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An aftereffect of adaptation to mean size

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The visual system rapidly represents the mean size of sets of objects (Ariely, 2001). Here, we investigated whether mean size is explicitly encoded by the visual system, along a single dimension like texture, numerosity, and other visual dimensions susceptible to adaptation. Observers adapted to two sets of dots with different mean sizes, presented simultaneously in opposite visual fields. After adaptation, two test patches replaced the adapting dot sets, and participants judged which test appeared to have the larger average dot diameter. They generally perceived the test that replaced the smaller mean size adapting set as being larger than the test that replaced the larger adapting set. This differential aftereffect held for single test dots (Experiment 2) and high-pass filtered displays (Experiment 3), and changed systematically as a function of the variance of the adapting dot sets (Experiment 4), providing additional support that mean size is adaptable, and therefore explicitly encoded dimension of visual scenes.

Keywords: Mean size; Adaptation aftereffect; Summary representations.

The visual system can only represent a few objects at a time in any detail (Irwin, 1991; Nakayama, 1990; Rensink, 2000; Simons & Levin, 1998; but see Simons & Rensink, 2005). However, we perceive the world around us as vibrant and complete. This discrepancy between processing capacity and perception has led to the proposal that the system may represent sets or collections of objects in a qualitatively different manner than individual objects, encoding average size along a single visual dimension. Here, we examined whether the mean size of sets is explicitly encoded as a basic

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dimension of visual scenes, like texture density (Durgin, 1995, 2008; Durgin & Huk, 1997; Durgin & Proffitt, 1996) or numerosity (Burr & Ross, 2008), by testing for an adaptation aftereffect.

Ariely (2001) first reported that observers could determine whether a test circle presented immediately after a collection of heterogeneously sized circles represented the mean size of the set, but could not reliably determine whether the test circle was present in the set. Based on these results, Ariely concluded that the visual system encodes a representation of the average size of sets of similar or redundant objects, without including precise information about the individual objects comprising the set. In 2003, Chong and Treisman reported that observers could quickly judge which of two sideby-side displays of heterogeneous circles had the larger mean size, with similar speed and precision as they could judge which of two single circles, or two homogeneous displays of circles had the larger average size. When they independently varied the density, number, and average size of circles comprising the sets, Chong and Treisman (2005) reported that only average size manipulations had much of an effect on the perceived size of the set of circles, providing further support for the proposal that observers were relying on a representation of the mean size of the set.

Building on these findings, here we examined whether mean size is encoded as a basic visual dimension of sets by testing for an adaptation aftereffect. Adaptation along a particular visual dimension can be explained in terms of independent mechanisms selectively sensitive over a limited range (e.g., Campbell & Robson, 1968). For example, following adaptation to visual motion in one direction, a subsequently viewed static image appears to drift in the opposite direction (e.g., Anstis, Verstraten, & Mather, 1998). Although such adaptation aftereffects are well established for "low level" stimulus features such as orientation (e.g., Gibson & Radner, 1937), and direction of motion (e.g., Anstis et al., 1998), it is less clear whether adapting to the average size of a group of objects can cause a similar perceptual bias. An aftereffect specific to mean size adaptation would provide further support for the proposal that mean size is automatically processed as a basic visual dimension, and not simply inferred from other stimulus properties.

Recent findings suggest several other dimensions of sets are adaptable, and therefore encoded along a single visual dimension. Unlike previously reported texture size/density aftereffects that could be reduced to spatial frequency aftereffects (e.g., Anstis, 1974), Durgin and colleagues have repeatedly demonstrated differential aftereffects from adaptation to the density of a variety of textures (Durgin, 1995, 2008; Durgin & Proffitt, 1996) that cannot be accounted for by differences in spatial frequency or orientation (Durgin & Huk, 1997). Similarly, Burr and Ross (2008) have demonstrated that when observers adapt to two sets of dots with different numerosities, their perceptions of the numerosity of dots in subsequently presented test patches are differentially biased such that test patches presented to regions adapted to a high numerosity appear less numerous than the same test patches presented to regions adapted to a lower numerosity.

