Separate banks of information channels encode size and aspect ratio

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Size and aspect ratio are ecologically important visual attributes. Relative size confers depth, and aspect ratio is a size-invariant cue to object identity. The mechanisms of their analyses by the visual system are uncertain. In a series of three psychophysical experiments we show that adaptation causes perceptual repulsion in these properties. Experiment 1 shows that adaptation to a square causes a subsequently viewed smaller (larger) test square to appear smaller (larger) still. Experiment 2 reveals that a test rectangle with an aspect ratio (height/width) of two appears more slender after adaptation to rectangles with aspect ratios less than two, while the same test stimulus appears more squat after adaptation to a rectangle with an aspect ratio greater than two. Significantly, aftereffect magnitudes peak and then decline as the sizes or aspect ratios of adaptor and test diverge. Experiment 3 uses the results of Experiments 1 and 2 to show that the changes in perceived aspect ratio are due to adaptation to aspect ratio rather than adaptation to the height and width of the stimuli. The results are consistent with the operation of distinct banks of information channels tuned for different values of each property. The necessary channels have log-Gaussian sensitivity profiles, have equal widths when expressed as ratios, are labeled with their preferred magnitudes, and are distributed at exponentially increasing intervals. If an adapting stimulus reduces each channel's sensitivity in proportion to its activation then the displacement of the centroid of activity due to a subsequently experienced test stimulus predicts the measured size or aspect ratio aftereffect.

Introduction

A sequence of mechanisms in the visual system transforms retinal images into codes for increasingly complex form representations (Cadieu et al., 2007; Felleman & Van Essen, 1991; Hubel & Wiesel, 1968; Lennie, 1998). The mechanisms are often comprised of populations of neurons individually sensitive to a narrow range of a particular stimulus dimension but collectively sensitive to the whole range of that dimension (Clifford, 2014; Clifford et al., 2007; Kohn, 2007; Storrs & Arnold, 2012). Neurons of the primary visual cortex (V1) are locally selective for orientation and spatial-frequency (Blakemore & Campbell, 1969; De Valois, Yund, & Hepler, 1982; Hubel & Wiesel, 1968) and in V2 they can, in addition, analyze angles and curves (Hegde, 2000; Ito & Komatsu, 2004). These properties could be considered one-dimensional as they concern the properties of a line. In V4, populations of neurons selective for the relative positions of such properties present on a boundary are used in the analysis of the complex two-dimensional shape of objects (Badcock, Almeida, & Dickinson, 2013; Bell, Dickinson, & Badcock, 2008; Bowden, Dickinson, Fox,

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& Badcock, 2015; Dickinson, Bell, & Badcock, 2013; Dickinson, Cribb, Riddell, & Badcock, 2015; El-Shamayleh & Pasupathy, 2016; Pasupathy & Connor, 1999, 2001, 2002), while a response to perceived size (Mikellidou et al., 2016) and shape (Ellison & Cowey, 2009; Silson et al., 2013) have been reported in LO1 and LO2, respectively. Although analyses of the boundaries of objects are frequently of critical importance to their identification it is often a contrast in visual properties between the interior of the boundary of the object and its background that defines the position of the boundary (Tan, Dickinson, & Badcock, 2013). Aggregation of the responses of V1 neurons with consistent or smoothly varying orientation, spatial frequency, color, or disparity can, therefore, allow perceptual segmentation of the visual field.

Clearly the introduction of a second dimension to a shape, creating a contained area, results in a dramatic increase in the complexity of analysis. This study investigates the analysis of size (area) and aspect ratio which, being the product and quotient of two perpendicular linear distances, are perhaps the simplest measures of two-dimensional shape. The mechanisms of size and aspect ratio analysis in the visual system are investigated using rectangular stimuli defined by their height and width. These are, therefore, the simplest stimuli that might be analyzed on the basis of their area and aspect ratio. Of course, for the results to have broader significance to the study of the visual system they would have to be shown to generalize to more complex stimuli but we have chosen rectangles here to avoid the complication that might arise by local tilt aftereffects also contributing to the results.

The study exploits figural aftereffects (Kohler & Wallach, 1944), changes in the perceived geometry of test stimuli that arise as aftereffects of exposure to adapting stimuli with different geometrical properties (Westheimer, 2008). One concern that can be levelled at adaptation experiments is that afterimages can build up during prolonged exposure to an adapting stimulus presented to the same region of the visual field (Ganz, 1964, 1966a, 1966b). A control experiment was, therefore, performed to inform decisions concerning stimulus design. This experiment is described in the Visual Stimuli subsection of the General Methods.

Perceived size and aspect ratio are influenced by the sizes and aspect ratios of previously experienced stimuli (Regan & Hamstra, 1992; Sagara & Oyama, 1957). Such aftereffects of adaptation are common in the visual system. One familiar example is the spatial frequency aftereffect. In this case, adapting to a one-dimensional grating causes a subsequently viewed grating to be perceived as having a larger difference in spatial frequency to the adaptor than is actually the case (Blakemore & Campbell, 1969; Blakemore & Sutton, 1969; Pantle & Sekuler, 1968). That is, the spatial frequency of a subsequently presented test grating is perceptually repelled from the spatial frequency of the adaptor. Adaptation to a grating of a specific spatial frequency also reduces sensitivity to contrast for stimuli at, or near, the adapting spatial frequency. This implies that sensitivity across the range of spatial frequencies arises from the operation of a bank of channels, with channels individually sensitive to a narrow band of spatial frequencies but distributed to cover the whole range of sensitivity (Blakemore & Campbell, 1969; Braddick, Campbell, & Atkinson, 1978; Clifford et al., 2007). When sufficiently different, stimuli characterized by spatial frequency are discriminable at the same contrasts at which they can be detected indicating that the channels carry labels for their preferred spatial frequency (Watson & Robson, 1981). Such channels are known as information channels. The repulsive aftereffect is then explained as arising from a reduction in the sensitivities of the individual channels produced by adaptation (Bekesy, 1929) leading, in this instance, to a shift in the centroid of the response to the test pattern in the population of spatial frequency selective information channels. We propose that size and aspect ratio are encoded in an analogous manner.

If size and aspect ratio are encoded by two banks of channels sensitive to the product and quotient of perpendicular distances respectively then we are obliged to consider how such distances are encoded. They might be encoded by banks of channels in an analogous manner to spatial frequency and therefore also express repulsive aftereffects of adaptation. These could arise in two different ways. First there may be units sensitive to the distance between the edges of the object and aftereffects due to adaptation to size or aspect ratio may result indirectly from distance aftereffects. Second there may be units directly sensitive to the product (size) or quotient (aspect ratio) and the aftereffects may arise from alterations in the sensitivity of those units. If this were the case then the measures of size and aspect ratio would not be susceptible to aftereffects of distance adaptation. This would allow aftereffects of size, aspect ratio, and linear distances to be decorrelated.

We hypothesize, then, that both size and aspect ratio are encoded in the centroid of activity of discrete populations of information channels. Moreover, as size and aspect ratio measures would be more useful if their aftereffects were uncorrelated, because of their different perceptual roles, we expect investigations to reveal that the aftereffects of size and aspect ratio arise from adaptation within populations of channels encoding size and aspect ratio and not from aftereffects of adaptation to linear distances.

It has previously been shown that, as the size difference between the adaptor and test increases, the magnitude of the repulsive size aftereffect initially increases but then begins to decrease beyond a certain size ratio (Sagara & Oyama, 1957). If size is specified as the area of the stimuli then the aftereffect maxima are at adaptor/test ratios of approximately 1/4 and 4. These two ratios are reciprocally related, suggesting that it is the ratio in size between adaptor and test that determines the size of the aftereffect rather than the absolute size difference. If the aftereffect is plotted against the adaptor-to-test size ratio on a logarithmic axis then the graph approximates the familiar first derivative of a Gaussian (D1) form characteristic of the tilt aftereffect (Clifford, 2002; Clifford, Wenderoth, & Spehar, 2000; Dickinson, Almeida, Bell, & Badcock, 2010; Dickinson, Harman, Tan, Almeida, & Badcock, 2012; Tang, Dickinson, Visser, & Badcock, 2015) predicted by a shift in the centroid of activity in a bank of channels (Clifford et al., 2000; Dickinson et al., 2012). If a linearly distributed bank of Gaussian profile channels is used in the model of the tilt aftereffect a Gaussian function proves a good fit to the population response of the channels to a specific test stimulus. The equivalent model of the encoding of a dimension where quantities are better represented as increasing exponentially requires the channels to have log-Gaussian sensitivity profiles distributed at exponentially increasing intervals. Under such circumstances a D1 function would be expected to fit the relationship between the log of the aftereffect and the log of the ratio of magnitudes of the adaptor and test. We propose that such a model will account for the aftereffects of adaptation to size and hypothesize that the same model might also be applied to account for aftereffects of adaptation to aspect ratio. In the modelling section of this paper the proposed model is shown to result in the predicted D1 function.

A model of aspect ratio aftereffects has previously been proposed by Regan and Hamstra (1992) based on adaptation within two pools of neurons with preferred sensitivities at the extreme ends of sensitivity to aspect ratio. This suggestion arose when they obtained a monotonic increase in the aspect ratio (height/width) discrimination threshold as aspect ratio diverged from a value of 1 (i.e., square). This places stimuli with an aspect ratio of 1 in a privileged position on the dimension encoding aspect ratio and no aspect ratio aftereffect should be expected from adaptation to a stimulus with an aspect ratio of 1. Adaptation to aspect ratios other than 1 should, however, result in the perceived aspect ratio being shifted towards the least adapted pool. The model that we hypothesize to account for the aftereffects of adaptation to aspect ratio, though, places no particular significance on an aspect ratio of 1 and we would expect a test stimulus to be perceived veridically after exposure to an adaptor with the same aspect ratio.

