen. Subjects were instructed to keep their gaze on the red target throughout the trial. An arrow indicated the direction of the head tilt at the beginning of each trial. The subject initiated the trial by pressing the space bar when she/he placed her/his head on the head-rest appropriately. A tilted adapting face was presented then at the fixation point for 6 seconds. The planar angle of the
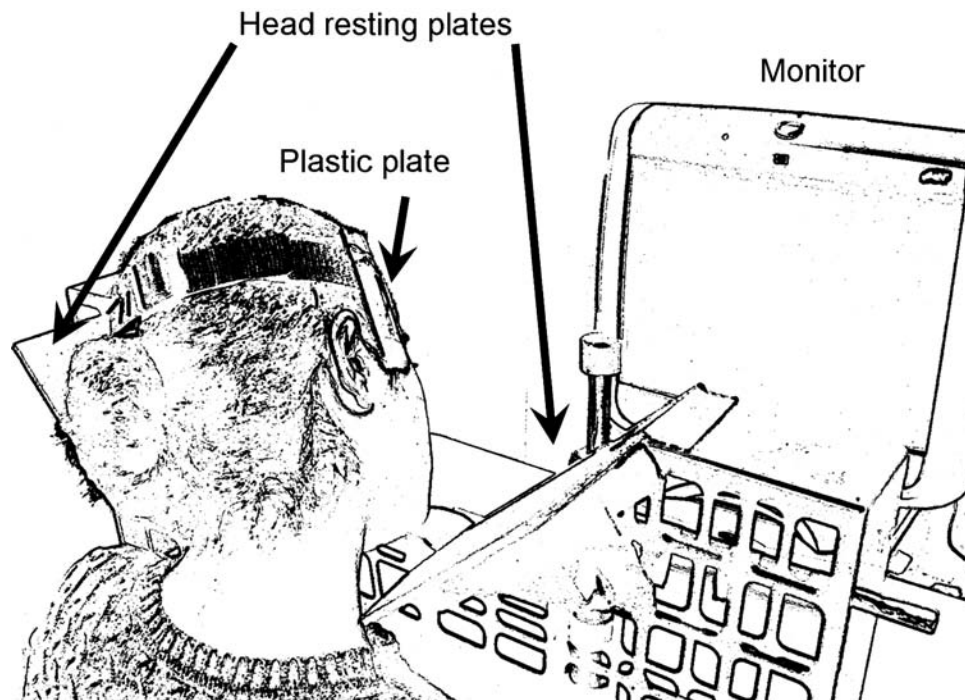
Figure 3. The V-shaped head-rest. Rectangular plastic plates were attached tightly to the temporal bone of the subjects with a head band. Subjects were asked to tilt their head and keep the plastic plate attached to the resting plates on the V-shaped head rest according to the trial instruction.

adapting face was chosen in a way to match the vertical meridian of the retina (based on the measurement of the retinal cyclotorsion). In other words, the adapting face was presented upright and vertical on the retina. This translates to a ∼45° tilt away from the vertical midline of the screen (the exact angle varies slightly from subject to subject depending on their cyclotorsion factor, and is ∼45° left or ∼45° right depending on the trial). Following the adaptation, the adapting face disappeared and an arrow indicated that the subject has to tilt her/his head to the opposite direction from that held during adaptation. The subject pressed the space bar again after completion of the head movement. The time delay between disappearance of the adaptor and the second space bar press was recorded for future use. The test stimulus was presented then at either the spatiotopic angle (matching the adapting angle on the screen) or the control angle, rotated ∼180 deg from the adapting stimulus on the screen. The spatiotopic angle was the same angle as the adapting stimulus (about 45 deg, half way between upright and horizontal on the screen, and oriented either to the left or right depending on the trial). Note that although the adapting and test stimuli are shown with the same angle on the screen in this spatiotopic condition, their angle has changed by almost 90 deg in retinotopic coordinates. The adapting stimulus is shown at the vertical meridian of the retina and the test stimulus is deviated from the vertical meridian to a direction opposite to the head-tilt direction producing a total shift on the retinal of almost 90 deg. The control angle was chosen to produce mirror symmetric deviation

of the test face from the vertical meridian relative to the spatiotopic angle (∼135° tilted away from the vertical orientation on the screen, about half way between horizontal and upside down) and so be about 90 deg shifted on the retina, in the opposite direction from the spatiotopic test, and therefore about 180 degrees rotated from the orientation of the spatiotopic test on the retina. Thus, the retinal angular distance between the adaptor and the test was identical and opposite in the two conditions (see Figure 4). The actual deviation of the test stimuli from the vertical meridian of the retina in the spatiotopic and control conditions varied across subject (between 84.4° and 75.9°) depending on their retinal cyclotorsion measurements.

Head-movement conditions (spatiotopic and control) were blocked together and no-head-movement conditions (retinotopic and non-adapted) were run in separate blocks. 336 trials were collected from each of the subjects. The inter-stimulus interval (the delay between the adaptor and the test stimulus) varied from trial to trial in the head-movement conditions (depending on how fast the subjects could make the movement). The inter-stimulus intervals for the retinotopic condition for each subject were selected pseudorandomly (without repetition) from the recorded inter-stimulus interval profile of the same subject for the head-movement conditions. Thus, the average and the distribution of inter-stimulus intervals were the same for the retinotopic condition and the two head-movement conditions. In the retinotopic adaptation condition, subjects maintained their head position to the left or right
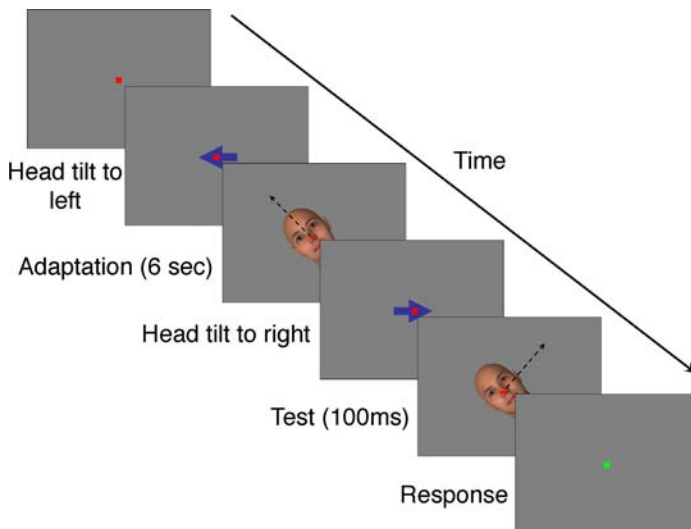
Figure 4. Experiment 2. Subjects started the trial by tilting their head to a lateral angle (±45°). The adapting face, aligned with the vertical meridian of the retina (~45° tilted away from the vertical midline of the screen), was presented for 6 seconds (the dashed arrow indicates the retinal vertical meridian and the arrow head points to the top of the retina). Subjects then tilted their head to the opposite direction and pressed the space bar. The test stimulus was presented then either at the same spatial angle as the adaptor (spatiotopic condition, shown here) or at the opposite angle relative to the vertical meridian of the retina (control condition −~135° tilted away from the vertical midline of the screen). The retinal cyclotorsion (see the text) is set to zero in this illustration so the angle between the test stimulus and the retinal vertical meridian is 90° (84.4° and 75.9° in the actual experiment).