Here we employ similar logic to test whether mean size was subject to adaptation. We adapted observers to two side-by-side patches of heterogeneously sized dots, one patch with a larger arithmetic mean diameter than the other, and tested the effects on the perceived size (diameter) of test patches presented in the adapted locations. If mean size is encoded as a basic visual dimension of sets, we should observe a differential adaptation aftereffect, such that the test patch presented in the location adapted to the larger mean size appears smaller than the test patch presented in the region adapted to the smaller mean size. In Experiment 1, we began by testing the effects of adaptation to mean size on the perceived size of two test patches with multiple dots of heterogeneous sizes. To examine whether mean size adaptation similarly affects the perceived size of a single test object, we conducted Experiment 2, using two single test circles. Next, we conducted Experiment 3 to rule out alternative explanations that global, low spatial frequency components of the adapting displays were driving the observed aftereffect. Finally, in Experiment 4, we measured the size of the aftereffect with adapting displays of constant mean sizes, across three different variance conditions to ensure that observers were, in fact, adapting to the mean size of the displays, and not to the size of a particular dot on each trial.

EXPERIMENT 1: MULTIPLE DOT TEST DOTS

We began by adapting observers to two side-by-side patches of dots with different mean sizes (diameters), and testing the effects on the perceived average dot sizes of two test patches. Importantly, we randomized the position of each of the individual dots comprising the adapting and test displays on every trial. Therefore, the size of an individual dot in any given location within our adapting and test patches was not consistently larger or smaller than any other dot; only the sizes of the individual dots comprising the adapting displays, and thus the difference in mean dot size (diameter) between the two adapting sets were constant over the course of the experiment. If mean size is encoded as a basic visual dimension, then we should observe a differential adaptation aftereffect, such that observers perceive the test patch presented in the region adapted to larger mean size set of dots as having a smaller average dot size than the test patch presented in the region adapted to the smaller mean size dot patch.

Methods

Participants

Five graduate students at the University of California, Davis (one woman and four men, aged 23–30) with normal or corrected-to-normal vision voluntarily participated in two 45-min sessions. All procedures and protocols were in accordance with the University of California, Davis's Institutional Review Board.

Task

On each trial, we asked observers to indicate which of two side-by-side test dot patches, the left or the right, appeared to have the larger average dot diameter, by pressing the "z" key on a computer keyboard with the left index finger, or the "/" key with the right index finger, respectively. The experimenter informed participants to respond as quickly and accurately as possible on each trial, and to remain focused on the 0.5° of visual angle fixation cross that was always present in the centre of the screen.

Apparatus

A Dell PC presented the black dots against a 79 cd/m² white background on a 19-inch Dell monitor with a vertical refresh rate of 75 Hz (1280 pixel \times 1024 pixel resolution), and recorded responses made using a computer keyboard. Matlab[®] software (Version 7.4a) controlled all the display, timing, and response functions. Participants were seated 57 cm away from the centre of the monitor, and restrained by a combination chin-andhead rest.

Stimuli

Adapting displays (Figure 1). The adapting stimulus consisted of two sets of 14 dots. Each set of 14 dots was composed of two concentric rings: An outer ring of eight dots initially positioned at one of eight cardinal or 45° intercardinal locations around an imaginary circle with a radius of 4° of visual angle, and then jittered independently in the x- and y-directions by a random factor between -0.469° and $+0.469^{\circ}$ of visual angle, and an inner ring of six dots initially positioned around an imaginary circle with a 2° radius at the 30° , 90° , 150° , 210° , 270° , and 330° positions, then jittered in the same manner as the outer dots. Within each of the two 14-dot patches, we restricted the positions of the dots such that no individual dot was within 0.125° of any other dot in either the x- or y-direction.