This study, then, critically evaluates our hypothesis that size and aspect ratio are encoded in the population responses of banks of information channels and makes the following testable predictions:

- The data describing the logarithm of the size (aspect ratio) of test stimuli at the PSE versus the logarithm of size (aspect ratio) of the adaptor should conform to the D1 function predicted by the bank of channels model.
- The point of inflection on the D1 function should occur where the magnitudes of the adaptor and test pattern are the same.
- The aspect ratio of a test stimulus at the PSE should depend on the aspect ratio of the adaptor and be independent of the relative sizes of adaptor and test.

General methods

Observers

Four experienced psychophysical observers participated in the study. Two observers, KT and KS, were naïve to the implications of the experimental conditions and two, ED and SM are authors. Observers gave their informed consent prior to their participation in the study. The study was approved by The University of Western Australia Research Ethics committee and, therefore, was performed in accordance with the tenets of the Declaration of Helsinki. The four observers represent replications of the same experimental conditions. All observers had normal or corrected-to-normal visual acuity. Observer ED has a strabismus and so performed the experiment monocularly with the left eye patched. No observers were excluded and no data was excluded for any of the four observers.

Apparatus

Visual stimuli were created in MATLAB and presented from the frame buffer of a Cambridge Research Systems (CRS) 2/3 graphics card (Cambridge Research Systems, Rochester, Kent, UK) to a Sony G420 monitor (Sony Corporation, Tokyo, Japan) refreshed at 100 Hz. Monitor calibration was performed using a CRS Optical (Cambridge Research Systems) and its associated software. Luminance was specified for 1,024 by 768 individual pixels over a linear eight-bit range with a maximum of 90 cd/m^2 and minimum near zero. Observers viewed the monitor from a position, stabilized by a chinrest, 115 cm along the normal to the center of the screen. At this distance each pixel subtended 1′ of visual angle. Observer responses were recorded using two buttons on a CRS CB3 button box.

Visual stimuli

Visual stimuli used in experiments investigating adaptation to size were square and specified by area, the product of the vertical and horizontal linear dimensions. Those used in experiments investigating adaptation to aspect ratio were rectangular, specified by the quotient of the vertical and horizontal linear dimensions and, other than the adapting stimuli used in Experiment 3, had a constant area of one square degree.

To ameliorate the risk that the aftereffects measured were simply due to the repulsion of the boundaries of the test stimuli from the boundaries of afterimages we employed short adaptation periods of only 160 ms, a gray rather than black background to the stimuli, and jittered the position of adapting stimuli across trials. Further, we performed a control experiment to inform our choice of the luminance characteristics of the stimuli, which compared the magnitudes of size aftereffects for adapting and test stimulus pairs that had the same ratio of sizes but different luminance profiles. Aftereffect magnitudes for filled rectangular stimuli with a Weber contrast of 1 used in this study were compared with stimuli defined by a narrow Gaussian luminance boundary ($\sigma = 1$ minute of visual angle) and stimuli matched for luminance energy (the contrast of the stimuli was scaled in inverse proportion to their area). The jittering of the positions of the stimuli ensured that the boundaries of the boundary-defined stimuli were typically not spatially coincident across trials preventing the buildup of afterimages. In the case of the stimuli matched for luminance energy, differences in the magnitudes of boundary repulsion might be expected since light scatter will be larger with higher luminance. Across the three stimulus types, however, the magnitudes of the aftereffects were consistent with being equal, engendering confidence that the aftereffects observed in this study would constitute geometrical aftereffects rather than boundary repulsion whichever of the three stimulus types we chose. For simplicity we chose the filled stimuli. Figure A1 of Appendix A illustrates the stimuli used and Figure A2 presents the aftereffects measured.

Stimuli, then, were filled rectangles with a Weber luminance contrast of 1 relative to the uniform background luminance of 45 cd/m^2. The boundaries of the stimuli were smoothed to background luminance using a one-sided Gaussian function with a standard deviation of 1 minute of visual angle to allow the sizes and aspect ratios to be specified on a continuous range rather than being quantized by pixel size. Square and rectangular stimuli were preferred to circular and elliptical stimuli because successively presented elliptical stimuli would have a range of local orientation differences and would, therefore, suffer from confounding aftereffects of adaptation to local orientation. Successively presented rectangular stimuli can only differ locally in their boundary orientation by 90°, which would not induce tilt aftereffects (Clifford et al., 2000).

Procedure

Aftereffects of adaptation were examined using a comparison of test stimuli centered 4.27°, on average, to the left and right of a fixation marker permanently present at the center of the screen. To prevent the buildup of afterimages of the stimuli due to repeated presentation, the stimuli were varied in their horizontal and vertical position by a distance of up to 1/16 of the average of their linear dimensions, at random, for each trial. For all trials the adaptor and test stimuli were presented for 160 ms with a 500 ms interstimulus interval of the same background luminance interposed between them.

The method of constant stimuli (MOCS) was used to determine a point of subjective equality for the two test stimuli. That is, the point at which the two test stimuli were subjectively equal in size (or aspect ratio). For conditions measuring size adaptation nine different sizes of square test stimuli were used. These had linear dimensions of 1.05^n, $n = \{-4, -3, -2, -1, 0, 1, 2, 3, 4\}$ degrees of visual angle. The two test stimuli in each trial had reciprocal linear dimensions. For example, if the left hand stimulus subtended 1.05^3 degrees of visual angle vertically and horizontally then the right hand stimulus subtended 1.05^{-3} degrees. The areas of the test stimuli were, therefore, 1.05^{2n}, $n = \{-4, -3, -2, -1, 0, 1, 2, 3, 4\}$.

For conditions measuring adaptation to aspect ratio the test stimuli had a range of nine aspect ratios. The heights and widths of the test stimuli were $2^{1/2} \times 1.02^n$ and $2^{-1/2} \times 1.02^{-n}$, $n = \{-4, -3, -2, -1, 0, 1, 2, 3, 4\}$, respectively. The aspect ratios of the test stimuli were, therefore, 2×1.02^{2n}, $n = \{-4, -3, -2, -1, 0, 1, 2, 3, 4\}$. Again the aspect ratios of the left and right test stimuli were modified by reciprocal ratios. For example if the left stimulus had an aspect ratio of 2×1.02^4 then the right hand test stimulus had an aspect ratio of 2×1.02^{-4}.

For the experiments investigating size adaptation observers were required to report, via the button box, whether the stimulus that was perceived to be largest was on the left or right. For each adapting condition observers completed 540 trials over three blocks of 180 trials divided equally over the nine pairs of test stimuli. Within a block all trials were of the same condition. The probability of responding that the largest test pattern was on the left, p(left), was determined for each adapting condition and a cumulative Gaussian distribution fitted to the data describing that probability as a function of the logarithm of the area of the left test stimulus. When the left hand test stimulus was at its largest the observers typically reported it as largest at a probability of 1 and when at its smallest a probability of 0 and so no lapse rate was incorporated in the fit. The fitted function is shown as Equation 1 below with X representing the area of the left test stimulus.

$$p(\text{left}) = 0.5 \times \left(1 + erf\left(\frac{\log(X) - \mu}{\sigma\sqrt{2}}\right)\right) \quad (1)$$

The point of subjective equality (PSE), at which the test squares were perceived to be equal in size, was defined by the point on the function specifying an equal probability of responding that the largest test stimulus was on the right or left. The logarithm of the size of the left stimulus at the PSE was given by the value of μ in Equation 1 and the anti-log yielded the reported size of the left stimulus at the PSE. The function *erf* is the error function and σ is the standard deviation. The R^2 values for the fits to the size adaptation data are presented in Table B1 of Appendix B.

For the experiments examining aspect ratio adaptation, the observers reported whether the pattern with the largest aspect ratio (tall and thin rather than short and fat) was on the left or right. Again, for each condition of adaptor, 540 trials were performed over three blocks of 180 trials divided across the nine pairs of aspect ratio test stimuli. The probability of responding that the test pattern with the largest aspect ratio was on the left was calculated for each pair of test stimuli. A cumulative Gaussian function was fitted to the data describing this probability versus the logarithm of the aspect ratio of the left hand test stimulus (X in Equation 1) and the PSE determined. The logarithm of the aspect ratio of the left hand test pattern at the PSE was then determined from the fitted function and the aspect ratio provided by the anti-log. The R^2 values for the fits to the aspect ratio adaptation data are presented in Table B2 of Appendix B. The specific conditions of adaptation differed across experiments and are reported within the sections describing those experiments.