while the adapting face (the same as the other two conditions) was presented for 6 seconds at one of the two lateral angles randomly. The test stimulus was presented at the same angle following the inter-stimulus interval (see above). The non-adapted condition was the same as the retinotopic condition with the exception that there was no adapting stimulus.

As in the previous experiment, the female face was used as the adaptor. Face stimuli used for the test phase spanned seven levels of morphing (including the average face and four levels in each direction) between 18.75% male and 18.75% female prototypes. Note the smaller range of test stimuli compared to the previous experiment. This range is selected to avoid saturation of the psychometric performance because the stimuli were presented in the fovea in this experiment and they were easier to distinguish. To investigate the possible effect of head movements on the retinotopic adaptation 3 of the subjects underwent a "head movement retinotopic" condition. In the head movement retinotopic condition, subjects titled their head to one side and the adapting face was presented at the vertical meridian of the retina. Then subjects tilted their head to the opposite direction and the test stimulus was presented at the vertical meridian of the retina again.

Note that in this condition, the test stimulus is shown at a different angle on the screen compared to the adapting stimulus. Other stimulus and apparatus parameters were the same as the first experiment.

Data analysis

The same data analysis procedures as the first experiment were used in this experiment.

Results

On average it took 1.19 seconds (Standard deviation = 0.3) for the subjects to tilt their head in head tilt trials (average inters-stimulus interval for all adaptation conditions). Figure 5A shows the results of Experiment 2 for one of the subjects. Just like the first experiment, the largest shift of the psychometric function was observed for the retinotopic condition in all of the subjects. Both spatiotopic and control curves were significantly shifted rightwards from the non-adapted curve (logistic regression, $p < 0.05$ for all subjects). FAE was significantly larger for the retinotopic condition in contrast to both spatiotopic and control conditions (logistic regression, $p < 0.05$ for all subjects). No significant difference was observed between the spatiotopic and control conditions (logistic regression, $p > 0.6$ for all subjects). Figure 5B shows the average shift of the psychometric function (from the non-adapted curve) for all of the subjects across various experimental conditions. Repeated measures ANOVA revealed the significant effect of experimental condition on the FAE magnitude ($F(2, 6) = 43.4$, $p < 0.001$). FAE was significantly smaller for both spatiotopic (paired sample t-test, $t(3) = 8.5$, $p < 0.01$, Bonferroni corrected) and control (paired sample t-test, $t(3) = 8.6$, $p < 0.01$, Bonferroni corrected) conditions in contrast to the retinotopic condition. No significant difference was observed between the shift values of the spatiotopic and control conditions (paired sample t-test, $t(3) = 0.26$, $p = 0.8$). In "head movement retinotopic" condition the FAE was as big as the main retinotopic condition and no significant difference was observed between the main retinotopic condition and the head movement retinotopic condition (logistic regression, $p > 0.7$ for all subjects).