Each two-ringed adapting dot set was centred at 8° of eccentricity along the horizontal meridian, relative to the centre of the monitor. The smaller



Figure 1. A sample trial sequence in Experiment 1: Each condition began with 2 min adaptation display (the Big on Right adapting condition is shown here) followed by cycling 2 s top-up adaptation displays, and 250 ms test patch displays, then a blank screen until observers responded, or for 3 s, whichever came first.

adapting set always contained the same 14 individual dots ranging in diameter from 0.737° to 1.375° in 0.049° steps, with a constant mean size of 1.056° of visual angle. The larger adapting set always contained the same 14 individual dots ranging in diameter from 1.473° to 2.112° , also in 0.049° steps, with a constant mean size of 1.792° of visual angle. The positions of the 14 dots in each set were randomized on every trial, such that no location within either patch consistently contained a dot that was larger or smaller than any other dot in the set.

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Test displays (Figure 1). There were 11 test stimuli in Experiment 1. Each of the 11 stimuli consisted of two side-by-side patches of 14 dots, as in the adapting displays. Also, as in the adapting displays, each test patch was composed of an inner ring of six dots subtending 4° of visual angle, and an outer ring of eight dots subtending 8° of visual angle, with individual dot positions jittered by a random factor between -0.469° and $+0.469^{\circ}$ in the x- and y-directions on every trial. The left test patch was composed of one of 11 different test sets. Each test set contained 14 individual dots, with the smallest dot in each test set ranging from 0.781° to 1.719°, in 0.094° steps. Within each test set, individual dots increased in size from the respective smallest dot in 0.031° steps. Unknown to subjects, the right test patch served as a standard, and always consisted of the same 14 dots in the sixth of the 11 test sets, ranging in size from 1.250° to 1.656° . For the 11 possible combinations of right standard and left test patches, the average dot diameter in the left test patch differed from the average dot diameter in the standard right test patch by: -0.469° , -0.375° , -0.281° , -0.188° , -0.094° , 0° , 0.094° , 0.188° , 0.281°, 0.375°, and 0.469° of visual angle, respectively. Note that negative numbers indicate the average left test dot diameter was smaller than the average right test dot diameter, and 0° indicates the two test patches had identical average dot diameters. We adopt this convention of negative valence for smaller left tests in all subsequent experiments. As in the adapting displays, the positions of the 14 dots in each right and left test set were randomized on every trial, such that no location within either patch consistently contained a dot that was larger or smaller than any other dot in that set.

Procedure

Each observer participated in two experimental conditions; one in which they adapted to the set of dots with the larger mean size on the left side of the screen (Big on Left), and one session with the set of larger dots on the right side of the screen (Big on Right), on separate days. We counterbalanced the order of the two adapting conditions between subjects.

As the sample sequence in Figure 1 illustrates, each block began with an initial adaptation phase, during which subjects fixated while viewing a display of two side-by-side adapting patches for 2 min. After this initial adaptation, each trial consisted of a top-up adaptation display presented for 2 s, followed by a test display for 250 ms, and then a blank screen until observers responded, or for 3 s, whichever came first. We excluded responses made later than 3 s after the display offset from further analysis. We used top-up displays after each test presentation to ensure that participants remained adapted to the two different mean sizes over the course of the experimental session. Using the method of constant stimuli, we presented each of the 11 possible test combinations 10 times per block, in random sequence. Observers

performed five blocks of trials, for a total of 50 trials per test combination and 550 total trials in each of the two adapting conditions (Big on Left, Big on Right).

Results

For each subject, in each adapting condition (Big on Left, Big on Right), we computed the average probability of a response that the average dot size of the left test patch appeared larger than the average dot size of the right patch. Using maximum likelihood estimation, we next fit each participant's averaged responses over the 11 test combinations to two separate logistic functions (one for the Big on Left condition, and one for the Big on Right condition), with lower and upper bounds of 0 and 1, respectively. Goodness of fit was evaluated with deviance scores, calculated as the log-likelihood ratio between a fully saturated, zero-residual model and the data model. A score above the critical chi-square value indicated a significant deviation between the fit and the data (Wichmann & Hill, 2001). All curves, shown in Figure 2, represent significant fits to the data, as all deviance scores were below the critical chi-square value, $\chi^2(11, 0.95) = 19.68$. There was a significant difference between the logistic fits to each adapting condition, for each subject, all $t_s(10) > 2.98$, all $p_s < .015$. Individual logistic fits for the Big on Left adapting condition were shifted rightward relative to leftwardshifted logistic fits for the Big on Right condition, indicating all observers experienced a negative adaptation aftereffect.