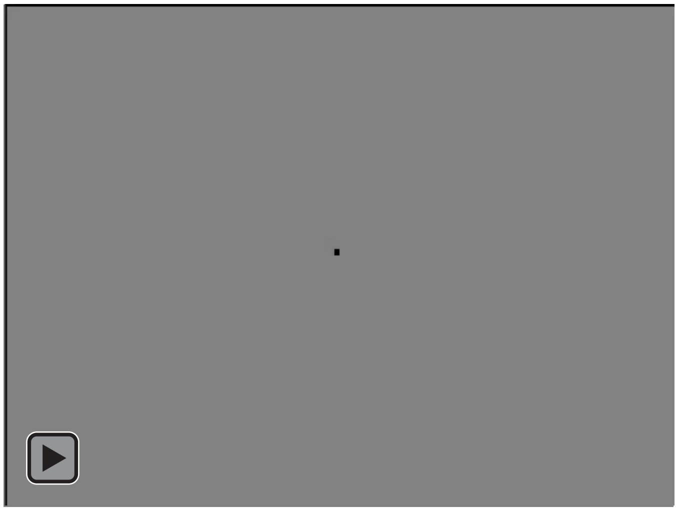
Experiment 1: Size is encoded by a bank of size selective channels

Introduction

Size, or area as we are choosing to define it in this study, is specified in units of square degrees. This choice of unit is arbitrary and, therefore, there is no intrinsic importance to the value of 1 for the adapting stimuli. If size is indeed encoded in a bank of size selective channels then the aftereffects of adaptation to any size should be repulsive in the sense that any subsequently experienced stimulus should appear more different in size to the adaptor than it actually is regardless of the size of the adaptor. The defining characteristic of a multiple, narrow-band, channel based system is, however, that the effects of adaptation first increase in magnitude as the difference between adaptor and test increases on the dimension encoded by the channels but then decrease as the channels sensitive to adaptor and test become more discrete. Experiment 1 examines size adaptation to verify that the graph describing the log of the aftereffects as a function of the log of the difference in size between adaptor and test conforms to the predicted D1 function.

Methods

Square adaptors were presented to the left and right of a marker that the observers were required to fixate. The adaptors varied in size between 1/64 and 64 square degrees with proportional increases in size from one square degree on one side matched with equivalent proportional decreases on the other side. Square test stimuli were also paired with each pair having a geometric mean size of one square degree. The observers were required to report which of the two test patterns appeared the larger and the point of subjective equality (PSE) was determined as the size of the left test pattern of the test pair that the observer judged to be of equal size to its partner, post adaptation (see General methods section). This PSE was determined for each of the adaptor pairs examined (observer ED made observations for 13 adaptor pairs and observers SM, KS, and KT 7 each). Movie 1 demonstrates the size aftereffect. The rationale behind the experimental procedure can be appreciated by viewing Movie 1 from different distances. The effect is always observed, which illustrates that it is the ratio in size difference between the adaptor and test that determines the size and direction of the aftereffect, rather than the difference in their absolute sizes. Having two adaptors with reciprocal ratios in size to the test patterns ensures a large effect. To confirm that both adaptors contributed equally to the combined effect two control conditions were conducted with the adaptor only present on the left. Two adaptor size ratios were tested using a single adaptor; one-fourth and four times the size of the test (1/4 and 4 square degrees).



Movie 1: A demonstration of the Size aftereffect. The area of the adaptor on the left is four times that of the test and on the right it is one-quarter of the area. The two test stimuli are of equal area. After adaptation the test on the left appears smaller than the test on the right. Significantly, the effect is observed regardless of the distance from which the video is viewed.

Results

The results of Experiment 1 are presented in Figure 1 for each observer separately, with the sizes of the left hand test stimuli at the PSE plotted against the size of the left hand adapting stimuli. The data are fitted by the function shown as follows.

$$\ln(Y) = -\ln(A)\left(\frac{1}{\sigma^2}\right)\ln\left(\frac{X}{X_0}\right)e^{-\left(\frac{\left(\ln\left(\frac{X}{X_0}\right)\right)^2}{2\sigma^2}\right)} + \ln(Y_0) \quad (2)$$

This function is a D1 function with the dependent and independent variables being the log of the perceived magnitude of the test stimulus when the two squares are perceived to be the same size and the log of the magnitude of the adaptor respectively. The free parameters in the fit are A, σ, X_0, and Y_0. Parameter A determines the amplitude of the D1 function, σ the width, X_0 the magnitude of the independent variable when the aftereffect is zero and Y_0 the magnitude of the

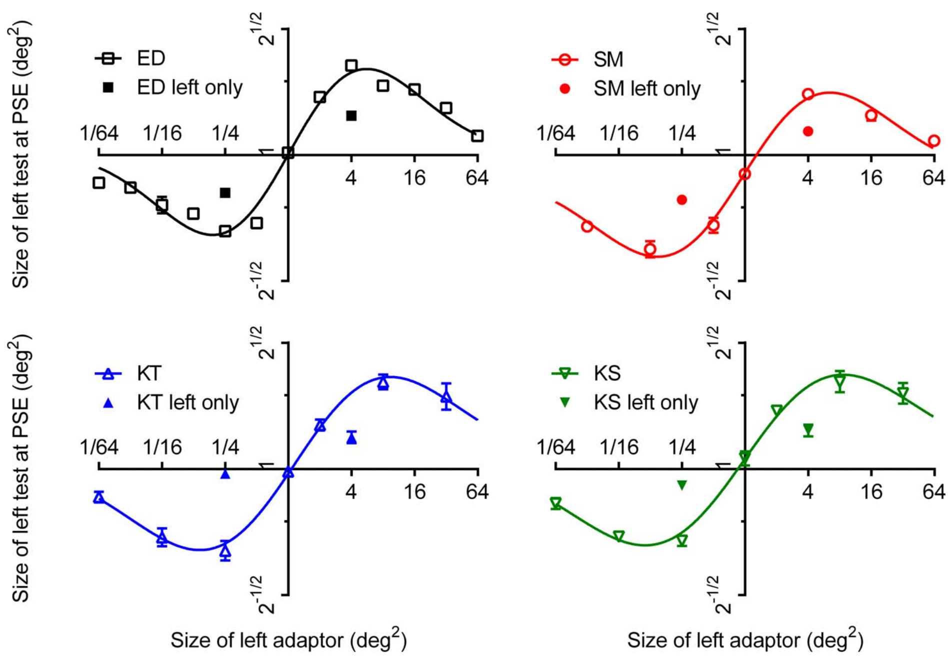


Figure 1. The size of the left hand test stimulus at the PSE as a function of the size of the left-hand adapting stimulus. The size of the left-hand test stimulus at the PSE is initially seen to increase (decrease) as the size of the left hand adapting stimulus is increased (decreased). The magnitude of the effect does, however, peak and then decline as the size of the adaptors become progressively more different from the sizes of the test stimuli. Both axes are logarithmic so the fitted function that has the form of the first derivative of a Gaussian (D1) actually illustrates the symmetry in variation of the logarithm of the size of the left-hand test stimulus at PSE versus the logarithm of the size of the left hand adaptor. Open symbols define data points for conditions where two adaptors were used which had reciprocal sizes. Filled symbols show the results of conditions where only the left-hand adaptor was presented. Error bars show the 95% confidence intervals in the mean of the cumulative normal functions fitted to the psychometric data but are often smaller than the symbols. The R^2 values for the fits are 0.973, 0.988, 0.997, and 0.993 for observers ED, SM, KT, and KS, respectively.

dependent variable when the aftereffect is zero. The aftereffect at a particular point on the function is given by the ratio between the dependent variable at that point and the value of Y_0.

The D1 function specified as Equation 2 is a very good fit to the data for each observer (The R^2 values for the fits are 0.973, 0.988, 0.997, and 0.993 for observers ED, SM, KT, and KS respectively). The free parameters Y_0 and X_0 in the fit specify the position of the point of inflection of the D1. Values of 1 for Y_0 and X_0 would indicate that the size of the left test stimulus at the PSE was 1 square degree after prior exposure to an adapting stimulus of 1 square degree. The geometric mean (and 95% confidence intervals) of the free parameter Y_0 in the fit across the four observers is 1.00 (0.94 lower 95% CI, 1.06 upper 95% CI). For parameter X_0 the geometric mean is 1.04 (0.91 lower 95% CI, 1.18 upper 95% CI). This result is consistent with the test stimulus being perceived as having its true size when the adapting and test stimuli are the same size. The free parameters σ and A pertain to the form of the D1. The geometric mean of σ in the fits to the data of the four observers is 1.95 (1.63 lower 95% CI, 2.33 upper 95% CI). The value of σ determines the positions of the points of maximum amplitude on the D1 function. The derivative of Equation 2, the second derivative of the Gaussian, is zero when $\ln(X/X_0)$ is equal to $\pm\sigma$. If we assume X_0 to be 1, then the maximum amplitudes, calculated from the geometric mean of σ across the observers, are at adaptor sizes of 7.0 (5.3 lower 95% CI, 10.3 upper 95% CI) and 0.14 (0.10 lower 95% CI, 0.19 upper 95% CI). These values are reciprocally related and can be considered to indicate that the largest aftereffects are observed when the left hand adapting stimulus is 7.0 times and 1/7.0 times of the size of the test pattern. The geometric mean of the parameter A, which determines the amplitude of the D1 function, across the observers was 0.47 (0.41 lower 95% CI, 0.55 upper 95% CI). Assuming the values of X_0 and Y_0 to be 1 and substituting the values of 7.0 and 0.14 for X into Equation 2 we arrive at values for the size of the left test at the maximum amplitudes of 1.26 (1.20 lower 95% CI, 1.32 upper 95% CI) and 0.79 (0.76 lower 95% CI, 0.83 upper 95% CI).

