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Shape Adaptation Exaggerates Shape Differences

Katherine R. Storrs
The University of Queensland and MRC Cognition and Brain Sciences Unit, Cambridge, United Kingdom

Derek H. Arnold
The University of Queensland

Adaptation to different visual properties can produce distinct patterns of perceptual aftereffect. Some, such as those following adaptation to color, seem to arise from recalibrative processes. These are associated with a reappraisal of which physical input constitutes a normative value in the environment—in this case, what appears "colorless," and what "colorful." Recalibrative aftereffects can arise from coding schemes in which inputs are referenced against malleable norm values. Other aftereffects seem to arise from contrastive processes. These exaggerate differences between the adaptor and other inputs without changing the adaptor's appearance. There has been conjecture over which process best describes adaptation-induced distortions of spatial vision, such as of apparent shape or facial identity. In 3 experiments, we determined whether recalibrative or contrastive processes underlie the shape aspect ratio aftereffect. We found that adapting to a moderately elongated shape compressed the appearance of narrower shapes and further elongated the appearance of more-elongated shapes (Experiment 1). Adaptation did not change the perceived aspect ratio of the adaptor itself (Experiment 2), and adapting to a circle induced similar bidirectional aftereffects on shapes narrower or wider than circular (Experiment 3). Results could not be explained by adaptation to retinotopically local edge orientation or single linear dimensions of shapes. We conclude that aspect ratio aftereffects are determined by contrastive processes that can exaggerate differences between successive inputs, inconsistent with a norm-referenced representation of aspect ratio. Adaptation might enhance the salience of novel stimuli rather than recalibrate one's sense of what constitutes a "normal" shape.

Keywords: shape perception, adaptation, visual aftereffects, neural coding, spatial vision

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Visual aftereffects along different sensory dimensions might involve qualitatively distinct processes. Some appear to arise from recalibrative processes that reference the appearance of inputs relative to malleable normative values (Anstis, Verstraten, & Mather, 1998; Webster, 2011; Webster & Leonard, 2008). For instance, one might have the impression that a particular hue and saturation is a neutral gray and that all other combinations of hue and saturation are colorful. One might then update one's impression of what appears gray, thereby changing the apparent color of all points in color space (Webster, 1996).

Other aftereffects appear to arise from contrastive processes that exaggerate differences between adapting and other inputs. The tilt aftereffect (Gibson, 1933; Vernon, 1934), for instance, is induced by prolonged exposure to a stimulus of a particular orientation. Afterward, differences between this and other similar orientations tend to be exaggerated, but the apparent orientation of the adaptor itself seems unchanged (Mitchell & Muir, 1976). Similar "locally repulsive" aftereffects are found following adaptation to spatial frequency (Blakemore & Sutton, 1969) or to a particular direction of motion (Clifford, 2002; Mather, 1980).

It has been suggested that shapes, faces, and other complex spatial stimuli are encoded relative to perceptual norms (Freiwald, Tsao, & Livingstone, 2009; Kayaert, Biederman, Op de Beeck, & Vogels, 2005; Leopold, Bondar, & Giese, 2006; Leopold, O'Toole, Vetter, & Blanz, 2001; Loffler, Yourganov, Wilkinson, & Wilson, 2005; Panis, Wagemans, & Op de Beeck, 2011; Rhodes et al., 2005; Webster & MacLin, 1999). According to these proposals, the appearance of complex forms can be distorted via adaptation-induced reappraisals of what constitutes a normative input (McKone, Jeffery, Boeing, Clifford, & Rhodes, 2014; O'Neil, Mac, Rhodes, & Webster, 2014; Pond et al., 2013; Susilo, McKone, & Edwards, 2010; Webster & MacLeod, 2011; Webster & MacLin, 1999). For example, after adapting to an unusual face, one's impression of what constitutes a normal face might be updated to more closely resemble the unusual face. This would impact on the appearance of all faces. Both the adapting face and more "extreme" versions of it, for instance, would appear more normal after adaptation (e.g., Susilo et al., 2010).

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Katherine R. Storrs, School of Psychology, The University of Queensland, and MRC Cognition and Brain Sciences Unit, Cambridge, United Kingdom; Derek H. Arnold, School of Psychology, The University of Queensland.

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Correspondence concerning this article should be addressed to Katherine R. Storrs, MRC Cognition and Brain Sciences Unit, 15 Chaucer Road, Cambridge, CB2 7EF, United Kingdom. E-mail: katherine.storrs@mrc-cbu.cam.ac.uk

Although facial appearance is popularly thought to be subject to recalibrative perceptual aftereffects, there is some contention on this point, with some having suggested that these perceptual distortions are better explained as contrastive aftereffects (Ross, Deroche, & Palmeri, 2014; Storrs, 2015; Storrs & Arnold, 2012, 2015b; Zhao, Seriès, Hancock, & Bednar, 2011). From a conceptual perspective, this would mean that adaptation-induced distortions of complex form, such as facial appearance, are qualitatively similar to distortions of attributes often described as low-level, such as spatial frequency and orientation (Blakemore & Sutton, 1969; Mitchell & Muir, 1976). We therefore felt it would be interesting to closely examine an intermediately complex spatial attribute—the aspect ratio of a two-dimensional shape.

The apparent aspect ratio of a shape can be distorted via adaptation. A circle can appear vertically elongated after adapting to a horizontally elongated ellipse and can appear horizontally elongated after adapting to a vertically elongated ellipse (Köhler & Wallach, 1944; Regan & Hamstra, 1992; Sagara & Oyama, 1957; Suzuki & Cavanagh, 1998). These changes in what looks "circular" could be explained by a recalibrative aftereffect, which updates one's impression of what constitutes a normal circular shape (Regan & Hamstra, 1992; Suzuki, 2005). They could be equally well explained by a contrastive aftereffect, which exaggerates aspect ratio differences between the adapted and other shapes (Badcock, Morgan, & Dickinson, 2014; see Figure 1, Panels b and c).