For each of the adapting conditions, we defined the magnitude of an individual subject's aftereffect as the Point of Subjective Equality (PSE), the 50% point on the psychometric function. The PSE quantifies the physical difference in average dot size for the two test patches to appear equal in average dot diameter. A paired *t*-test examining the effect of adapting condition (Big on Left vs. Big on Right) on participants' PSEs indicated a negative aftereffect over the five observers, t(4) = 8.309, SEM = .04116, p = .001.

Discussion

We observed a differential aftereffect such that the appearance of the average dot size of a test dot patch was inversely dependent on the average dot size of a preceding adapting dot patch. All subjects in Experiment 1 experienced this adaptation aftereffect; on average, they perceived the average dot size of a test patch replacing the adapting patch with the smaller mean dot size as being larger than a test patch replacing the adapting patch with the larger mean size. This conclusion is supported by the significant differences between the respective logistic fits to each participant's averaged "Left



Figure 2. Experiment 1 results (multiple test dots): Logistic fits (lines) and actual data (points) for the average probability of responding that the left test patch appeared to have the larger average size over the 11 left/right test size differences in each adapting condition (Big on Right, Big on Left), for each participant in Experiment 1. On average, observers more often perceived the test patch on the left as having the larger average dot size when they were adapted to the set of dots with the larger mean size on the right ("Big on Right", solid lines; squares), and the left dot patch as having the smaller mean dot size when adapted to the set of dots with the larger mean size on the left ("Big on Left", dashed lines; circles). In each plot, the dashed horizontal line delimits the proportion of responses (y-axis) for which the observer was equally likely to respond that the test patch on one side appeared to have a larger average size than the other test patch, and the vertical dashed lines mark the corresponding PSEs (x-axis) for each adapting condition in terms of the difference in the average sizes of the test dot patches necessary for this perceived equality.

appears larger" responses for the 11 test combinations in the Big on Left and Big on Right adapting conditions. In addition, there was a significant difference between the PSE parameters of the logistic functions fit to each subject's averaged responses in the two adapting conditions, confirming an overall shift in the perceived sizes of the test dots between the two conditions. Therefore, the results of Experiment 1 demonstrate a differential aftereffect of mean size, supporting the proposal that mean size is adaptable, and therefore an explicitly encoded dimension of visual scenes.

EXPERIMENT 2: SINGLE TEST DOTS

Although the results of Experiment 1 provide support for the proposal that mean size is an explicitly encoded visual dimension, susceptible to adaptation, the possibility remained that the observed aftereffect was specific to the perceived density of the test patches (cf. Durgin, 2008; Durgin & Huk, 1997). To help control for such local density effects, we randomized the positions of individual dots in our adapting and test displays on every trial in Experiment 1. Yet, within the larger average size adapting patch, there was still more area covered by individual dots (higher density) than in the smaller adapting patch. Therefore, a density aftereffect, if present, may have biased subjects' reports of which test array appeared larger. As density aftereffects do not transfer to single features (single dots), we conducted a second experiment to examine whether the size aftereffect resulting from adaptation to many dots would transfer to affect the perceived size of a single test dot. In Experiment 2, we replaced the multiple dot test patches with single test dots. Given that single, filled test dots do not differ in density, a replication of the differential aftereffect we observed in Experiment 1 would offer further support that the mean size of the adapting displays, and not the density of the dots comprising each display, was driving observers' misperceptions of size.