Data were also collected for conditions where the adaptor was presented only on the left. Adaptor sizes of one quarter and four times the mean size of the test stimuli were used to directly test the assumption that in our paired adaptor conditions the reciprocal adaptor/test size ratios did, indeed, have the same magnitude of effect. For these conditions the size of the left test stimulus at PSE was determined. The value of the parameter Y_0 fitted in Figure 1 predicts the size of the left test stimulus when there is no effect of adaptation. Values other than 1 indicate a systematic bias in the perception of size of the test stimuli. The sizes of the left test stimuli at PSE for the single adaptor conditions were, therefore, divided by the value of Y_0 for each of the four observers to remove each observer's bias. Following this the geometric mean of the sizes for the small adaptor, 0.93 (0.88 lower 95% CI, 0.98 upper 95% CI), did equate to the geometric mean of the reciprocals of the sizes for the large adaptor, 0.91 (0.88 lower 95% CI, 0.94 upper 95% CI) demonstrating that the aftereffects of adaptation to stimuli with one quarter and four times the area of the test stimuli are consistent with being equal in magnitude when expressed as ratios.

Conclusions

The results closely match the predicted D1 function mapping the log of the size of the adapting stimulus to the log of the size of the left hand test stimulus at the PSE. Because the aftereffect first increases in magnitude and then diminishes as the sizes of the adaptor and test diverge we can reject any suggestion that size is encoded within just two antagonistic pools of neurons with maximal sensitivities at the ends of the spectrum of sizes encountered. The control conditions demonstrated that the aftereffects are equal in magnitude for reciprocal ratios between adaptor and test, if the aftereffects are expressed as a ratio of the size of the test. This outcome indicates that it is the relative sizes of the adaptor and test that predict the aftereffect rather than the absolute sizes. The implications of this observation can be appreciated by viewing Movie 1 from differing distances. The aftereffect is always repulsive regardless of the distance from which the video is viewed demonstrating that the choice of one square degree for the size of the test stimuli in the experiment is arbitrary. If size were encoded by two pools of neurons with sensitivity at the extreme ends of sizes encountered in the visual environment then a large adaptor, for example, would diminish the sensitivity of the pool of neurons more sensitive to large stimuli more than the pool of neurons sensitive to small stimuli. Any subsequently presented test stimulus would then be perceived as smaller than its actual size irrespective of its size relative to the adaptor. The aftereffect would then be seen as repulsive if the test were smaller than the adaptor but attractive if it were larger. The fact that the aftereffects of adaptation are always repulsive argues against the two pool model. A model for the encoding of size in a bank of size selective channels is shown to predict the size aftereffect in the modelling section that follows the experimental sections of this paper.

Experiment 2: Aspect ratio is encoded by a bank of aspect ratio selective channels

Introduction

The stimuli employed in Experiment 1 were treated as having the dimensions of area (height multiplied by width). We define aspect ratio as the vertical distance between opposite borders divided by the comparable horizontal distance and it is, therefore, dimensionless. Despite the quantities being dimensionally different, aspect ratio can be treated in an analogous manner to size. Here we examine whether a bank of channels selective for aspect ratio can account for aspect ratio aftereffects. Again, results demonstrating that the log of the aspect ratio of the left hand test stimulus at the PSE conformed to a D1 function of the log of the adaptor aspect ratio would be taken as evidence for a channel based system. Further we expect the point of inflection of the D1 to occur when the aspect ratio of the adaptor is the same as the aspect ratio of the test. Unlike size, a value of 1 for aspect ratio represents a midpoint between the two ends of the spectrum of possible aspect ratios. A two pool model for encoding of aspect ratio would predict that exposure to a stimulus with an aspect ratio of 1 would produce symmetrical adaptation in the two pools likely resulting in no change in the encoded aspect ratio of any subsequently experienced stimulus (Regan & Hamstra, 1992).

In order to explicitly test whether the point of inflection of the D1 occurs at the aspect ratio of the adapting stimulus rather than at an aspect ratio of 1, a geometric mean of 2 was chosen (see General methods section) for the aspect ratios of the pairs of test stimuli used to determine the aspect ratio of the left hand test at the PSE. The adapting stimulus was presented only on the left-hand side. The value of this arrangement lies in the fact that the perceived aspect ratio of an adapted test is directly compared with an unadapted but variable aspect ratio test stimulus. Absence of adaptation will be indicated by the pair of test stimuli appearing to have the same aspect ratio when they do have the same physical aspect ratios. This allows us to determine which adapting aspect ratio produces no change. This aspect ratio will be 1 if a two-pool system of encoding is employed by the visual system and 2 if a channel based system is employed. Further, the magnitude of the aftereffect will increase monotonically from 1 if a two-pool system is employed. If, however, a channel-based system is employed the log of the aspect ratio of the test at the PSE will conform to a D1 function of the log of the aspect ratio of the adaptor with a point of inflection at 2. This provides for a strong test of our prediction that aspect ratio is encoded in a channel based system.

Movie 2: A demonstration of the aspect ratio aftereffect. To experience the aspect ratio aftereffect fixate on the black fixation point while the video cycles. The adapting stimulus on the left has an aspect ratio of 1 (square). Both of the test stimuli have an aspect ratio of 2 but after adaptation the test of the left appears to have a larger aspect ratio, appears taller and thinner, than the one on the right.

Methods

Observers were required to indicate which of the test stimuli, left or right, had the greatest aspect ratio (the most tall and thin) and the aspect ratio of the left test pattern was determined at the PSE over a range of adaptor aspect ratios (all observers made observations for 11 adaptor aspect ratios: 1/32, 1/16, 1/8, 1/4, 1/2, 1, 2, 4, 8, 16, and 32). Movie 2 demonstrates the aspect ratio aftereffect.

Results

For each observer individually the aspect ratio of the left test stimulus at the PSE is plotted against the aspect ratio of the solitary left hand adaptor in Figure 2 using logarithmic axes.

The function specified as Equation 2 is fitted to the data displayed in Figure 2. Again the free parameters Y_0 and X_0 in the fit specify the position of the point of inflection of the D1. In this case values of 2 for Y_0 and X_0 would indicate that the aspect ratio of the left test stimulus at the PSE was 2 after prior exposure to an adapting stimulus with an aspect ratio of 2. The geometric mean for the parameter Y_0 across the four

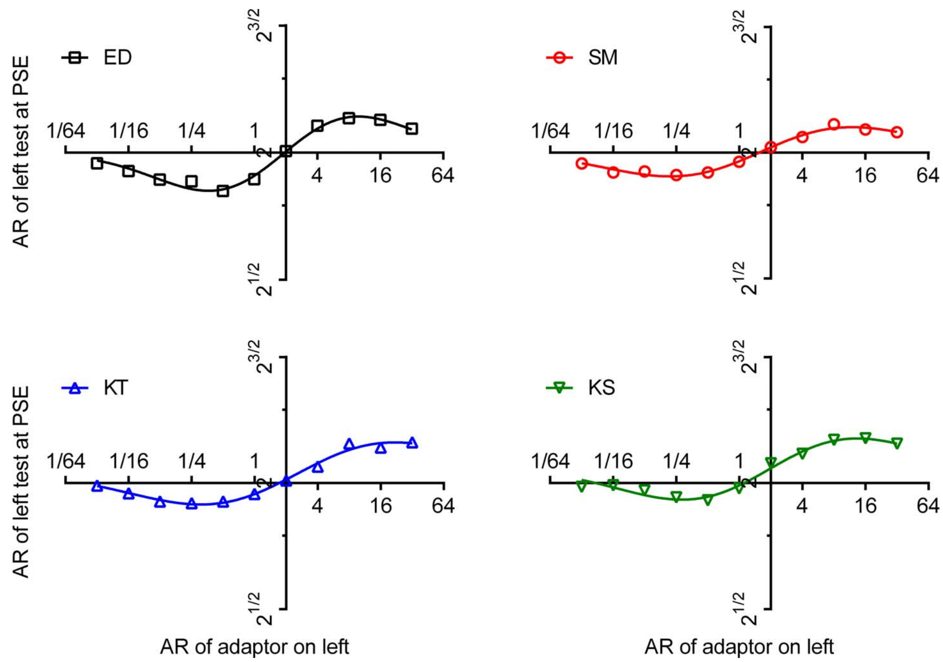


Figure 2. The aspect ratio of the left-hand test stimulus at the PSE as a function of the aspect ratio of the adapting stimuli presented only on the left hand side. Note: The axes of the graphs intersect at the point (2, 2). That is the x-axis is intersected at an adaptor aspect ratio of 2 by the y-axis and the y-axis is intersected by the x-axis at an aspect ratio for the left-hand test stimulus of 2. The aspect ratio of the left hand test stimulus at the PSE is initially seen to increase (decrease) as the size of the left hand adapting stimulus is increased (decreased) from a value of 2. The magnitude of the effect peaks and declines as the aspect ratio of the adaptor becomes progressively more different from the aspect ratios of the test stimuli. Both axes are logarithmic so the fitted function that has the form of the first derivative of a Gaussian (D1) illustrates the variation of the logarithm of the aspect ratio of the left hand test stimulus at the PSE versus the logarithm of the aspect ratio of the left hand adaptor. Error bars show the 95% confidence intervals in the mean of the cumulative normal functions fitted to the psychometric data. The R^2 values for the fits are 0.988, 0.989, 0.985, and 0.979 for observers ED, SM, KT, and KS respectively.

observers is 2.03 (1.97 lower 95% CI, 2.10 upper 95% CI) and for the parameter X_0 it is 1.98 (1.45 lower 95% CI, 2.71 upper 95% CI). The result is, therefore, consistent with the test stimulus being perceived as having its true aspect ratio when the adapting and test stimuli have the same aspect ratio. The intersection of the x-axis and y-axis has been moved to point (2, 2) in Figure 2 to highlight this point. The geometric mean of σ is 1.92 (1.61 lower 95% CI, 2.29 upper 95% CI), consistent with the result obtained for size adaptation. Again, the derivative of Equation 2 is zero when $\ln(X/X_0)$ is equal to $\pm\sigma$. Here, if we assume X_0 to be 2, then the maximum amplitudes, calculated from the geometric mean of σ, are at adaptor aspect ratios of 13.6 (10.5 lower 95% CI, 19.7 upper 95% CI) and 0.29 (0.20 lower 95% CI, 0.40 upper 95% CI). As the aspect ratio of the test patterns was 2 these values are indicate that the largest aftereffects are observed when the adapting stimulus is 6.8 times and 1/6.8 times the aspect ratio of the test pattern. The geometric mean of parameter A across the observers was 0.77 (0.73 lower 95% CI, 0.81 upper 95% CI). Assuming the values of X_0 and Y_0 to be 2 and substituting the values of 13.6 and 0.29 for X into Equation 2 we arrive at values for the aspect ratio of the left test at the maximum amplitudes of 2.17 (2.14 lower 95% CI, 2.21 upper 95% CI) and 1.84 (1.81 lower 95% CI, 1.87 upper 95% CI).