Discussion

The results of Experiment 2 show that FAE is maximal when the retinal orientations of the adaptor and test are matched even if the head tilts between adaptation and test phases. Although the FAE transfers across a broad range of orientation, it remains strongest at its retinotopic angle of adaptation and spreads symmetrically from this retinal orientation to the spatiotopic and control orientations which are both about a 90 deg rotation, in opposite
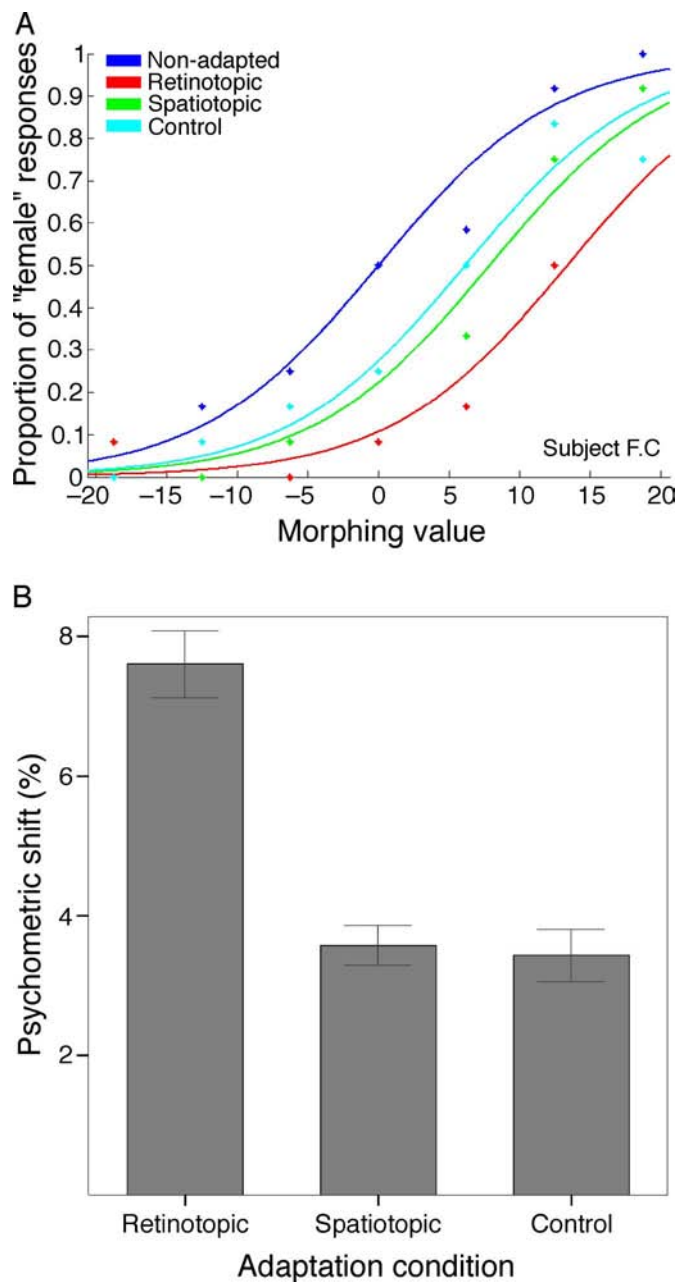
Figure 5. The FAE as a function of orientation match between adapt and test. A) Psychometric functions for one of the subjects. The horizontal axis shows the face morphing level. Positive values indicate female faces and negative values stand for male. The vertical axis indicates the proportion of female responses. Colored curves show the logistic fits to the psychometric results for the four experimental conditions. The rightward shift of each psychometric curve from the non-adapted curve (shown in blue) indicates the magnitude of the face aftereffect for that condition. B) Face aftereffect strength for the three experimental conditions. The vertical axis shows the magnitude of the face aftereffect (the shift of the psychometric function from the baseline condition) on a scale of 0–100 (spanning the entire range between the male and the female prototype). The bars indicate the average FAE across subjects for the three experimental conditions. Error bars show ±1 *SE* of mean.

directions, on the retina. On the screen, the spatiotopic test is oriented about halfway between the upright and horizontal whereas the control is oriented about halfway between the upside down and horizontal. In other words there is a face-inversion component possible in the control angle in screen coordinates—although both land sideways (90 rotation) on the retina in opposite directions. Indeed, although on the screen the control condition is more or less inverted and the spatiotopic test is not, the FAE spreads equally to both. Here again, as in the previous experiment, we find strong evidence for retinotopy, now over the dimension of orientation, and none for spatiotopy.

Experiment 3

Introduction

Change of the retinal image size due to head movements is another major geometrical image change that cannot be corrected by eye movements. As we move toward or away from visual stimuli their retinal size change drastically without any physical change in the actual size of the stimulus. In the third experiment, we measure the effect of the change in the retinal size on the FAE and contrast it for the retinotopic and spatiotopic conditions as well as the control which is neither retinotopic nor spatiotopic. The general logic of the experiment is similar to the previous experiments; the retinal size of the test stimulus changes relative to the adapting stimulus following a head movement. This retinal size change reflects either no physical change in the stimulus size on the screen (spatiotopic condition) or actual change of the stimulus size on the display (control condition). The retinal size is kept unchanged in the retinotopic condition.

Methods
Subjects and procedure

Four subjects including one of the authors participated in Experiment 3. To control the distance of the eyes from the screen effectively a special forehead/backhead-rest was used (see Figure 6). The distance between the forehead rest and the backhead rest was adjusted to the skull size of each individual to provide 28.5 cm range for the movement of the eyes plane. The screen was 57 cm away from the eyes when subjects held their head on the backhead rest. By this arrangement, the distance between the eyes and the display screen varied from 57 cm to 28.5 cm as the subjects moved their head from the backhead rest to the forehead rest. Subjects were trained to hold their head on the head rest (forehead or backhead rest depending on the condition) and move it forward or
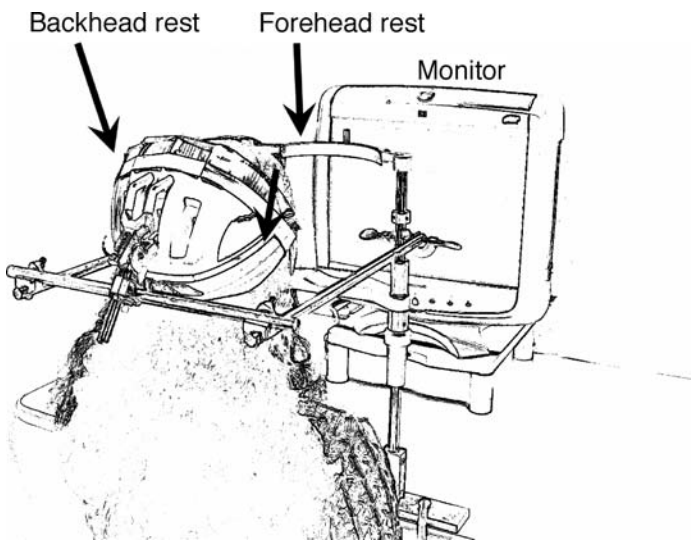
Figure 6. The forehead/backhead rest. The head rest was designed to control the distance of the eyes from the display screen. Subjects were asked to rest their head on the backhead rest and move it forward to the forehead rest when instructed. Or vice versa.

backward (upon the instruction) as fast as possible when instructed.