Methods

Except for the switch from multiple dot test patches to single dot test stimuli, the participants and methods of Experiment 2 were identical to those of Experiment 1. As in Experiment 1, there were 11 pairs of test stimuli. However, in Experiment 2, each test pair consisted of only two side-by-side single dots, presented simultaneously to the respective adapted regions. Subjects were now instructed to indicate whether the left or right test dot appeared larger (in diameter). Similar to the methods of Experiment 1, unknown to subjects, the right test dot served as a standard and the left dot ranged in size relative to the standard right dot. The right standard dot was a constant 1° of visual angle. For subjects DH and TH, who had become rather well-practised over the

course of pilot experiments and Experiment 1, this left test dot differed from the right standard dot by -0.227° , -0.182° , -0.136° , -0.091° , -0.045° , 0° , 0.045° , 0.091° , 0.136° , 0.182° , and 0.227° . For subjects JK, KB, and ND, the left test dot differed from the 1° standard right dot by -0.385° , -0.308° , -0.231° , -0.154° , -0.077° , 0° , 0.077° , 0.154° , 0.231° , 0.308° , and 0.385° . We randomized the positions of the test dots within the two 8° adapted regions from trial-to-trial, so that no given location in either adapted region was consistently probed, making it more likely that the mean size of the entire display of adapting dots was responsible for any observed effects on the perceived size of the individual test dots.

Results

For each subject, in each adapting condition, we again computed the average probability of a response that the left test dot appeared larger. We again used maximum likelihood estimation to fit each participant's averaged responses to separate logistic functions with upper and lower bounds of 0 and 1, respectively, for the Big on Left and Big on Right adapting conditions. The resultant curves in Figure 3 represent significant fits for each participant, as all deviance scores were below the critical chi-square value, $\chi^2(11, 0.95) = 19.68$. Again, all subjects showed a significant difference between the logistic fits for the two adapting conditions, all *ts*(10) > 2.9, all *ps* <.017, and we defined the magnitude of their aftereffects in the two adapting condition as the PSEs of their respective psychometric functions. As in Experiment 1, a paired *t*-test revealed significant differences across subjects' PSEs between the two adapting conditions, *t*(4) = 10.301, *SEM* = .02272, *p* =.001.

Discussion

The results of Experiment 2 suggest that the differential adaptation aftereffect of mean size observed for test displays of multiple dot elements in Experiment 1 transfers to affect the perceived size of single test circles. On average, each subject perceived the test dot that replaced the smaller mean size adapting display as larger than the test dot that replaced the larger mean size adapting display. In addition, there was a significant difference between the PSE parameters of the logistic functions fit to subjects' averaged responses in the two adapting conditions, confirming an overall shift in the perceived sizes of the test dots between the two conditions. As the aftereffect observed in Experiment 1 for multiple test dot displays held for single test dots, the results of Experiment 2 provide additional support that the aftereffect was specific to the mean sizes of the adapting patches, not just an aftereffect of the perceived density of the test displays.



Figure 3. Experiment 2 results (single test dots): Logistic fits (lines) and actual data (points) for the average probability of responding that the left test dot appeared larger over the 11 left/right test size differences in each adapting condition (Big on Right, Big on Left), for each participant in Experiment 2. On average, observers more often perceived the test dot on the left as larger when they were adapted to the set of dots with the larger mean size on the right ("Big on Right", solid lines; squares), and the left test dot as smaller when adapted to the set with the larger mean size on the left ("Big on Left", dashed lines; circles). In each plot, the dashed horizontal line delimits the proportion of responses (y-axis) for which the observer was equally likely to respond that the test dot on one side appeared larger than the other test dot, and the vertical dashed lines mark the corresponding PSEs (x-axis) for each adapting condition in terms of the difference in the sizes of the test dots necessary for this perceived equality.

While Experiment 2 helped to rule-out alternative accounts based on density aftereffects, it was still possible that the adaptation effect occurred due to the differences in global spatial frequencies between the adapting displays in the first two experiments. As the adapting display with the larger average size also contained more power in the lower end of the visible spatial frequency spectrum than the adapting display with the smaller average size, we conducted Experiment 3 with both adapting and test patches equated in the spatial frequency domain, to rule out this alternative explanation.