Aspect ratio is an interesting case in which to test for recalibrative versus contrastive aftereffects for several reasons. First, the human visual system appears to have dedicated mechanisms for encoding aspect ratio (Badcock et al., 2014; Nachmias, 2011; Regan & Hamstra, 1992; Stankiewicz, 2002). Second, aspect ratio aftereffects likely arise from adaptation at a reasonably late stage of processing, because they reflect *perceived* differences between the adapted and test values, rather than differences in the physical aspect ratios of retinal images (Storrs & Arnold, 2013). Finally, several groups have proposed that aspect ratio mechanisms encode shapes relative to a "neutral" norm corresponding to an apparent 1:1 aspect ratio (Kayaert et al., 2005; Regan & Hamstra, 1992; Suzuki, 2003, 2005; Suzuki & Rivest, 1998).

Because adaptation to spatial patterns likely occurs at multiple levels of visual processing (e.g., Dickinson, Almeida, Bell, & Badcock, 2010; Dickinson & Badcock, 2013; Xu, Liu, Dayan, & Qian, 2012) and we wanted to investigate shape-specific adaptation, it was important to mitigate, as far as possible, the effects of adaptation in mechanisms encoding local contrast or orientation. For example, when adapting and test shapes overlap, any observed effect could be strongly impacted by contour repulsion or tilt aftereffects, likely produced in primary visual cortex rather than later shape-specific stages of processing (Dragoi, Sharma, & Sur, 2000; Jin, Dragoi, Sur, & Seung, 2005). To overcome this we used an adapting stimulus that was intermittently repositioned about the physical test location, such that the external contours of the adaptor traced a symmetrical outline about the test location (see Figure 2c). Moreover, we diminished the influence of precortical adaptation by adapting and testing with shapes rendered in dynamic white noise, which had the same average luminance over time as did the gray display background. With these two precautions, adapting stimuli had no persistent luminance-defined contour that could

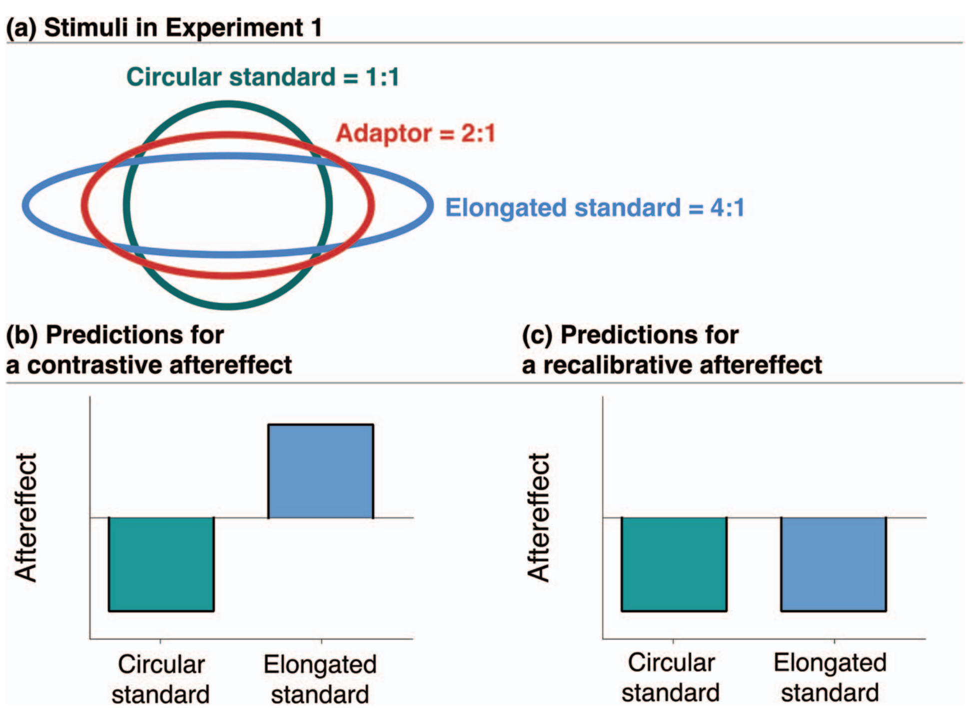

Figure 1. Aspect ratios of adapting and standard test shapes used in Experiment 1 (Panel a). Schematic predictions for how the perceived aspect ratio of each standard test should change after adaptation in a contrastive aspect ratio aftereffect (Panel b) and in a recalibrative aspect ratio aftereffect (Panel c). See the online article for the color version of this figure.