Conclusions

The D1 function described by Equation 2 is again a good fit to the data (the R^2 values for the fits are 0.988, 0.989, 0.985, and 0.979 for observers ED, SM, KT, and KS, respectively). The magnitude of the aftereffect is seen to increase to a maximum and then decrease as the aspect ratios of the adapting and test stimuli diverge, supporting the prediction that aspect ratio is encoded in the population response of a bank of channels sensitive to specific aspect ratios and not two opposing pools of aspect ratio sensitive units. Moreover, there are no aftereffects of adaptation when the adapting and test stimuli have an aspect ratio of 2. A two-pool model might be expected to predict that there would be no adaptation for an adaptor with an aspect ratio of 1 (Regan & Hamstra, 1992) and that a substantial aftereffect for an aspect ratio of 2 would be observed, but these predictions are not supported by the data.

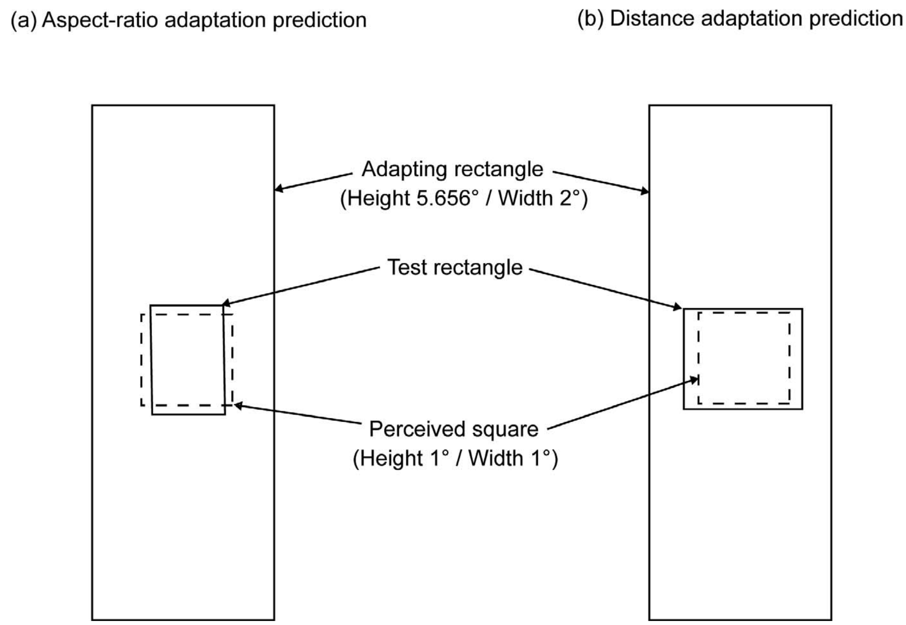


Figure 3. An illustration of the competing predictions of adaptation to aspect ratio versus linear distances. (a) Adaptation to a large rectangle with an aspect ratio of 2.828 causes a smaller rectangle with an aspect ratio greater than one to appear square (dashed square). (b) Adaptation to the linear dimensions of a large rectangle with a height of 5.656 degrees of visual angle and a width of 2 degrees causes a squat rectangle with a height of slightly more than 1° and a width of a little more than that to appear square.

The average position of the point of inflection of the D1 functions across the observers is consistent with being at the point (2, 2) providing further evidence for a bank of channels model for the encoding of aspect ratio.

Experiment 3: Aspect ratio aftereffects are explained by adaptation to aspect ratio rather than perpendicular linear distances

Introduction

Although the preceding experiments are consistent with separate aftereffects of size and aspect ratio it could still be argued that these are also consistent with aftereffects of adaptation to perpendicular linear distances, the height and width for the stimuli used in Experiments 1 and 2. That is, height and width could be encoded in the population responses of independent banks of channels selective for distance in the vertical and horizontal respectively. The perceived height and width would then be expected to be susceptible to distance adaptation. Aspect ratio adaptation might then be explained by independent adaptation within the banks of channels encoding height and width. Here, by exploiting the result that size aftereffects are seen to diminish when the size difference between adaptor and test exceeds a factor of 7, we present a direct test of this possibility by choosing the sizes of the adapting and test stimuli to create conditions in which opposite direction of outcomes arise from aspect ratio adaptation and adaptation to perpendicular linear distances.

If the aftereffects of adaptation in Experiment 2 are genuinely due to the ratio of aspect ratios between adaptor and test then the magnitude of the aftereffect should be indifferent to the relative sizes of the adaptor and test rectangles. This allows us to scale the adapting rectangle to a size that would produce the opposite aftereffect on the test stimulus if the aftereffect was, instead, due to the effects of adaptation in banks of channels encoding the vertical and horizontal extent of the stimuli. Such a condition is illustrated in Figure 3. In Panel (a) of Figure 3 a large rectangle with an aspect ratio of 2.828 causes a rectangle with an aspect ratio of slightly greater than 1 to appear square, a repulsive aftereffect consistent with the results of Experiment 2. In Panel (b) of Figure 3 the alternative prediction of distance adaptation is shown. This prediction can be understood through consideration of Figure 1. If the putative size adaptation were instead due to adaptation to height and width then we can predict the effects of adaptation to distance by comparing the measured size aftereffects for adaptors of area 4 and 32 square degrees (the squares of the height and width of the adapting rectangle considered here). For all observers the repulsive aftereffect is larger for an adaptor size of 4 square degrees than for 32 square degrees. The repulsive aftereffect in the width would be larger than

Movie 3: A trial demonstrating the aspect ratio aftereffect for an adapting stimulus that would produce the opposite sense of aftereffect if aspect ratio aftereffects were due to adaptation to linear dimensions. The adapting stimulus on the left has an aspect ratio of 0.354 and that on the right 2.828. After adaptation the left-hand test stimulus appears taller and thinner than the left hand stimulus consistent with adaptation to aspect ratio rather than distance.

that in the vertical. This would result in a test rectangle that is wider than it is tall appearing square post-adaptation, the opposite of the prediction for aspect ratio adaptation.

Methods

Using test stimuli with aspect ratios having a geometrical mean of 1 and widths and heights with geometrical means of 1 degree of visual angle, we employed adapting stimuli with linear dimensions of 2 and 5.656 degrees of visual angle. Two conditions were tested. In the first the adaptor on the left had a height and width of 2 and 5.656 degrees of visual angle respectively, an aspect ratio of 0.354, and that on the right 5.656 and 2 degrees of visual angle, an aspect ratio of 2.828. In the second the positions of the adapting stimuli were reversed. These two conditions allow us to definitively determine a direction of aftereffect that we can compare with predictions for adaptation to aspect ratio and adaptation to linear distances which are in opposite directions as illustrated in Figure 3.

Again, three blocks of 180 trials were performed for each condition and blocks were interleaved. Observers were required to report which of the two test stimuli, left or right, had the greatest aspect ratio and the aspect ratio of the left hand test stimulus determined at the PSE. Movie 3 demonstrates an example trial. The aspect ratios of the test stimuli at the PSE are presented

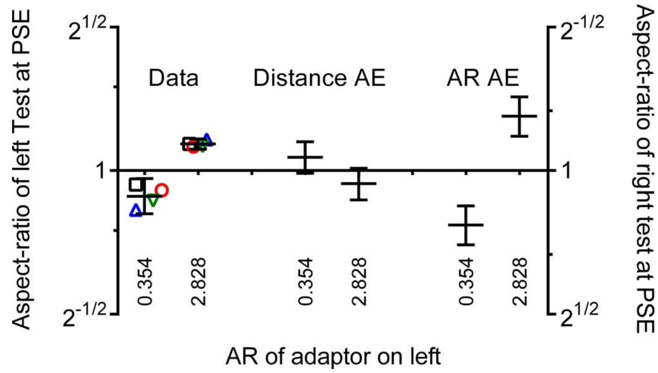


Figure 4. The aspect ratio at PSE of test stimuli following adaptation to adaptors with aspect ratios of 0.354 and 2.828 compared with predictions based on adaptation to linear distance (Distance AE) and to aspect ratio (AR AE). The points representing the data of the four observers are plotted using the same symbols as for Experiments 1 and 2: ED, black squares; SM, red circles; KT, blue triangles; and KS green inverted triangles.

in Figure 4. Also shown in Figure 4 are predictions for these aspect ratios based on the previously-measured size and aspect ratio aftereffects.