EXPERIMENT 3: HIGH-PASS FILTERED DISPLAYS

The possibility remained that differences in the brightness or spatial frequencies of the adapting sets could have contributed to the results we observed in the previous two experiments. In other words, the adapting set with the larger mean size also tended to have a lower global spatial frequency (a greater number of black pixels) than the adapting set with the smaller mean size. To rule out the alternative explanation that the difference in spatial frequency between the two adapting displays was driving the aftereffect, in Experiment 3, we used a high-pass filter to limit the spectral energy of the test and adapting stimuli used in Experiment 1. If the effects observed in the previous two experiments are due to differences in the relative spatial frequencies or brightness of the stimuli, then we should no longer observe a differential aftereffect when controlling for these possible differences using high-pass filtered displays. If we again observe an adaptation aftereffect in Experiment 3, we can better attribute the results to the differences in the mean size of the dot sets in the adapting/top-up displays.

Methods

The methods of Experiment 3 were identical to those of Experiment 1, with the exceptions that: (1) The adapting, top-up, and test displays were highpass filtered to remove spatial frequencies below 12.5 cpd,¹ helping to control for differences in the power spectrum of the adapting or test stimuli that may otherwise have led to the results obtained in the previous two experiments, and (2) subjects DH, ND, TH, and two new subjects, SM and MM, participated in Experiment 3. All procedures and protocols were in

¹We chose 12.5 cpd as the cutoff frequency to avoid exceeding the sampling limit of experimental monitor's resolution (1280×1024 pixels), and to maintain the highest cutoff frequency possible while preventing the fast Troxler's fading that tended to occur when we tested for adaptation with higher cutoff frequencies.

accordance with the University of California, Davis's Institutional Review Board.

Results

The results of Experiment 3 again revealed a differential aftereffect of mean size. Each participant's average proportion of "Left appears larger" responses across the 11 test patch combinations in both conditions were fit to two separate logistic functions, as in the previous two experiments (Figure 4); all curves represent significant fits using maximum likelihood estimation, with all deviance scores below the critical chi-square value, $\chi^2(11, 0.95) = 19.68$. All subjects showed a significant difference between the logistic fits for the two adapting conditions, all ts(10) > 2.91, all ps < .016, and there was again a significant within-subjects effect of adapting condition on their PSEs, t(4) = 6.996, SEM = .02973, p = .002.

Discussion

Controlling for differences in the spatial frequency energy of the adapting and test displays in Experiment 3 yielded the same pattern of results as obtained in the previous two experiments. Although the magnitude of the effect was somewhat reduced compared to that observed in the first two experiments, this reduction is most likely due to the fact that the stimuli in Experiment 3 were overall lower in contrast, and perhaps less salient than those in the preceding experiments. Therefore, the results of Experiment 3 help to rule out the alternative explanation that the differential aftereffect of mean size observed in the present investigation could otherwise be attributed to differences in the spatial frequencies of the larger and smaller adapting displays. Instead, these results provided additional evidence that observers' perceptions of size were biased from adapting to the mean sizes of the two sets of large and small dots.

EXPERIMENT 4: ADAPTING SET VARIANCE

The three preceding experiments provide strong evidence that observers experienced a differential adaptation aftereffect of mean size based on a summary representation of the adapting dot sets. However, the possibility remains that observers could be adapting to the most prominent (largest or smallest) individual dot in each display instead of the mean size of the set. This alternative is unlikely given that recently two separate groups have used equivalent noise paradigms manipulating the variance in individual element diameters to demonstrate convincing evidence that observers use more than a few items to estimate the mean size of a set (Dakin, Greenwood, & Bex,



Figure 4. Experiment 3 results (high-pass filtered displays): Logistic fits (lines) and actual data (points) for the average probability of responding that the left test patch appeared to have the larger average size over the 11 left/right test size differences in each adapting condition (Big on Right, Big on Left), for each participant in Experiment 3. On average, observers more often perceived the test patch on the left as having the larger average size when they were adapted to the set of dots with the larger mean size on the right ("Big on Right", solid lines; squares), and the left test patch as having the smaller average size when adapted to the set with the larger mean size on the left ("Big on Left", dashed lines; circles). In each plot, the dashed horizontal line delimits the proportion of responses (y-axis) for which the observer was equally likely to respond that the test patch on one side appeared to have a larger average size than the other test patch, and the vertical dashed lines mark the corresponding PSEs (x-axis) for each adapting condition in terms of the difference in the average sizes of the test dot patches necessary for this perceived equality.