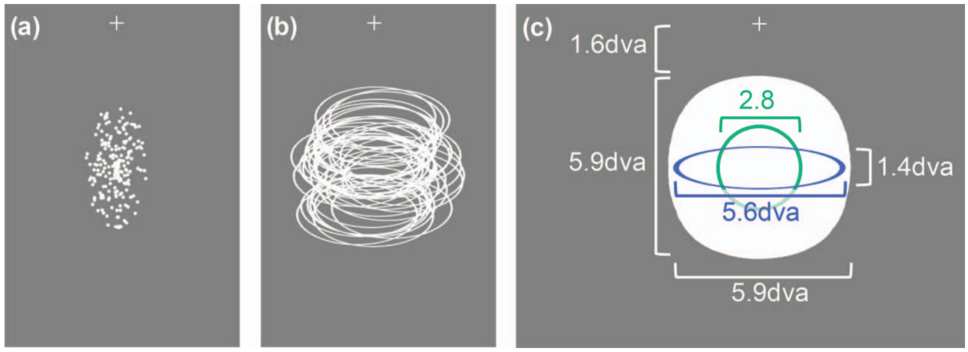

Figure 2. Illustration of how adaptor positions were “jittered.” Panel a: Every 100 ms during adaptation the location of the center of the adapting shape was resampled from within a vertically elongated ellipse region (aspect ratio 1:2) centered on the test location. Dots depict a random sample of 200 possible adaptor locations. Locations were uniformly sampled in polar coordinates, with the result that locations near the test location occurred more frequently than did locations further away. Panel b: White ellipses show the contours of a random sample of 40 adaptor locations, representative of the range of adaptor locations seen by an observer during a 4-s adaptation period (note that in the experiment adaptors were rendered in dynamic white noise). Panel c: Using this sampling method, the region within which adaptor edges could appear approximated a circular shape with a 1:1 aspect ratio (shown as a solid white region). For reference, the outlines of the circular (green) and elongated (blue) standard test shapes are also shown. The sizes of each test shape, and the size and distance from fixation of the adapted region, are indicated in degrees of visual angle (dva). See the online article for the color version of this figure.

induce adaptation at the initial tightly retinotopic stages of processing (C. L. Baker & Mareschal, 2001).

To distinguish between the possibilities that shape aspect ratio aftereffects involve recalibrative or contrastive processes, we first had observers adapt to moderately horizontally elongated ellipses and examined the effect this had on the appearance of both more horizontally elongated shapes and less elongated shapes (circles). If shape aftereffects involve the recalibration of a norm for aspect ratio, both types of test should look *less* horizontally elongated and more vertically elongated after adaptation. If shape aftereffects involve a contrastive process, circular tests should look less horizontally elongated (i.e., vertically elongated), whereas the horizontal elongation of more-elongated tests should be further exaggerated—that is, one should find opposite distortions for the two types of tests (see Figure 1).

Experiment 1: Aspect Ratio Adaptation

Method

Participants. Ten observers, composed of the two authors and eight additional experienced psychophysical observers naïve to the research hypotheses, participated. Experiment 1 was approved by the School of Psychology Ethics Committee at the University of Queensland.

Stimuli and apparatus. Stimuli were presented on a 19-in. Samsung SyncMaster 950SL, a 19-in. Samsung SyncMaster 950p+, or a 19-in. Dell Trinitron monitor, all set to a 1,280 × 1,024 pixel resolution and a refresh rate of 75 Hz. Stimuli were generated using the Psychophysics Toolbox for Matlab (Brainard, 1997; Pelli, 1997). Participants viewed stimuli from a distance of 57 cm, using a chinrest to stabilize their heads.

Stimuli were elliptical patches of dynamic white noise updated every 10 ms, rendered on a gray background. By defining stimuli using dynamic noise textures, we minimized adaptation in precortical sites and in those V1 neurons that act as linear luminance filters (C. L. Baker & Mareschal, 2001). In runs of trials involving adaptation, the adapting stimulus had an aspect ratio of 2 (i.e., a 2:1 width-to-height ratio). Two standard test stimuli were used: a circular standard with an aspect ratio of 1 and an elongated standard with an aspect ratio of 4 (see Figure 1a). The area of adapting and test shapes was held constant at 14,400 pixels^2—approximately 7.8 square degrees of visual angle (dva). The circular standard therefore subtended 2.8 (width) × 2.8 (height) dva, the elongated standard subtended 5.6 × 1.4 dva, and the adaptor subtended 4.0 × 2.0 dva. Adapting and test stimuli were centered 4.6 dva above or below a central fixation cross, which subtended 0.5 dva (see Figure 2).

The spatial location of the adapting stimulus jittered randomly within an allowable region (see Figure 2 and the movie in the online supplemental material, which presents a simple demonstration of aftereffects induced by the “jittering adaptor” method, using two oppositely elongated adaptors in two spatial locations and circular tests). By ensuring no systematic retinotopic overlap between the contours of adapting and test shapes, we could minimize location jitter contributions from “contour repulsion” and tilt adaptation, both of which can be driven by channels sensitive to second-order stimuli such as ours (Whitaker, McGraw, & Levi, 1997, and Larsson, Landy, & Heeger, 2006, respectively). The spatial jitter was implemented by randomly selecting a new adaptor location every 100 ms, from within a vertically elongated ellipse with an aspect ratio (1:2) opposite to that of the adaptor. The allowable adaptor region was equal in size to the adaptor and was centered on the test location (see Figure 2a). This resulted in the contours of adapting stimuli tracing an approximately circular region across a block of trials, which importantly had a 1:1 aspect ratio (with a width and height of 5.93 dva; see Figure 2c). Adaptors were presented above fixation for five participants and below fixation for the other five.

Procedure. Each participant completed one run of trials without adaptation, followed immediately by a run of trials with adaptation. During adaptation runs, the adapting shape was displayed for 4 s at the start of each trial. Test stimuli were presented using a dual-pair task (Kaplan, Macmillan, & Creelman, 1978; Rousseau & Ennis, 2001), in which four test stimuli were presented in two sequential pairs (see Figure 3). On each trial, three of the four stimuli were of a standard test aspect ratio (either circular or elongated, selected pseudorandomly on each trial), whereas the fourth varied according to a method of constant stimuli (described later). Each test pair was presented for 100 ms. The variable test was always presented in the unadapted location, in an interval chosen randomly on each trial. There was a blank interstimulus interval of 300 ms between each test pair and between the adaptor and tests.