Similar to the previous experiments there were four conditions in Experiment 3: spatiotopic, control (neither spatiotopic nor retinotopic), retinotopic and non-adapted. In the first two conditions (spatiotopic and control) a small red fixation target appeared in the center of the screen. Subjects were instructed to keep their gaze on the red target throughout the trial. The instructions about head position were presented on the screen when necessary (see Figure 7). The subject initiated the trial by pressing the space bar when she/he placed her/his head on the head rest (forehead or backhead rest, upon the instruction) appropriately. The adapting face of 6° of visual angle was presented at the fixation point for 6 seconds. Following the adaptation, the adapting face disappeared and a "Go" signal on the screen indicated that the subject has to move her/his head forward or backward (depending on the condition). The subject pressed the space bar again after completion of the head movement. The time delay between disappearance of the adaptor and the second space bar press was recorded for future use. The test stimulus was presented then at either 11.9° or 3° sizes. If the subject was adapted at the far location but was tested at the near location, the 11.9° stimulus has the same screen size as the 6° adaptor (spatiotopic condition). The 3° stimulus matches neither the retinal nor the screen size (it is the neither-retinotopic-nor-spatiotopic control condition). Alternatively, if the subject was adapted at the near location (28.5 cm distance from the screen), then moved to the far location for the test, the 3° stimulus has the same screen size as the adaptor (spatiotopic) and the

11.9° stimulus matched neither the size of the adaptor on the retina nor on the screen (control).

In the first retinotopic adaptation condition, subjects held their head on the backhead-rest or the forehead rest (depending on the trial) throughout the trial. The test stimulus was presented at 6° of visual angle following the inter-stimulus interval. The inter-stimulus interval was determined from the results of the head movement trials (see the Methods section of Experiment 2 for more details). The non-adapted condition was the same as the retinotopic condition with the exception that there was no adapting stimulus. In the second retinotopic adaptation condition, 3 of the 4 subjects underwent a "head movement retinotopic" condition. In the head movement retinotopic condition, subjects moved their head (forward of backward depending on the condition) after adaptation to a 6° adaptor. They were presented then with a 6° test stimulus. Note that in this condition, the test stimulus is shown at a different size on the screen compared to the adapting stimulus. Other stimulus and apparatus parameters were the same as the first experiment.
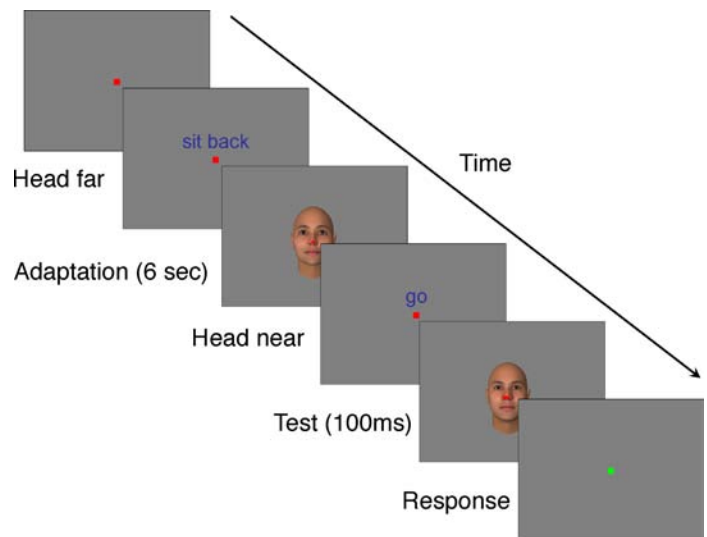

Figure 7. Experiment 3. Subjects started the trial by resting their head on the forehead or the backhead rest upon the instruction. The adapting face was presented for 6 seconds at the center of the display. Subjects moved their head (toward or away from the screen upon the instruction) and then pressed the space bar. The test stimulus was presented then either at a different (half or double depending on the condition) retinal size that corresponded to the same screen size as the adaptor (spatiotopic condition, shown here) or a different (half or double) retinal size that does not correspond to the screen size of the adaptor (control condition). In the retinotopic condition, the adapting and test stimuli were of the same retinal size. Note that in the control condition, the adapting and test stimuli matched neither in screen size not in retinal size but differed in retinal size by the same factor as did the spatiotopic adapt and test size (1 octave).

Data analysis

The same data analysis procedures as the previous experiments were used in this experiment.

Results

On average it took 1.3 seconds (Standard deviation = 0.15) for the subjects to move their head in head-movement trials (average inters-stimulus interval for all adaptation conditions). Figure 8A shows the results of Experiment 3 for one of the subjects. Just like the first experiment, the largest shift of the psychometric function was observed for the retinotopic condition in all of the subjects. Both spatiotopic and control curves were significantly shifted rightwards from the non-adapted curve (logistic regression, $p < 0.05$ for all subjects). FAE was significantly larger for the retinotopic condition in contrast to both spatiotopic and control conditions (logistic regression, $p < 0.05$ for all subjects). No significant difference was observed between the spatio-topic and control conditions (logistic regression, $p > 0.4$ for all subjects). Figure 8B shows the average shift of the psychometric function (from the non-adapted curve) for all of the subjects across various experimental conditions. Repeated measures ANOVA revealed the significant effect of experimental condition on the FAE magnitude ($F(2, 6) = 49.4$, $p < 0.001$). FAE was significantly smaller for both spatiotopic (paired sample t-test, $t(3) = 9.9$, $p < 0.01$, Bonferroni corrected) and control (paired sample t-test, $t(3) = 11.9$, $p < 0.01$, Bonferroni corrected) conditions in contrast to the retinotopic condition. No significant difference was observed between the shift values of the spatiotopic and control conditions (paired sample t-test, $t(3) = 0.16$, $p = 0.9$). In "head movement retinotopic" condition the FAE was as big as the main retinotopic condition and no significant difference was observed between the main retinotopic condition and the head movement retinotopic condition (logistic regression, $p > 0.6$ for all 3 subjects who ran in both conditions).