Results

Figure 4 plots the results of adapting to stimuli that would produce opposite predictions for adaptation to aspect ratio and distance. The adaptors had the dimensions of 2 by 5.656 degrees of visual angle and vice versa, defining the aspect ratios of 0.354 and 2.828. The fits to the size adaptation and aspect ratio adaptation data from the two previous experiments employing the same observers were used to calculate the predictions.

For the distance aftereffect prediction (Distance AE in Figure 4) the size aftereffect measured in Experiment 1 was assumed to result from adaptation to linear dimensions. The prediction for the aspect ratio of the test stimulus at the PSE was then calculated from the size adaptation data. Using the data presented in Figure 1 the predicted height of the test stimulus at the PSE was taken as the linear dimension of the square test stimulus at PSE after exposure to an adaptor with a linear dimension equal to the height of the adaptor in this experiment. The predicted width was derived similarly and the predicted aspect ratio calculated as the ratio between these linear dimensions.

For the aspect ratio prediction (AR AE in Figure 4) aspect ratios at PSE were derived from the aspect ratio aftereffect data measured in Experiment 2. The predictions were derived from a function with double the amplitude of the fitted function to account for the fact that, in this experiment, adaptors with reciprocal aspect ratios were presented at opposite sides of the visual field whereas in the aspect ratio adaptation experiment only a single adaptor was used. The standard deviation of the function was retained but values of 1 were used for parameters Y_0 and X_0 so that the point of inflection of the D1 function was at an aspect ratio of 1, the geometric mean of the aspect ratios of the test stimuli. The individual data for the observers is rendered using the same symbols as previously employed. The error bars represent 95% confidence intervals in the mean. The predictions were calculated for each observer individually and the mean and 95% confidence intervals plotted for comparison with the data.

The results shown in Figure 4 demonstrate that, postadaptation, the perceived shapes of the test patterns are consistent with adaptation to aspect ratio rather than distances.

Conclusions

The aspect ratios of the test stimuli at the PSE for the adaptors used are consistent with adaptation to aspect ratio rather than independent linear distances. The direction of aftereffects is opposite to that predicted if the effects were due to adaptation to distances. This indicates that different banks of channels, underpin size and aspect ratio aftereffects. The individual channels, because they are not susceptible to distance adaptation, are assumed to represent products and quotients of dedicated perpendicular distance estimates.

The results of this experiment also argue against the results of this study more broadly being predominantly due to repulsion between the borders of an after-image of the adaptor and the border of the test. Other than for a region of attraction when adjacent borders have a separation of less than 4 minutes of visual angle, the borders repel (Badcock & Westheimer, 1985a, 1985b). Beyond an interfigural distance of no more than about 10 minutes of visual angle, however, the magnitude of the repulsion declines. The closer borders of this experiment would, therefore, be expected to be repelled to the greater extent leading to a prediction in the same direction as the distance adaptation prediction, the opposite of what is observed.

Modeling

The results for the three psychophysical experiments argue for a channel-based encoding of size and aspect ratio in two distinct banks of channels but with a similar underlying channel organization. A graph describing tilt aftereffects as a function of the orientation difference between the adaptor and test conforms to a first derivative of a Gaussian or D1 (Clifford et al., 2000; Dickinson et al., 2012). The data describing the size and aspect ratio aftereffects obtained in this study also conform to a D1 if the log of the aftereffect is plotted against the log of the magnitude of the adaptor. This suggests that size and aspect ratio differences are best described as ratios. A channel based model of size and aspect ratio encoding analogous to that proposed by Dickinson et al. (2012) for orientation encoding would, therefore, be expected to have channels with log-Gaussian sensitivity profiles arranged at exponentially increasing intervals (see Dickinson et al., 2012 for details of the model proposed for the encoding of orientation). An implementation of this model is illustrated in Figure 5.

Figure 5 represents the adaptation of the bank of channels in response to exposure to a stimulus with a magnitude of 4 (four square degrees or an aspect ratio of 4) followed by exposure to a test stimulus with a magnitude of 1. Adaptation results in the sensitivity of the channels responding to the adaptor being reduced in proportion to their activation level. The activity of an individual channel is given by Equation 3 and the centroid of the population response to the test stimulus is given by Equation 4.

$$a_i = e^{-\left(\frac{\left(\log\left(\frac{x}{X_i}\right)\right)^2}{2\sigma^2}\right)} \quad (3)$$

$$X_p = \log^{-1}\left(\frac{\sum_i a_i \log(X_i)}{\sum_i a_i}\right) \quad (4)$$

In these equations X is the stimulus size or aspect ratio, X_i is the preferred magnitude of channel i, a_i is the activity in channel I, and X_p is the perceived size or aspect ratio. The standard deviation, σ, is distinct from the standard deviation of the fitted D1 function. In Panel (c) of Figure 5 it is evident that the centroid of activation in the channels that respond to the test stimulus with a magnitude of 1 is displaced toward smaller magnitudes because of the reduction of sensitivity of the channels that were activated by the adaptor.

Channel bandwidth strongly influences the width of the D1 function that describes the variation of the aftereffect with the changing ratio in size or aspect ratio between the adapter and test. Changes in the sensitivity reduction of the channels due to adaptation only weakly influence the width of the D1 but strongly influence the amplitude. The model was optimized by manipulating the channel bandwidth and adaptation depth to cause the model to predict D1 functions with an amplitude and width that matched the corresponding geometric means of the functions fitted to the data of the four observers. Figure 6 shows the model predictions and the fitted D1 functions for size

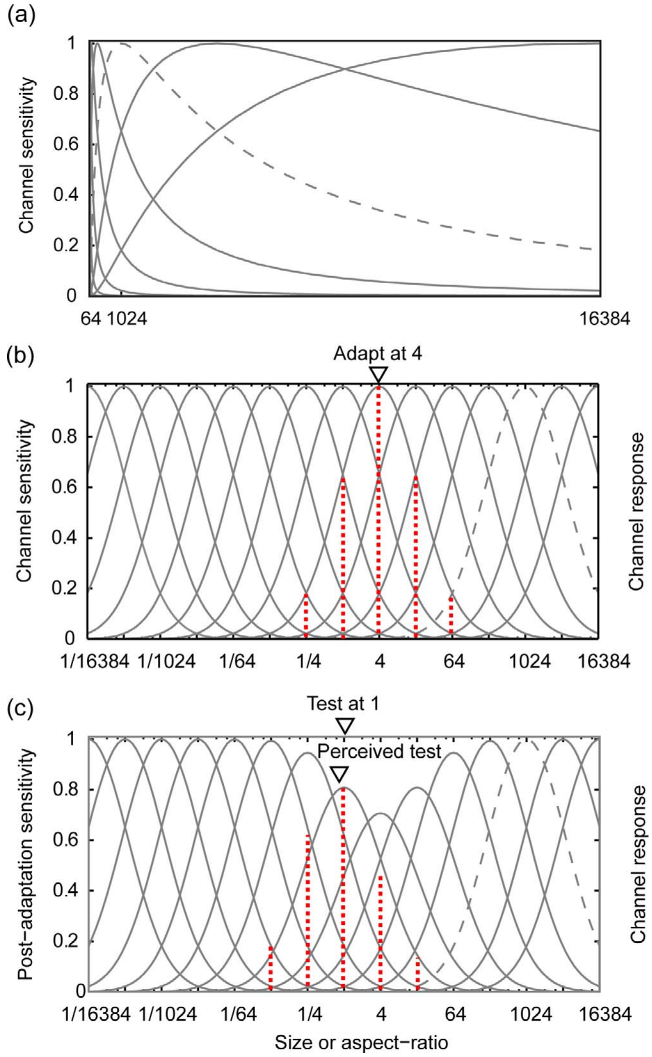


Figure 5. A model proposed to account for aftereffects of adaptation to size and aspect ratio. (a) Channels, illustrated in gray, have log-Gaussian sensitivities and are distributed at exponentially increasing intervals. (b) Channel bandwidths are equal in width when expressed as ratios, and channels are distributed at equal ratios of preferred magnitude. Channel response to an adapting stimulus with a magnitude of 4 is illustrated by vertical dotted red lines. The height to which the lines extend is the height at which a vertical line at the adapting magnitude would intersect each channel's sensitivity profile. The lines themselves are, however, drawn at the preferred magnitude of stimulus for each channel. In this un-adapted state the centroid of the response of the population of channels evoked by the adaptor is at the magnitude of the adaptor. (c) After exposure to an adapting stimulus the channels are decreased in sensitivity in proportion to the degree to which they were activated by the adaptor. Subsequent exposure to a test stimulus results in a channel population response that is modified by prior exposure to the adaptor (activation of the adapted bank of channels is indicated again by dotted red lines). The perceived magnitude of the test stimulus is defined by the centroid of the population response. The end points of the →

adaptation, Panel (a), and aspect ratio adaptation, Panel (b).