The observers' task was to indicate via a key press whether the nonidentical pair (i.e., the pair containing the variable test) had appeared first or second. Observers were instructed to choose the interval containing the larger difference if both intervals appeared to contain nonidentical shapes. This is expected to be the case in many trials after adaptation, unless the variable test shape exactly matches the adaptation-induced distortion of the standard test shape. The point of subjective equality (PSE) between adapted and unadapted locations occurs at the value for which the adaptation-induced distortion of the variable test compensates for its physical difference from the standard. Near this value, the adaptation-induced difference between the physically identical standards appears larger than that between the variable test and standard, and observers should respond systematically incorrectly. The peak in the proportion of incorrect responses can therefore be taken as an estimate of the observers' PSE.

On each trial the standard test was pseudorandomly selected to be of either the circular or elongated standard aspect ratio. The variable test was selected pseudorandomly according to a method of constant stimuli from one of seven aspect ratios, centered logarithmically about the respective standard stimulus. For trials involving circular standards (aspect ratio 1), variable tests were selected from aspect ratios of 0.59, 0.71, 0.84, 1.00, 1.19, 1.41, or 1.68. For trials involving elongated standards (aspect ratio 4) tests were selected from aspect ratios of 2.38, 2.83, 3.36, 4.00, 4.76, 5.66, or 6.73. Variable tests had the same area as did standard tests and the adaptor. Within a run of trials, eight samples of each variable test aspect ratio were presented for each of the two types of standard test, yielding a total of 112 trials.

Results

Trials involving circular and elongated standard test stimuli were analyzed separately. For each, data were expressed as the proportion of trials on which the observer had incorrectly reported on the order of the variable test interval. A Gaussian function was fitted to the proportion of incorrect responses as a function of variable test aspect ratios. The peak of the fitted function was taken as an estimate of the point of subjective equality (PSE) in terms of aspect ratio between the adapted and unadapted locations. A proportional aftereffect score was calculated by dividing the log(PSE

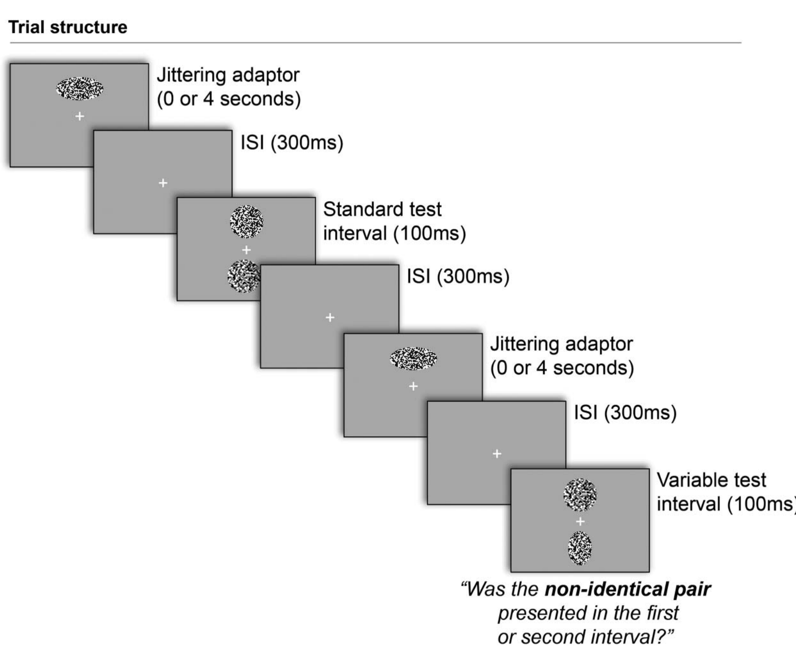

Figure 3. Example trial structure. Adapting stimuli "jittered," appearing at a different location every 100 ms, whereas test stimuli appeared in a fixed location. Both adapting and test stimuli were rendered in white noise that updated every 10 ms. The interval in which the variable test stimulus appeared was randomly chosen on each trial. ISI = interstimulus interval.

estimate derived from adaptation runs of trials) by the log(PSE estimate derived from baseline runs of trials).

After adapting to an aspect ratio of 2, circular standard stimuli were matched to more-contracted ellipses relative to baseline trials (proportional aftereffect -0.12 ± 0.01), $t(9) = -9.08$, $p < .001$ (see Figure 4a). An oppositely directioned aftereffect was observed for tests more elongated than the adaptor (0.12 ± 0.03), $t(9) = 4.75$, $p = .001$. This bidirectional pattern of perceptual changes was found for each observer (see Figure 4b).

These results demonstrate that the aspect ratio aftereffect manifests predominantly as a contrast between successive shapes. If it is *entirely* mediated by contrastive mechanisms, two additional results are predicted: First, when the test shape is identical to the adapting shape, there should be no change in the appearance of the test. Alternatively, a contribution from recalibrative processes predicts that the adapted aspect ratio will appear closer to circular after adaptation ("renormalization"). Experiment 2 tests this prediction. Second, in a contrastive aftereffect, adapting to a 1:1 aspect ratio should induce bidirectional aftereffects on test aspect ratios smaller or larger than 1:1. Recalibration predicts that adapting to a 1:1 shape should be uniquely ineffective in inducing aftereffects, because it is the norm for aspect ratio perception under this hypothesis. Experiment 3 tests this prediction.

Experiment 2: Testing for Renormalization of the Adapted Shape

Details were the same as for Experiment 1, with the following exceptions.