Discussion

Experiment 3 shows that the FAE spreads over a broad range of stimulus sizes. Following a head movement that changed the distance between eyes and the screen, the FAE remained strongest for tests matching the retinotopic size of the adaptor (which corresponds to a different screen size) and decreased for other stimulus sizes whether or not they matched the screen size of the adaptor (the spatiotopic test). As in previous experiments, again we found strong evidence for retinotopic coordinate frame for the FAE, now over the dimension of size, and no evidence in support of spatiotopy.
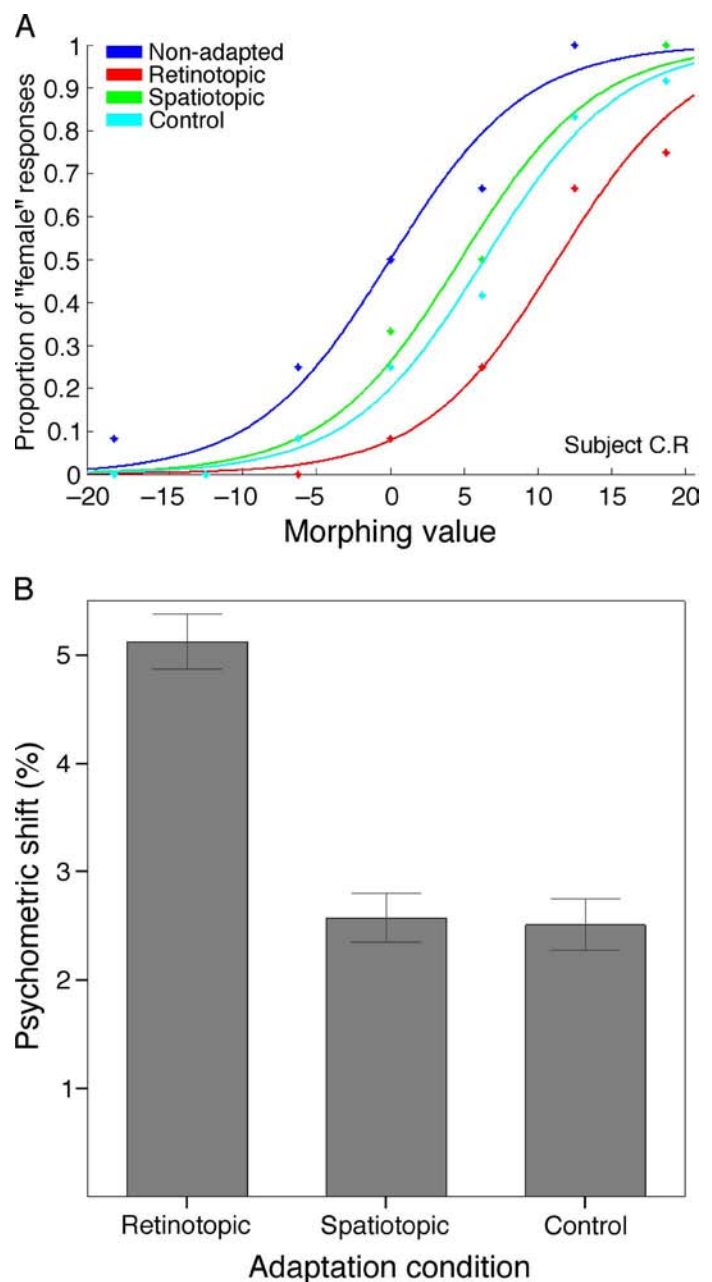

Figure 8. The FAE as a function of size match between adapt and test. A) Psychometric functions for one of the subjects. The horizontal axis shows the face morphing level. Positive values indicate female faces and negative values stand for male. The vertical axis indicates the proportion of female responses. Colored curves show the logistic fits to the psychometric results for the four experimental conditions. The rightward shift of each psycho-metric curve from the non-adapted curve (shown in blue) indicates the magnitude of the face aftereffect for that condition. B) Face aftereffect strength for the three experimental conditions. The vertical axis shows the magnitude of the face aftereffect (the shift of the psychometric function from the baseline condition) on a scale of 0–100 (spanning the entire range between the male and the female prototype). The bars indicate the average FAE across subjects for the three experimental conditions. Error bars show ±1 *SE* of mean.
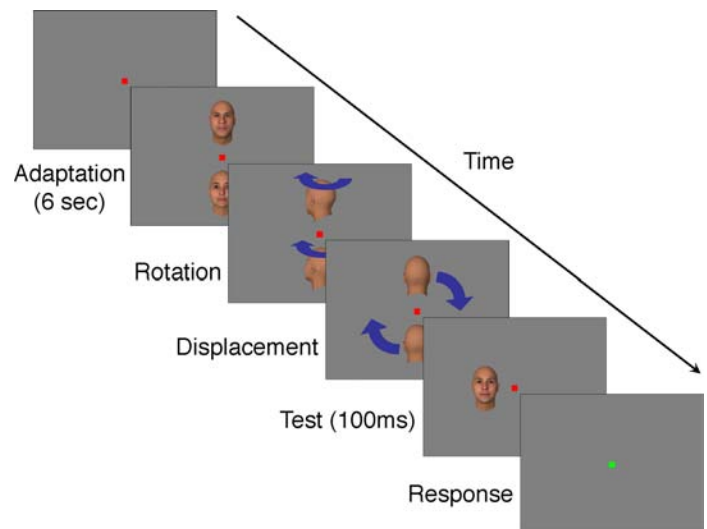
Experiment 4

Introduction

The idea of object-based remapping of visual features has been recently suggested as a possible mechanism for spatial constancy (Melcher, 2008). It has been claimed that following adaptation to features of a visual object at a given location on the screen, if that object moves to a new location, its aftereffect transfers to the new location on the screen even if the visual features of the object have been occluded during the displacement (Melcher, 2008). Experiment 4 put this idea to test for the FAE. It also included a condition with an eye movement during the interval between adaptation and test as suggested by Melcher (2008) to strengthen the object-specific adaptation.