2010; Solomon, Morgan, & Chubb, 2011). Along these lines, to provide further evidence that adaptation is specific to the mean size of the dots comprising the sets, and not simply accomplished by attending to the most prominent dots in each display, in Experiment 4, we compared the magnitude of the aftereffect across three different variance conditions. Specifically, we manipulated the variance in the diameters of the individual dots comprising the adapting displays over three conditions, but held the mean sizes of the large and small displays constant. In line with previous findings, if the aftereffect we report in the first three experiments here is sensitive to set variance, this would similarly suggest it is mediated by a summary statistical estimation of mean size that is not based on a sampling of any single dot in the array.

Methods

The methods of Experiment 4 were similar to those of Experiment 2. Observers adapted to side-by-side patches of heterogeneously sized dots with different mean sizes and judged the relative sizes of two single test dots presented in the adapted regions. The key difference in Experiment 4 was that each observer was adapted to three different types of displays, with Low, Medium, and High variance between the sizes of the individual dots comprising the adapting displays, respectively. Importantly, the variance of the adapting dot sets was manipulated over the three types of displays, and the sizes of the individual dots on each presentation were randomly selected as a function of the prespecified set variance, while the mean sizes of the large and small adapting displays remained constant over the duration of the experiment. We chose to manipulate the variance of the adapting sets and *not* their relative mean sizes, because with the latter manipulation, it would be much more likely that subjects could calculate an accurate estimate of the set mean by attending to only a few of the adapting dots.

Participants

Five subjects from the University of California, Berkeley (one woman and four men, aged 23–32) with normal or corrected-to-normal vision voluntarily participated in two hour-long sessions. All procedures and protocols were in accordance with the University of California, Berkeley's Institutional Review Board.

Stimuli

Adapting displays. As in all previous experiments, the adapting stimulus consisted of two sets of 14 dots, each centred at 8° of eccentricity along the horizontal meridian. The small and large adapting sets each contained

14 individual dots, with constant mean dot diameters of approximately 0.714° and 1.429°, respectively. Unique to Experiment 4, on each trial, the individual dots comprising the adapting displays were randomly drawn from normal distributions with the constant large and small set means, and a standard deviation of 0.107° around those respective means in the low variance condition, a standard deviation of 0.321° in the medium variance condition, and a standard deviation of 0.536° in the high variance condition. As in the three preceding experiments, the positions of the dots within each adapting display were randomized on each trial. Note that to avoid confounding individual dots sizes with set means and variances, the 14 individual dots comprising the large and small adapting displays within each variance condition were not the same sizes on every trial (as in the large and small adapting sets used in the three preceding experiments). While this manipulation did cause the small and large set means to fluctuate very slightly from trial to trial, the overall adapting set means never deviated from the respective 0.714° and 1.429° by more than 0.018° on any given trial.

Test displays. Similar to the methods of Experiment 2, the eight test dot pairs in Experiment 4 differed by -0.286° , -0.214° , -0.143° , -0.071° , 0.071° , 0.143° , 0.214° , and 0.286° . The positions of the single test dots were randomized within the two 8° adapted regions from trial to trial.

Procedure

In Experiment 4, each observer participated in two adapting conditions (Big on Left and Big on Right), conducted at least 2 hours apart. Each adapting condition consisted of three blocks; one block of each of three prescribed set variances (low, medium, and high). The order of variance blocks (low, medium, and high) was counterbalanced for each observer in each adapting condition, and the order of adapting conditions was counterbalanced within each session over observers.

Using the method of constant stimuli, we presented each of the eight possible test combinations 20 times per variance block, in random sequence. Observers performed one block of 160 trials adapting to each of the three variance blocks (low, medium, high), in each of the 2 adapting conditions (Big on Left, Big on Right), for a total of 960 trials per observer in Experiment 4.