Method

Participants. Ten observers, including the first author, four experienced psychophysical observers naïve to hypotheses, and five inexperienced observers recruited from the MRC Cognition and Brain Sciences Unit volunteer panel, who were compensated with £6 (US$7.75) per hr for their time, participated. Experiments 2 and 3 were approved by the Cambridge Psychology Research Ethics Committee.

Stimuli and apparatus. Stimuli were presented on a 17-in. Dell P791, set to a 1,024 × 768 pixel resolution and a refresh rate of 75 Hz. In runs of trials involving adaptation, the adapting stimulus had an aspect ratio of 2. Three standard test stimuli were used: a narrower standard with an aspect ratio of 1.5, an identical standard with aspect ratio 2, and a wider standard with aspect ratio 2.67. Stimuli were centered 6.8 dva above or below a central fixation cross, which subtended 0.7 dva. The area of adapting and test shapes was held constant at 28,800 pixels^2—approximately 33.3 dva^2. The narrower standard therefore subtended approximately 7.1 × 4.7 dva, the identical standard or adaptor subtended 8.2 × 4.1 dva, and the wider standard subtended 9.4 × 3.5 dva. Each pair of test stimuli was presented for 200 ms.

Procedure. On each trial a standard test was pseudorandomly selected from among the narrower, identical, and wider aspect ratios. The variable test was selected pseudorandomly according to a method of constant stimuli from one of seven aspect ratios, centered logarithmically about the respective standard stimulus. For trials involving narrower standards, variable tests were selected from aspect ratios of 1.06, 1.26, 1.40, 1.50, 1.61, 1.78, and 2.12. For trials involving identical standards tests were selected from aspect ratios of 1.41, 1.68, 1.87, 2.00, 2.14, 2.38, and 2.83; and for trials involving wider standards, tests were selected from aspect ratios of 1.89, 2.42, 2.49, 2.67, 2.89, 3.17, and 3.77. Eight samples of each variable test aspect ratio were presented for each standard test within a run of trials, yielding a total of 168 trials. On runs of trials involving adaptation, the adapting stimulus was

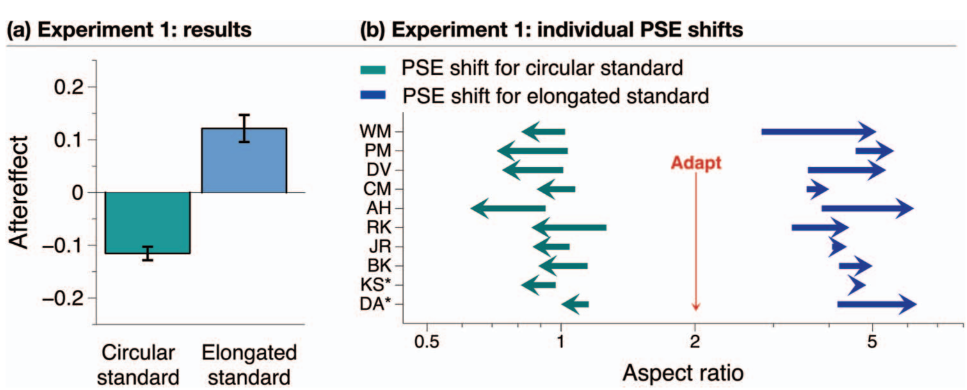

Figure 4. Panel a: Mean proportional aftereffect on trials involving circular (aspect ratio 1:1) and elongated (aspect ratio 4:1) standard test stimuli. Error bars indicate ± 1 standard error of the mean. Panel b: The same data displayed as individual point of subjective equality (PSE) shifts for each participant for each standard stimulus. The tail of each arrow indicates the baseline PSE estimated during trials involving circular (green arrows to the left of the vertical arrow) or elongated (blue arrows to the right of the vertical arrow) standard tests, and arrowheads indicate the corresponding postadaptation PSE estimate. The aspect ratio of the adapting stimulus is indicated by a vertical red arrow. Note that the abscissa is in log units. Initials along the y-axis represent individual participants. Authors' data are indicated by an asterisk. See the online article for the color version of this figure.

presented above fixation for five participants and below fixation for the other five.

Results

Trials involving each of the three standard test stimuli were analyzed separately. After adapting to an aspect ratio of 2, narrower standard stimuli were matched to more-contracted ellipses relative to baseline trials (proportional aftereffect −0.03 ± 0.01), $t(9) = -3.64$, $p = .005$ (see Figure 5). After adaptation, wider standards were matched to more elongated ellipses relative to baseline (0.04 ± 0.01), $t(9) = 3.47$, $p = .007$. In the critical condition, in which standard stimuli had the same aspect ratio as the adaptor, adaptation had no significant effect on aspect ratio perception (−0.01 ±.005), $t(9) = -1.43$, $p = .19$.

Results suggest that aspect ratio aftereffects can be characterized as contrastive, exaggerating differences between adapting and test aspect ratios without changing the appearance of the adapted aspect ratio. In Experiment 3, we tested a final point of difference between the contrastive and recalibrative hypotheses: whether adaptation to the putative norm (a 1:1 aspect ratio) induces aftereffects. In addition, we introduced a size change between the adapting and test stimuli, to assess the possibility that observers were adapting to width or height alone, rather than aspect ratio.

Experiment 3: Effect of Adapting to a 1:1 Aspect Ratio

Details were the same as for Experiment 2, with the following exceptions.

Method

Participants. Fifteen observers, including the first author, two experienced psychophysical observers naïve to hypotheses, and 12 inexperienced paid observers, participated.