Methods

Subjects and procedure

Four subjects including one of the authors participated in Experiment 4. Following presentation of a fixation point for 1 second, each trial started with simultaneous presentation of a male and a female face for 6 seconds. The faces were 2° of visual angle in size and were centered on the vertical midline of the screen at 3.6° eccentricity on top and bottom of the fixation point (see Figure 9). In half of the trials (randomly determined) the male face was presented on top and in the other half the female face was shown on top. Both faces rotated in depth then and turned the back of their heads to the observer. The 3D model of the heads was morphed in a way that the back of both heads (the male and the female ones) were identical. Rotation in depth took 400 ms. In non-adapted trials only the back of the heads were shown in this phase. Then the back of the heads moved smoothly on a circular path centered at the fixation point. They traveled 90° on this circular path and stopped at a new pair of locations at the left and right of the fixation point. We had shown previously that the FAE spreads in space, but following simultaneous adaptation to two opposite faces, the two effects cancel at locations equidistant from the two adaptors (Afraz & Cavanagh, 2008). With the two adaptors here being above and below fixation, any retinotopic aftereffects should cancel along the horizontal line between the two (the horizontal meridian). We re-confirmed this basic finding for the gender-specific FAE (the experimental procedure used here) in our pilot experiments. With the horizontal meridian as the destination of the two moving objects here, we should be able to measure the pure effect of any possible object-base aftereffect. The displacement of the two heads to the new, horizontally arranged locations took 0.75 seconds. The direction of the displacement motion was randomly determined for each trial (clockwise or counter-clockwise). The two heads stayed at

Figure 9. Experiment 4. Each trial started with simultaneous adaptation to a male and a female face. The adapting stimuli were aligned vertically on above and below the fixation point. Following the adaptation phase, the heads rotated smoothly, turning their back to the viewer. Then the heads moved on a circular path—centered at the fixation point—to the horizontally aligned new positions on the left and right of the fixation point. The subject had to track the identity of each head across this displacement. A test stimulus was then presented either at the retinotopic site of adaptation (where one of the adapting faces was originally shown prior to the displacement) or at the terminal location of one of the two heads after the displacement.

their new locations for 700 ms. The two heads disappeared then and following a blank period of 300 ms a single test stimulus was shown at one of the four cardinal directions with respect to the fixation point for 100 ms. The top and bottom locations are the retinotopic tests, which would be either a male or female adaptation test, depending on whether upper or lower was probed and the assignment of the male or female locations during adaptation. The left and right locations are the object-specific tests which would be either a male or female object-specific adaptation test, depending on whether left or right position was probed, whether the head shifts clockwise or counterclockwise following adaptation and the assignment of the male or female locations during adaptation. The total inter-stimulus interval between the adaptation phase and the test phase was 2150 ms.

The trials in which the test stimulus was presented on top or bottom of the fixation point were called retinotopic trials as the location of the test stimulus associated with the retinal location of the adaptor. Trials in which the test stimulus was shown on the horizontal midline (to the left or right of the fixation) were named *object-specific* trials as they were associated with the final location of the tracked object (in the absence of the gender signal). Subjects were instructed to covertly track the two faces across their displacements. To make sure that the subjects tracked the

stimuli properly, instead of directly reporting the gender of the test stimulus, they were asked to report if the test stimulus had the same gender as its adaptor by pressing one of the two keys on the keyboard with their right hand. Note that each test location was associated with one of the two adaptors as its original or terminal location. For non-adapted trials the subjects had to directly determine the gender of the test face by pressing keys with their left hand.

Each subject completed 420 experimental trials. There were 5 conditions in this experiment: male adapted retinotopic (when the test was presented at the retinotopic adaptation locus of the male adaptor), female adapted retinotopic (when the test was presented at the retinotopic adaptation locus of the female adaptor), male adapted object-specific (when the test was presented at the final position of the male adaptor after its displacement), female adapted object-specific (when the test was presented at the final position of the female adaptor after its displacement) and non-adapted. Different conditions were not blocked together and the order of various trial types was randomized. Other stimulus and apparatus parameters were the same as previous experiments.

Melcher (2008) claimed that making a saccadic eye movement during the object movement phase strengthens that object-based aftereffect. To investigate this possibility for the FAE, two of the subjects participated in a complementary experiment. All of the parameters were the same as the main experiment except that during the head displacement phase the fixation target moved to a peripheral location on the diagonal of the display screen, 6° of visual field away from the center for 400 ms. Subjects were instructed to saccade to the target when it moves to a new position. Then the fixation target moved back to its original central position and stayed there for the rest of the trial.

Data analysis

The same data analysis procedures as the previous experiments were used in this experiment.

Results

Figure 10 demonstrates the results of Experiment 4. Deviation of the psychometric curves of male and female adaptation from each other indicates the FAE. As demonstrated for a typical subject in Figure 10A also the average of all subjects in Figure 10B, the psychometric curves of male and female adaptation were significantly deviated from each other in all cases (logistic regression, $p < 0.01$, Bonferroni corrected) for the retinotopic condition. No significant effect was observed for the objectotopic condition (logistic regression, $p > 0.5$, Bonferroni corrected). The average of psychometric shift values (shifts from the baseline non-adapted condition) for all of the subjects also showed the significant difference between male adaptation

and female adaptation for the retinotopic condition (paired sample t-test, $t(3) = -22.3$, $p < 0.001$) but not for the objectotopic condition (paired sample t-test, $t(3) = -0.02$, $p = 0.9$). The results of the complementary experiment were the same as the main experiment and the application a saccade in the middle of the trial did not change the results. More specifically, no significant difference was observed between the male adapted and female adapted curves for the objectotopic condition in the complementary experiment (logistic regression, $p > 0.4$).

Discussion

The results of Experiment 4 show that the FAE remains strongest at the retinotopic location of the adaptor even if the adaptor moves to a different position after the adaptation. The FAE did not follow the object to its new location. We have previously shown that the FAE transfers over space (Afraz & Cavanagh, 2008). We have also shown that simultaneous adaptation to two opposite faces produces a cancellation of the two FAEs halfway between the two adaptors. An object-specific FAE should therefore be the only FAE evident at locations equidistant from both adaptors (along the horizontal meridian in this case), so following adaptation, we displaced the adapting stimuli to this neutral zone to increase the chance of observing the hypothesized object-specific component of the FAE. However we failed to observe any such effect. It has been suggested that introducing an eye movement between the adaptation and test phases increases the strength of an object-specific aftereffect, at least in the case of the tilt (Melcher, 2008); nevertheless, our results were not influenced by a saccade introduced between adapt and test. One might claim that the aftereffect was reduced by stimulus motion or the longer delays between the adaptation and test phases, but the existence and strength of the FAE at the retinotopic test location makes this unlikely. The magnitude of the FAE at the retinotopic location here is comparable to our previous measurements of the FAE with simultaneous adaptation to two opposite faces using the same stimulus size and eccentricity (Afraz & Cavanagh, 2008).