The geometric means of the parameters A and σ in the D1 functions fitted to the size adaptation data were 0.47 and 1.95, respectively. A D1 with parameter values of 2.13 (the reciprocal of 0.47 to account for the inversion of the D1 function) and 1.95 was predicted by the model if the gain applied to the channel maximally sensitive to the adaptor was 0.58 and the channel bandwidth was a factor of 32.25 at full width half maximum. For aspect ratio adaptation the geometric means of the fitted parameters A and σ were 0.77 and 1.92, respectively. The reciprocal of the value of A is 1.3. The adaptor was, however, only present on the left and the aspect ratios of the test stimuli were constrained to have a geometric mean of 2 meaning that the aspect ratio of the left hand test stimulus at the PSE was only responsible for nulling half of the aftereffect. The modeled value for A was, therefore, 1.69, the square of 1.3. These values for A and σ were predicted by the model if the gain applied to the channel maximally sensitive to the adaptor was 0.68 and the channel bandwidth was a factor of 28.66.

Discussion

The results for size and aspect ratio adaptation are well described by D1 functions supporting the proposal that these dimensions are encoded by banks of channels that are individually selective to restricted ranges on those dimensions but collectively sensitive to the whole range. A monotonic increase in the magnitude of the aftereffect from a size or aspect ratio of 1 would have lent support for a two pool model but this possibility is clearly ruled out by the results of Experiments 1 and 2, respectively. Moreover the point of inflection of the D1 function that described the results of Experiment 2, using test patterns with a geometric mean of 2, was shown to be at the point (2, 2), meaning that after adapting to rectangle with an aspect ratio of 2 a test rectangle with an aspect ratio of 2 would be perceived veridically. This provides compelling evidence in support of a channel based encoding of aspect ratio. Experiment 3 showed that the aspect ratio aftereffects could not be accounted for by adaptation to the vertical and horizontal linear dimensions of the adapting

← banks of channels correspond to stimuli that would have side lengths of 1/128 degrees of visual angle and 128 degrees of visual angle. These choices are arbitrary but are close to the resolution limit of the visual system and the maximum angular extent of the visual field respectively. There is no necessity for the channels to extend this far.

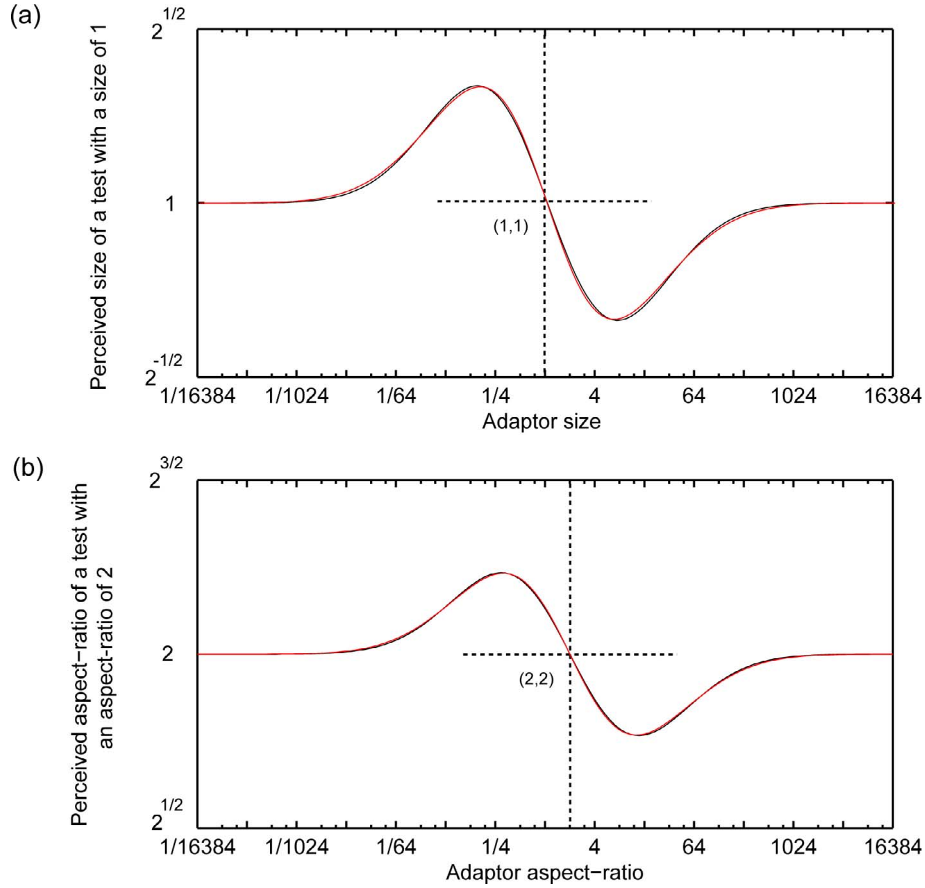


Figure 6. Model predictions of the perceived magnitude of a test stimulus as a function of the magnitude of the adaptor. The predicted size or aspect ratio is given by the centroid of the population response of the bank of channels (see Equation 2). Predictions are made at intervals of factors of $2^{0.1}$ using the model and interpolated using red lines. The predictions are fitted using the D1 function shown as black lines. (a) The model predictions over a range of magnitudes of adaptor size for a test stimulus with a magnitude of 1. (b) The model predictions over a range of adaptor aspect ratios for a test stimulus with a magnitude of 2. In both cases at the point of inflection of the D1 the test stimulus is perceived veridically after adaptation to a stimulus of the same magnitude. The D1 function is inverted with respect to the functions fitted to the psychophysical data because the model predicts the perceived size or aspect ratio of a test stimulus of constant size or aspect ratio while the data represents the size of the test stimulus at the PSE (a value that nulls the aftereffects of adaptation).

stimuli. Precise measures of lengths might also be expected to be provided by a channel-based system and so the absence of any evidence for adaptation to the vertical and horizontal dimensions of the rectangles used in this study suggests that dedicated measures of the height and width of the stimuli are used in the mechanisms that comprise the measures of size and aspect ratio. This in turn requires the measures of size and aspect ratio to be independent.

The results of Experiments 1 and 2 are consistent with the channels of the inferred banks of channels having log-Gaussian sensitivity profiles distributed at exponentially increasing intervals. The aftereffects of adaptation are predicted to arise from a reduction in sensitivity of the channels responding to the adaptor in proportion to the degree to which they are stimulated. This causes a repulsion of the centroid of the population response of the channels that is dependent on the difference between the adaptor and the test stimuli (specifically the ratio of the magnitudes of the adaptor and test). The magnitudes of repulsive aftereffects of adaptation to size are seen to peak for adaptor-test size ratios of both approximately 1/7 and 7. No aftereffect is observed when the adaptor and test are the same and the misrepresentation of the test tightly conforms to the D1 function predicted by the proposed channel-based system for encoding of size or aspect ratio. In Experiment 1 examining the encoding of size the test stimuli had a geometric mean size of one square degree. This choice of size is, of course, as arbitrary as the division of a circle into 360 parts is arbitrary and a number of studies have shown that the aftereffects of adaptation to size are repulsive regardless of the size of the test stimuli (Sagara & Oyama, 1957). The results imply that the point of inflection of the D1 function can be expected to occur at the test size, whatever that might be (there will, of course, be upper and lower limits to the sampling by channels but we have not pursued that question here).

Our aspect ratio adaptation results are consistent with the encoding of aspect ratio in the population response of a bank of aspect ratio selective channels. This solution differs from the two-pool model preferred by Regan and Hamstra (1992) that was proposed to account for a monotonic increase in aspect ratio discrimination threshold from an aspect ratio of 1 (a square). Our model as presented does not account for the improvement in discrimination threshold at an aspect ratio of 1 but it is conceivable that the noise associated with an estimate of aspect ratio is lowest for an aspect ratio of 1. This would be the case if the uncertainty associated with a particular aspect ratio was derived by adding the uncertainty in the estimates of the two linear dimensions in quadrature and the uncertainty in the estimates of each of the linear dimensions was proportional to the square root of its magnitude as might be predicted if dedicated measures of height and width were used in the aspect ratio estimates. Figure 7 shows this prediction for data taken from Regan and Hamstra. The fitted function is

$$Th = C\left(\left(\sqrt{H}\right)^2 + \left(\sqrt{W}\right)^2\right)^{0.5} \quad (5)$$

where Th is the aspect ratio discrimination threshold, C is a constant multiplier, H is the height of the rectangle and W the width (H and W are reciprocally related).

Figure 7 shows that the increasing uncertainty in the estimate of aspect ratio, and the concomitant increase in discrimination threshold can be accounted for by uncertainty in the estimates of height and width. This is consistent with Morgan (2005) who argued for an estimate of aspect ratio based on a combination of noisy estimates of height and width. Our model, however, is mute on this point.