Stimuli and apparatus. Adapting shapes had an area of 14,400 pixels^2—approximately 16.6 dva^2. In runs of trials involving adaptation, the adapting stimulus had an aspect ratio of 1 (i.e., circular) and subtended 4.1 × 4.1 dva. Four standard test stimuli were used: *small* and *large* narrower standards, with an aspect ratio of 0.8, and *small* and *large* wider standards, with an aspect ratio of 1.25. The square root of the area of *small* test stimuli was set to ¾ the square root area of the adaptor, and the square root area of *large* test stimuli was set to $^4/_3$ the square root area of the adaptor. The spatial location of the adapting stimulus jittered randomly within a circular region, such that, across a block of trials, its contours inscribed a circle subtending 8.7 × 8.7 dva. Standard stimuli subtended 2.7 × 3.4 dva (*small* narrower standard), 3.4 × 2.7 dva (*small* wider standard), 4.9 × 6.1 (*large* narrower standard), or 6.1 × 4.9 dva (*large* wider standard). It is important to note that *small* test stimuli were smaller in both width and height than adapting stimuli, whereas *large* test stimuli were larger in both width and height than adaptors. Any aftereffect induced by adaptation to unidimensional width or height should therefore distort the aspect ratio of both narrower and wider standards in the same direction (within a size condition), contrary to the predictions of a locally repulsive aspect ratio aftereffect. For example, if adapting to width, both narrower and wider *large* test stimuli should appear more elongated in aspect ratio, because both have a larger width than does the adaptor. Adaptors were presented above fixation for eight participants and below fixation for the other seven.

Procedure. On each trial the variable test was presented with the same area as the standard stimulus selected for that trial. For trials involving narrower standards (aspect ratio 0.8), variable tests were chosen from aspect ratios of 0.57, 0.67, 0.75, 0.80, 0.86, 0.95, or 1.13. For trials involving wider standards (aspect ratio 1.25) tests were chosen from aspect ratios of 0.88, 1.05, 1.17, 1.25, 1.34, 1.49, or 1.77. A run of trials consisted of 224 trials.

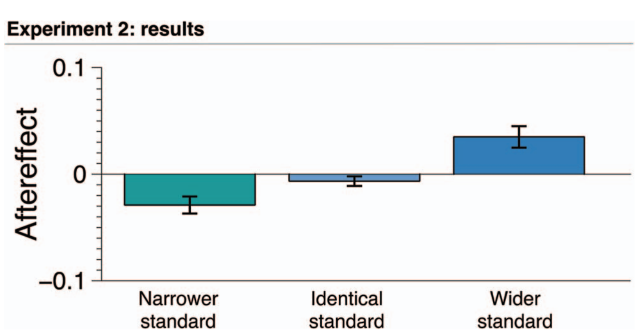

Figure 5. Mean proportional aftereffects in Experiment 2, following adaptation to an ellipse with aspect ratio 2:1, for trials involving standard test stimuli of a narrower (1.5:1), identical, or wider (2.67:1) aspect ratio. Error bars indicate ± 1 standard error of the mean. See the online article for the color version of this figure.

Results

Trials involving each of the four standard test stimuli were analyzed separately. For *large* test stimuli, after adapting to a circle, narrower standard stimuli were matched to more-contracted ellipses relative to baseline trials (proportional aftereffect −0.02 ± 0.01), $t(14) = -2.38$, $p = .032$ (see Figure 6b), and wider standards were matched to more-elongated ellipses relative to baseline (0.01 ± 0.01), $t(14) = 2.93$, $p = .011$). For *small* test stimuli, narrower standards were matched to narrower ellipses than during baseline trials (−0.01 ± 0.01), $t(14) = -2.80$, $p = .014$). Wider standard stimuli were matched to slightly wider shapes than during baseline, but this difference was not significant (0.01 ± 0.01), $t(14) = 1.05$, $p = .313$.

General Discussion

Our data imply that aspect ratio aftereffects arise from a contrastive process, which perceptually exaggerates differences between adapting and test shapes. We are confident that these data reflect a perceptual effect because we used a signal detection task (a two-alternative forced-choice task, in which observers choose the interval containing nonidentical tests) in order to minimize the potential impact of decisional response bias. We are also confident that these data cannot be accounted for by positional repulsion between contours, tilt adaptation to local edges, or adaptation to a single shape dimension (width or height). We used stimuli rendered in dynamic white noise to minimize the contribution of processing in precortical and some V1 mechanisms, which adapt well to luminance-defined stimuli but not dynamic white noise (C. L. Baker & Mareschal, 2001). Moreover, we