Discussion

The results of all four experiments confirm that FAE is at maximum strength for tests that match the original retinal values of position, orientation and size. The effect does spread to other test locations around the original retinotopic ones, falling to a value about half its maximum at a spatial offset of 10°, an orientation difference of ~80° and a size difference of 1 octave. The range of spread is only approximately determined here but they show a tuning for the FAE that is far broader than that seen in the
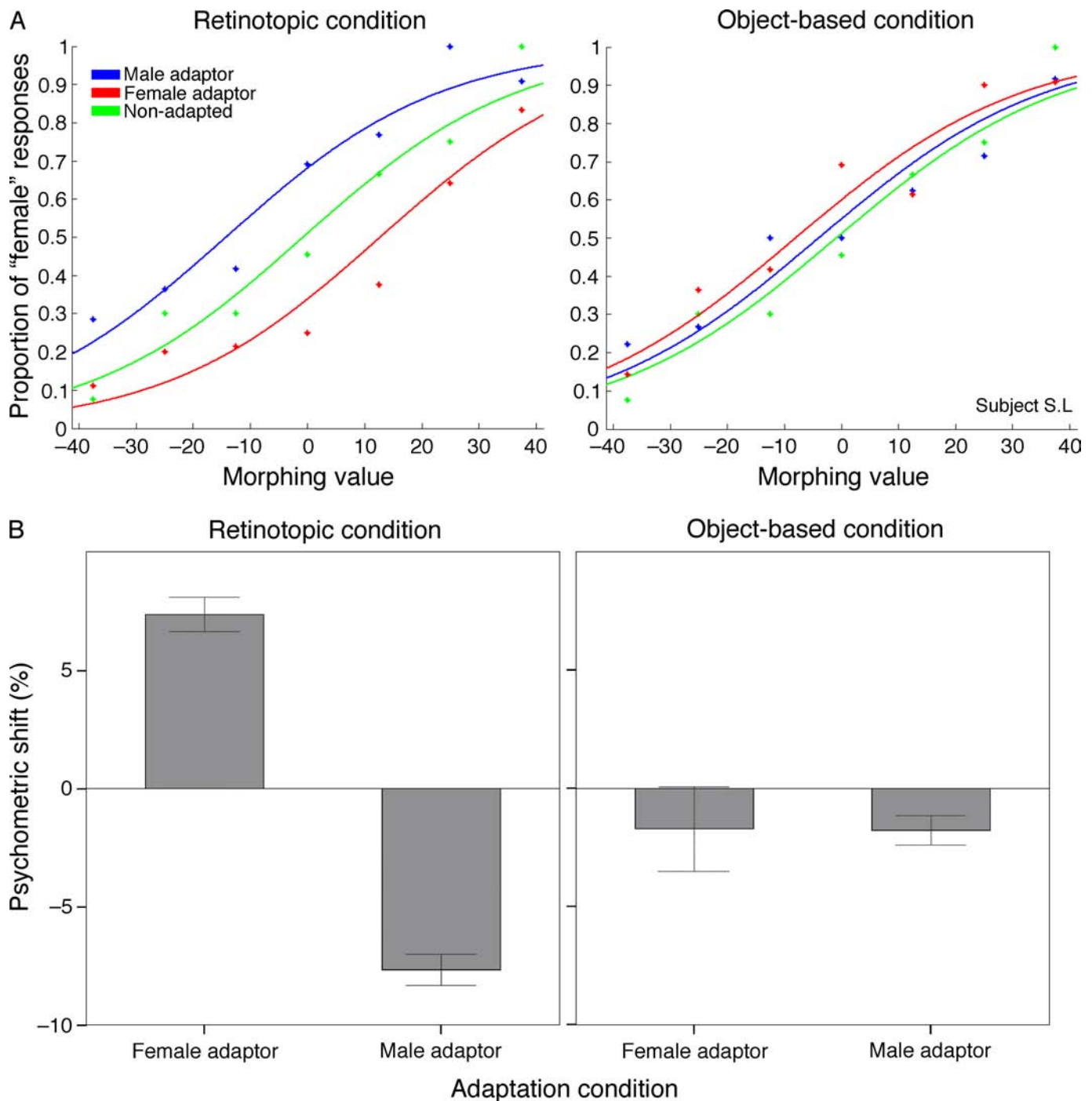
Figure 10. The results of Experiment 4. A) Psychometric functions for one of the subjects. Deviation of male adapted and female adapted curves from each other indicates the FAE. The left plot shows the results for the retinotopic location and the right plot shows the results at the object-specific location (see the text for more details) condition. B) Face aftereffect strength for various experimental conditions. The scale of the vertical axis is the same as Figure 2B. The face aftereffect was robust at the retinotopic test location. No significant face aftereffect was observed for the object-specific test location. Error bars show ±1 SE of mean.

aftereffects that are related to adaptation in early visual cortices. The aftereffects for orientation and spatial frequency drop to about half their maximum at offsets of ~1–3° of visual angle from the adaptor's location (Ejima & Takahashi, 1984, 1985; Williams, Wilson, & Cowan, 1982). In terms of transfer across differences in orientation

and size, these aftereffects decline to half maximum with ~15° orientation difference (Greenlee & Magnussen, 1988) and ~0.5 octave size difference (Greenlee & Magnussen, 1988) between the adapting and test stimuli. Based on the much broader gradient of transfer of the FAE over these dimensions, we suggest, as others have

(Leopold et al., 2001; Moradi et al., 2005; Webster & MacLin, 1999; Yamashita, Hardy, De Valois, & Webster, 2005; Zhao & Chubb, 2001) that the FAE is based in high-level visual cortex such as the FFA or LOC, human equivalents of the inferotemporal face areas in monkey as these areas show evidence of similar range of tuning (Bulthoff, Edelman, & Tarr, 1995; Lawson, 1999; Op De Beeck & Vogels, 2000).