We reject the two-pool model on the combined evidence that the aftereffect conforms to a D1 function of adaptor aspect ratio and that the point of inflection of the D1 function fitted to the aspect ratio data occurred at an aspect ratio of 2, the aspect ratio of the test pattern, not at 1, as the proposed two pool model would predict. Consistent with Regan and Hamstra, we show that the relative size of the adaptor and test is irrelevant to adaptation to aspect ratio, indicating that the analyses of size and aspect ratio are independent. Specifically we show that aftereffects of adaptation to patterns with differing aspect ratios are predicted by adaptation to aspect ratio rather than adaptation to linear distances. This implies that the channels encoding aspect ratio use dedicated measures of perpendicular distances rather than population measures of distance. The utility of this arrangement is that the measures of size and aspect ratio would be robust to

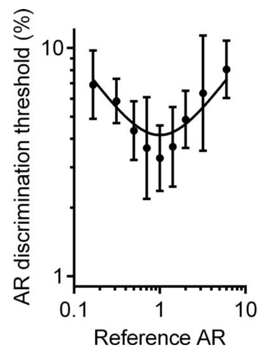


Figure 7. Aspect ratio discrimination thresholds versus reference aspect ratio, compared with a prediction based on noisy estimates of height and width. The plotted data points are the geometric means of the points plotted in panels B, E, H, and K of Figure 1 of Regan and Hamstra (1992) plotting discrimination thresholds versus aspect ratio of the reference stimulus. These points represent the data for four observers for discrimination of rectangles with an area of 1 square degree on the basis of aspect ratio. Error bars are 95% confidence intervals in the geometric mean of the discrimination thresholds of the four observers. The fitted function is given as Equation 5.

changes in the visual statistics of the environment. This would allow size to provide reliable comparisons of perceived distance and enable aspect ratio to be used as a distance-invariant cue to object identity. That is, aspect ratio is preserved as the distance to a target object is varied, perhaps allowing an object to be identified at different distances on the basis of its aspect ratio. In contrast, the retinal size of an image of an object that has been identified allows the distance to that object to be estimated based on knowledge of its physical size. The similar mechanisms of encoding provide information that is exploited in very different ways and therefore investigation of the encoding of size and aspect ratio in parallel might prove illuminating. Also of critical importance is the manner in which the measures of size and aspect ratio generalize to more complex stimuli. We argue that dedicated measures of height and width of rectangles encode their size and aspect ratio but it is difficult to extrapolate our results to objects with more complex boundaries than the rectangles employed here. Perhaps a crude representation of the extent of an object is provided by a coarse sampling of its boundary. If, however, complex objects are deconstructed into their component parts at matched concavities, as has been suggested (Biederman, 1987), then the simpler, predominantly convex, components would be more immediately amenable to analysis on the basis of height to width ratios.

Although this paper concentrates on developing an algorithmic model for the processing of size and aspect ratio it is based on the demonstration in neurophysiological studies that neurons of V1 are selective for spatial frequency. These channels have the same log-

Gaussian sensitivity profiles proposed for the size and aspect ratio channels and have been described as labelled information channels (Watson & Robson, 1981). The neural substrates of analogous size and aspect ratio channels are uncertain. A recent brain imaging study investigating activity in V1 showed that the area of the blood oxygen level-dependent (BOLD) fMRI response of V1 predicts the size adaptation illusion (Pooresmaeili, Arrighi, Biagi, & Morrone, 2013). More recently Mikellidou et al. (2016) showed that transcranial magnetic stimulation (TMS) applied to cortical area LO1 of the lateral occipital cortex (LOC) released observers from an aspect ratio illusion. The release from the illusion was not observed when the TMS was applied to LO2 or V1. Mikellidou et al. argued that the size illusion was therefore a result of feedback onto area V1 and that LO1 was critical to this illusory size-change. Silson et al. (2013) demonstrated differential effects of TMS applied to LO1 and LO2 on performance in the discrimination of orientation and shape. The oriented stimuli were circularly windowed sinusoidal gratings and the shape stimuli radial frequency (RF) patterns, patterns deformed from circular by a sinusoidal modulation of radius. Stimulation of LO1 and LO2 impaired orientation and shape discrimination, respectively. To reconcile these findings it might be reasoned that orientation discrimination might be impaired if it were in some way contingent on an accurate assessment of the aspect ratio of the window of the grating. It is the case that larger aspect ratios do result in a dominant orientation for a shape. Supporting this link Ellison and Cowey (2009) showed that TMS to a subregion of LOC, likely corresponding to LO1, does impede aspect ratio discrimination performance. If discrimination of the amplitudes of modulation of the RF patterns in fact depended on judgements of size of the overall envelope of the patterns then perhaps size judgements may be more closely linked to the operation of LO2. It would be desirable to determine whether aspect ratio and size can be selectively influenced by TMS to LO1 and LO2 as these areas might form a substrate for the separate banks of channels supported by the psychophysical data reported here.

Keywords: size, aspect ratio, adaptation, aftereffects, information channels, population encoding

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Appendix A

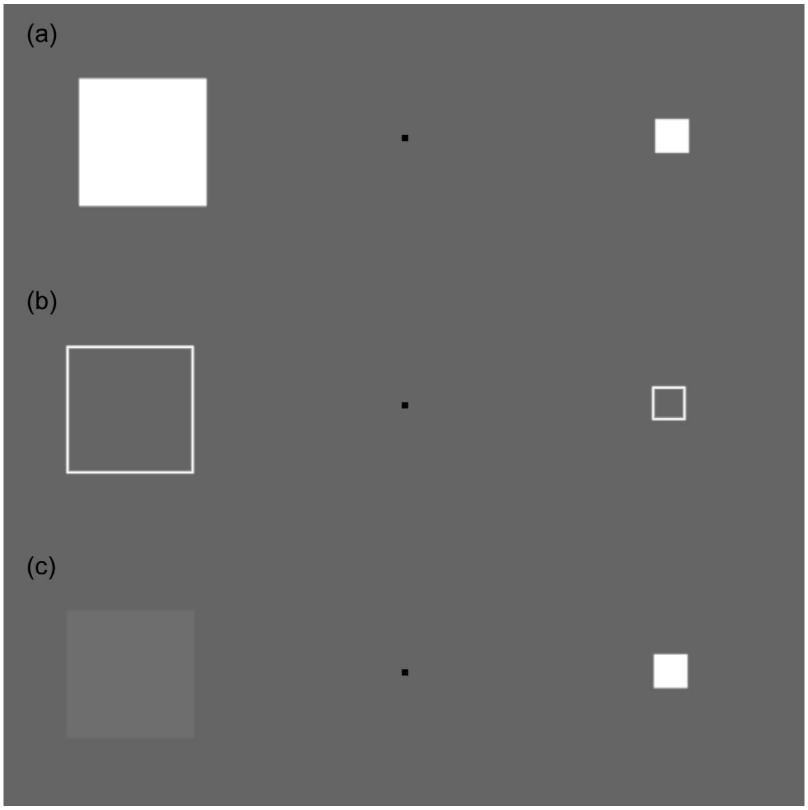

Figure A1. Adaptors used in a control experiment to verify that the aftereffects observed in this study could be attributed to adaptation to the geometry of the adapting stimuli, rather than repulsion of the boundaries of the test stimuli from the boundaries of afterimages accumulated over multiple trials. (a) An example of the filled stimuli used throughout Experiments 1, 2, and 3. (b) Adapting stimuli with the same size but defined by a narrow Gaussian luminance profile ($\sigma = 1$ minute of visual angle) boundary. (c) Adaptors matched for luminance energy (the total luminance contrast of the stimuli integrated over their area was matched). The test patterns for these control conditions were constructed in the same manner as the adapting patterns. The test patterns for condition (c) for example also had the same integrated contrast as the adapting patterns.

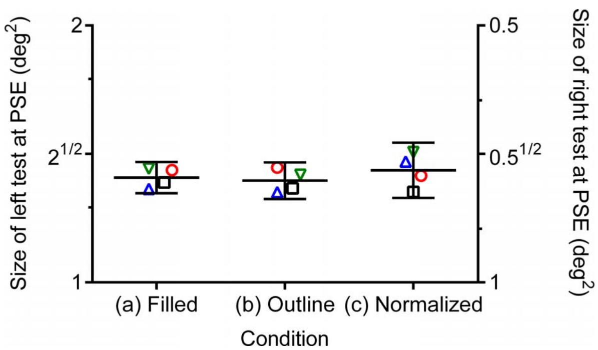

Figure A2. Sizes of the test patterns at PSE for the three control conditions illustrated in Figure A1. As demonstrated by the 95% confidence intervals, the aftereffect is consistent with being equal in size across the three conditions. The data analysis for these control conditions was identical to that for Experiment 1 but an adapting duration of 320 ms was used, rather than 160 ms, to exacerbate the effects of afterimages were they present. The symbols representing the data of the individual observers are the same as for the three main experiments: ED, black squares; SM, red circles; KT, blue triangles; and KS green inverted triangles.

Appendix B

	1/64	1/32	1/16	1/8	1/4	1/2	1	2	4	8	16	32	64
ED	0.98	0.99	0.94	0.99	0.98	0.99	0.99	0.99	0.99	0.97	0.99	0.99	1.00
SM		0.98		0.92		0.94	1.00		0.99		0.98		0.98
KT	0.98		0.94		0.92		0.98	0.98		0.95		0.86	
KS	0.97		0.98		0.97		0.96	0.99		0.89		0.90	

Table B1. R^2 values for the fits of cumulative Gaussian functions to the method of constant stimuli (MOCS) data for the size adaptation experiment, Experiment 1. The header line indicates the size of the left hand adapting stimulus.

	1/64	1/32	1/16	1/8	1/4	1/2	1	2	4	8	16	32	64
ED		0.94	0.97	0.98	0.96	0.96	1.00	0.99	0.97	0.93	0.96	0.96	
SM		0.97	0.96	0.99	0.98	0.99	0.96	0.92	0.96	0.91	0.98	0.98	
KT		0.95	0.96	0.98	0.98	0.97	0.94	0.92	0.96	0.93	0.96	0.95	
KS		0.98	0.98	0.96	0.96	0.96	0.94	0.96	0.97	0.85	0.96	0.94	

Table B2. R^2 values for the fits of cumulative Gaussian functions to the method of constant stimuli (MOCS) data for the aspect ratio adaptation experiment, Experiment 2. The header line indicates the aspect ratio of the sole adapting stimulus present on the left.