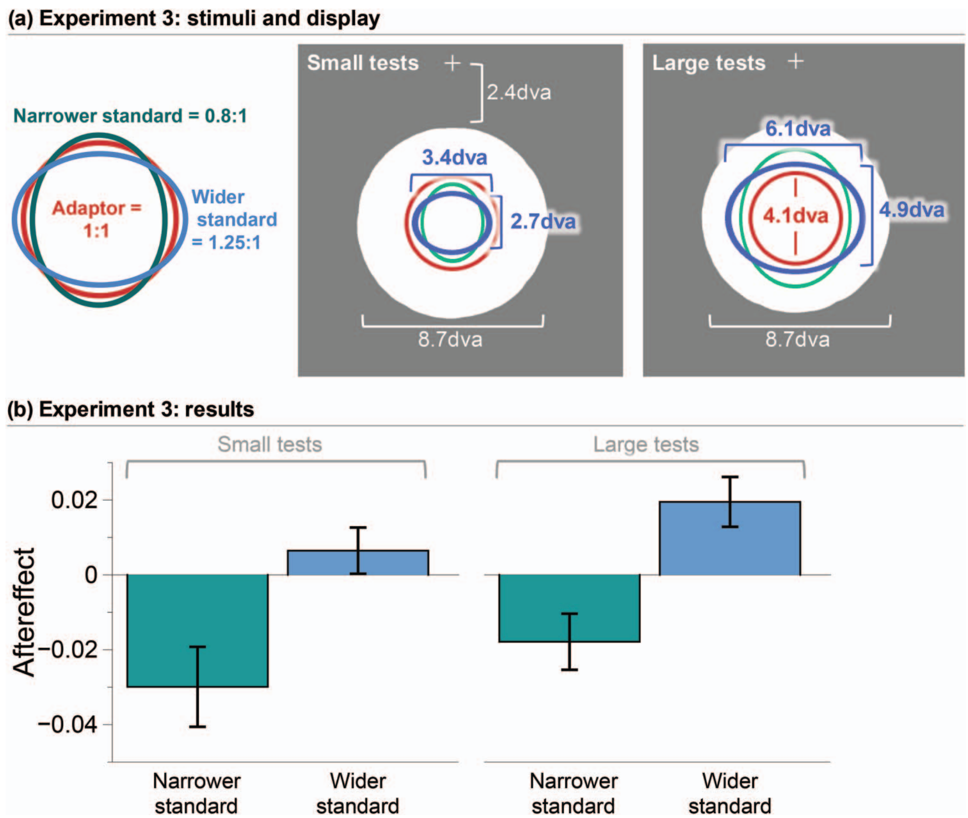

Figure 6. Panel a: Aspect ratios of adapting and standard (narrower: green vertical oval; wider: blue horizontal oval) test shapes used in Experiment 2 (left diagram). Schematic illustrations of stimulus displays, showing the relative sizes of adapting and test stimuli in *small* (middle diagram) and *large* (right diagram) test conditions in Experiment 2, respectively. The red perfect circle indicates the size of the adaptor, whereas the white disk indicates the region within which it could appear. Outlines of the narrower (lighter gray [green]) and wider (darker gray [blue]) standard tests are also shown. dva = degrees of visual angle. Panel b: Mean proportional aftereffects in Experiment 2. Error bars indicate ±1 standard error of the mean. See the online article for the color version of this figure.

minimized the influence of tightly retinotopic visual processes by using a novel jittering adaptor display (inspired by D. H. Baker & Meese, 2012), in which the adaptor's external contours did not systematically overlap with those of the test stimuli. In Experiment 3 we also introduced a size change, so that both the width and height of test stimuli were smaller or larger than those of the adaptor. If observers adapted to only the width or height of the adaptor, both narrower and wider test stimuli should be distorted in the same direction within a size condition. Instead, we found opposite aftereffects for narrower versus wider test shapes in the *large* test condition (aftereffects in the *small* test condition did not reach significance).

Our observations are inconsistent with a norm-based representation of aspect ratio, in which adaptation recalibrates the putative norm (Regan & Hamstra, 1992; Suzuki, 2003, 2005; Suzuki & Rivest, 1998). Norm-based aspect ratio coding predicts unidirectional recalibration after adapting to a nonnormative aspect ratio, rather than the bidirectional contrastive aftereffects we observed in all three experiments. Additionally, it predicts perceptual renormalization of an adapted shape toward a neutral aspect ratio, which we did not observe in Experiment 2. Finally, norm-based aspect ratio encoding predicts no aftereffect following adaptation to a 1:1 aspect ratio (the putative norm), whereas we found in Experiment 3 that adapting to a circle exaggerates the aspect ratios of tests away from circular.

The present results suggest the existence of multiple aspect ratio channels, each tuned to a different aspect ratio, which signal shape via the distribution of activity across the population of channels (Badcock et al., 2014; Storrs & Arnold, 2012, 2015b; Webster & MacLeod, 2011). Similar encoding schemes underlie the perception of orientation and spatial frequency (Blakemore & Campbell, 1969; Clifford, 2002; Goris, Putzeys, Wagemans, & Wichmann, 2013; Pouget, Dayan, & Zemel, 2000). Channels encoding aspect ratio are likely retinotopically localized, because we were able to induce and measure spatially contingent aftereffects. However, the relevant channels must have broad spatial receptive fields, because a shape jittering over approximately 6 degrees of visual angle was an effective adaptor.

Because our method measured differences in perceived aspect ratio between an adapted location and unadapted location, it would be insensitive to any retinotopically global adaptation. It therefore remains possible that there exists a location-tolerate stage of aspect ratio that conforms to recalibration, although deconfounding such nonlocalized adaptation from decisional bias is problematic (see, e.g., Morgan, 2014).

Previous Attempts to Characterize the Tuning of Shape Aftereffects

Regan and Hamstra (1992) were the first to propose a norm-based encoding of aspect ratio, on the basis of the observation that discrimination sensitivity is highest near a 1:1 aspect ratio (the putative norm). They presented a model comprising two channels oppositely tuned to high and low aspect ratios. The responsiveness of both channels as a function of input aspect ratio changed most steeply around an aspect ratio of 1:1, thereby predicting enhanced discrimination sensitivity about this value. This observation, however, is also compatible with a multiple-channel code with an uneven distribution of channels along the dimension of aspect ratio. Channels tuned to neutral aspect ratios might be more numerous and/or more narrowly tuned than are those preferring more-extreme aspect ratios. This would be analogous to the anisotropies found in orientation-tuned channels, which are thought to underlie individuals' superior discrimination ability about vertical and horizontal relative to oblique orientations (Girshick, Landy, & Simoncelli, 2011; Li, Peterson, & Freeman, 2003; Mannion, McDonald, & Clifford, 2010; Storrs & Arnold, 2015a).