Despite this broad gradient of transfer, there was no evidence of any privileged transfer to locations, orientations, or sizes that maintained a spatiotopic match between the adapt and the test stimulus (i.e. that kept the test stimulus fixed at the adapting location on the display screen while the subject moves his or her eyes or head between adaptation and test). Nor did we find any transfer of the FAE to a displaced location of the adapting head that turned around following adaptation and moved to a new location. Thus we have failed to replicate the spatiotopic FAE claimed by Melcher (2005) and we do not find any evidence of an object-specific FAE that would be equivalent to Melcher's (2008) report of an object-specific tilt aftereffect. We suggested earlier that higher level factors (such as the subject's strategy for attention allocation) might be responsible for Melcher's results but investigating the source of the difference is beyond the scope of the current paper. Here we have attempted to study spatiotopy for the gender-specific face aftereffect using the basic face aftereffect paradigm across a wide range of retinal transformations, including size and orientation as well as position. We found that spatiotopy is not a general property of face aftereffects although we cannot rule it out for his specific conditions.

Based on the results of Experiment 1, we estimate that FAE magnitude drops to half its maximum about 9.2° away from the adaptor. This number was 5.4° in our previously published estimates where much smaller (~2° of visual angle) faces were used. The larger range of transfer here might be a result solely of the larger stimuli. Specifically, the stimuli are about 4° larger here than in the previous study and the area of analysis also 4° larger. The larger faces may have fallen on more and so recruited more face analysis areas that are nevertheless of the same size as those previously measured.

Whatever the source of this difference in estimated size, the results here clearly demonstrate robust retinotopy for the FAE. As mentioned previously, our method here corresponds to the stand method of measuring aftereffects whereas the method used by Melcher (2005) has some potential flaws. Our current results support robust retinotopy, without spatiotopy, for the FAE across various dimensions and suggest that adaptable face analysis in the visual system is based in a retinotopic coordinate frame.

The strength of the retinotopic FAE measured in our 4 experiments varies widely from ~30% in Experiment 1 to between ~7 and ~5% in Experiments 2 and 3. However, the eccentricity of the adapting and test faces also varied across the four experiments. For example in Experiment 1, the stimuli were 6° in size and shown at 10° in the periphery, producing in the retinotopic condition an effect of about 30%. In Experiments 2 and 3, the faces were also 6° in size but presented in the fovea and the FAE was 5–7%. To pursue the possible effect of eccentricity on the size of the face aftereffect we measured the retinotopic face aftereffect in three subjects at two eccentricities (3° and 10°) and two sizes (stimulus sizes 4° and 1.2°). The face aftereffect was largest for the 4° stimulus centered at 10° eccentricity (median of the three subjects: 40%), the FAE was smallest for the 4° stimulus centered at 3° eccentricity (median: 7.5%). Interestingly, the effect was relatively large for the 1.2° stimulus at 3° eccentricity (median: 26%). These results suggest that the strength of the FAE increases as the stimulus size gets smaller, relative to the resolution level at the test eccentricity. Possibly a stimulus that activates a larger number of face analysis regions (large stimuli and/or small eccentricity) is less susceptible to adaptation. We chose the sizes of the smaller stimulus at the near position and the larger stimulus at the far position to be approximately matched in cortical size when corrected for cortical magnification factor of V1 (Rovamo & Virsu, 1979). Nevertheless, the aftereffect was still substantially larger for the far stimulus. This might reflect the increase in foveal bias beyond V1 (Hasson, Harel, Levy, & Malach, 2003). The effect of eccentricity on the face aftereffect is not the central topic of the current study, however, and further studies are required to investigate this interesting effect. The other possible explanation for the observed variation of the magnitude of the retinotopic FAE across our experiments is the variation of the delay between adaptation and test across these experiments. The delay is the shortest for Experiment 1 where the biggest retinotopic FAE is observed. However, the inter-stimulus interval is much longer in other experiments where smaller aftereffects are observed.

The question of spatiotopy has been studied in the vision science literature for a long time, classically as the contrast between head-centered or retinotopic coordinates and gravitational coordinates. Although some studies showed a contribution from gravitational coordinates (Nicholls, Smith, Mattingley, & Bradshaw, 2006) most of them showed stronger dependence of perception and aftereffects on retinotopic coordinates (Friederici & Levelt, 1990; Mast, Ganis, Christie, & Kosslyn, 2003; Wenderoth & Hickey, 1993). The face inversion effect also generally follows the retinotopic coordinate system (Lobmaier & Mast, 2007). Many years ago, Gestalt psychologist Gaetano Kanizsa (1913–1993) demonstrated the dependence of face perception on retinotopic orientation (as opposed to the gravitational orientation) in a simple way (Kanizsa, 1979). Figure 11 shows a typical ambiguous face cartoon (not the one used by Kanizsa). The identity of the face changes if you invert the page. If instead of rotating the page, you invert your head, or bend down and look at the image from between your legs, the

Figure 11. Ambiguous face illusion and spatiotopy (a simple observation from Gaetano Kanizsa). If you invert the page, the identity of this face will switch. Instead of inverting the page, turn your head about 180° or bend down and look at the image from between your legs. The spatiotopic arrangement of the stimulus will not change, so a spatiotopic face analysis would predict no change in the identity of the face. However, the change inverts the image on your retina and if the analysis is based in retinotopic coordinates, the identity of the stimulus should switch.

image remains upright in spatiotopic coordinates, but is inverted on your retina. As you can observe, the identity of the face depends on its orientation in the retinotopic coordinates.

This observation and other evidence in addition to our adaptation results here indicate that face selective neurons analyze the image based on afferent visual signals that are organized retinotopically. They do not have access to the visual world in spatiotopic coordinates. We nevertheless confirm a remarkably broad tuning of the FAE in position, orientation, and size. This broad tuning indicates that this strong and easily demonstrated aftereffect must be tapping high levels of visual processing well beyond that of area V1. Despite this high-level adapting site, the effect is retinotopic along all the dimensions we tested. Finally, even though the spread of the FAE is broad across the dimensions we tested, it is nevertheless tuned in each, showing a maximum at the retinotopic match. This tuning rules out global face analysis covering the entire visual field, all orientations, and all sizes.

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