Badcock et al. (2014) recently communicated via a conference abstract that they had measured spatially contingent aspect ratio aftereffects and also concluded that aspect ratio adaptation involves a local repulsion. They tested the influence of a range of adapting shapes on a test stimulus with a fixed aspect ratio of 2:1 and found a classic locally repulsive aftereffect tuning with a minimum value when adapting and test aspect ratios were identical. However, in these experiments, stimuli were defined by first-order luminance information, and the spatial overlap of adapting and test shapes was consistent. This left open the possibility that the data in question reflected adaptation to local contours rather than to shape aspect ratio. Our data show that locally repulsive aftereffect tuning for shape aspect ratio persists when this possibility is eliminated.

The only other previous attempt to assess the tuning of aspect ratio aftereffects, communicated via an edited book chapter and a conference abstract (Suzuki, 2005; Suzuki & Rivest, 1998), found evidence of recalibration. However, those authors used extremely brief adaptation (150 ms) and test (60 ms) periods, making the results difficult to compare to those of the present experiments.

What Computations Underlie Global Shape Perception?

The precise nature of computations underlying global shape perception are, as yet, unclear. It is, however, entirely possible that these will involve the activity of channels with retinally localized receptive fields that are attuned to different curvatures (Badcock et al., 2014). Related experiments have revealed aftereffects induced by the curvature of shapes that cannot be explained entirely by local tilt adaptation (Gheorghiu & Kingdom, 2007, 2008). These manifest as contrastive aftereffects rather than as a recalibration of curvature perception (Gheorghiu & Kingdom, 2007, 2008), and they have been successfully modeled by adaptation within a multichannel code (Gheorghiu, Kingdom, Bell, & Gurnsey, 2011). Our results might be mediated by the influence that sequential adaptation of such channels has on computations underlying global shape perception. Alternatively, the locus of adaptation might be more directly within channels that encode shape from broader retinal expanses. In either case, our data suggest that the product of shape adaptation is a contrastive aftereffect rather than a renormalization of shape perception.

Adaptation May Enhance the Salience of Novel Stimuli

Both multiple-channel and norm-based encoding schemes can predict improved discrimination sensitivity about adapted test values postadaptation, but these have not been found reliably. For instance, after adaptation to spatial patterns Clifford, Wyatt, Arnold, Smith, and Wenderoth (2001); Regan and Beverley (1985), and Oruç and Barton (2011) reported enhanced performance in psychophysical spatial discrimination tasks, whereas Barlow, Macleod, and van Meeteren (1976), Rhodes, Maloney, Turner, and Ewing (2007), and Westheimer and Gee (2002) reported no such advantage.

An intriguing recent suggestion is that perceptual distortions created by contrastive aftereffects might be behaviorally useful even in the *absence* of improved discrimination in a psychophysical task. According to this hypothesis, the perceptual distortions enhance the salience of novel inputs (McDermott, Malkoc, Mulligan, & Webster, 2010; Ranganath & Rainer, 2003). By perceptually exaggerating differences between the adapted environment and subsequent inputs, adaptation might ensure that scenes and objects that are statistically unusual in the context of the recent past capture attention. Adaptation might therefore rapidly and implicitly update one's knowledge of which stimuli are typical in the current context (e.g., Kayaert, Op de Beeck, & Wagemans, 2011) and provide a host of behavioral advantages for atypical stimuli, such as faster and more-accurate detection in cluttered environments (Kompaniez-Dunigan, Abbey, Boone, & Webster, 2015; McDermott et al., 2010; Wissig, Patterson, & Kohn, 2013). Our demonstration of a contrastive shape aftereffect is entirely consistent with this conjecture.

Norms Might Not Be the Norm in Spatial Vision

The theory that the brain represents spatial patterns relative to perceptual norms has gained traction over the past couple of decades (Freiwald et al., 2009; Kayaert et al., 2005; Leopold et al., 2001, 2006; Loffler et al., 2005; Panis et al., 2011; Rhodes et al., 2005; Webster & MacLin, 1999). Norm-based opponent-channel coding proposals have been particularly prevalent in the face perception literature (Giese & Leopold, 2005; Leopold et al., 2001; McKone et al., 2014; Pond et al., 2013; Rhodes et al., 2005; Valentine, 1991; Webster & MacLin, 1999). There is, however, mounting evidence questioning accounts of facial aftereffects that rely on norm-based encoding. Specifically, several studies have found that facial aftereffect patterns are not well described by opponent-channel-based hypotheses but can be better explained by multiple-channel models (Ross et al., 2014; Storrs, 2015; Storrs & Arnold, 2012, 2015b; Zhao et al., 2011).

The present data and other recent results (Badcock et al., 2014) similarly suggest that a norm-based opponent-channel hypothesis does not well explain shape aspect ratio aftereffects.

Instead, our data suggest a continuity in spatial vision, such that adaptation to a moderately complex spatial property (aspect ratio) creates a classical contrastive aftereffect similar to those found for simpler spatial properties, such as spatial frequency (Blakemore & Sutton, 1969), orientation (Mitchell & Muir, 1976), and curvature (Gheorghiu & Kingdom, 2008). This complements findings suggesting that adaptation to still more complicated spatial properties, such as facial gender and identity (Ross et al., 2014; Storrs, 2015; Storrs & Arnold, 2012, 2015b; Zhao et al., 2011), also produce contrastive aftereffects. It would seem, therefore, that local repulsion, rather than renormalization, might be the norm for aftereffects in spatial vision. In all contexts, aftereffects might serve to enhance the salience of changes to the spatial properties of the environment, whether those properties signal changes in objects, scenes, or faces.

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