Results

As predicted, if subjects were adapting to the mean sizes of the sets of dots in Experiment 4, the magnitude of the adaptation aftereffect decreased with increasing set variance. For each of the three variance blocks, we fit each participant's averaged responses in both adapting conditions to two separate logistic functions with lower and upper bounds of 0 and 1.0, respectively, using maximum likelihood estimation as in the three previous experiments. All fits were significant, with deviance scores below the critical chi-square value, $\chi^2(8, 0.95) = 15.51$.

We next conducted a 2 (adapting condition: big on left, big on right) $\times 3$ (variance block: low, medium, high) repeated-measures ANOVA on observers' averaged PSEs, revealing a significant main effect of adapting condition, F(1, 2) = 117.21, MSE = 0.20737, p < .001, and an interaction between adapting condition and variance block, F(2, 24) = 3.62, MSE = 0.00641, p = .042. Figure 5 illustrates the main effect of adapting condition, indicating a significant negative adaptation after-effect across all three variance blocks, and the interaction between adapting condition and variance block, signifying a reduced aftereffect in the high variance block as compared to the medium or low variance blocks.

Discussion

The results of Experiment 4 suggest that adaptation was sensitive to the mean size of the dots comprising the adapting displays. Specifically, the magnitude of the aftereffect decreased as the variance in the diameters



Figure 5. Experiment 4 results (adapting set variance): Grand average PSEs (point of subjective equality: Difference in relative sizes of the test dots necessary for participants to be equally likely to respond that the test dot on one side appeared larger than the other test dot) for each adapting condition (Big on Right, Big on Left) in Experiment 4. In general, as the variance in the diameters of the dots within the adapting sets increased from low and medium to high, the magnitude of the aftereffect (the difference in PSE between the two adapting conditions) decreased. Error bars are standard errors of the means, calculated using the method of Loftus and Masson (1994).

of the dots comprising the adapting dot sets increased from low and medium to high. As only the variance of the adapting sets, and not the overall mean dot diameters changed across variance blocks, for participants to be sensitive to the variance manipulation in this manner, they most likely adapted to the entire set of dots (or at least more than could be focally attended). Although the possibility remains that observers were selectively attending a small sample of a few "key" dots in each set (see Myczek & Simons, 2008, for a discussion of such subsampling strategies), such an intelligent sampling strategy is unlikely given that a simple simulation of randomly selecting two to four dots from each adapting set predicts equal magnitudes of the aftereffect across variance conditions. Our conclusion that the aftereffect is specific to the mean sizes of the adapting sets is further reinforced by the fact that we randomly chose the dots in each adapting set from a normal distribution with a constant mean and one of three different variances, allowing for the same dots to be shown in more than one variance block. In other words, as the mean estimate became less precise with increasing variance, the results of Experiment 4 suggest that observers adapted to a perceptual summary of the average size of each set, and not just the size of the most prominent dots in each display.

GENERAL DISCUSSION

Taken together, the results of these four experiments provide converging evidence that mean size is an adaptable dimension of sets, and is explicitly encoded by the visual system. In Experiment 1, on average, observers perceived the test patch that replaced the adapting set with the smaller mean size as having a larger mean size than the test patch that replaced the adapting set with the larger average size, regardless of which test patch had the physically larger average dot size. The same pattern of results held for Experiments 2 and 3 with single dot tests, and high-pass filtered displays, respectively, helping to rule out alternative explanations based on differences in the relative densities or spatial frequencies of the displays. Finally, Experiment 4 provided an additional confirmation that the size aftereffect was the result of adapting to the average of sizes of the sets, as the aftereffect decreased as the variance in the adapting dot diameters increased and the mean estimate became less precise.

Our results are in line with previous demonstrations of adaptation to ensembles or summary statistics of other stimulus dimensions, such as average direction of motion (e.g., Anstis et al., 1998), average orientation (e.g., Gibson & Radner, 1937), average texture density (Durgin, 1995, 2008; Durgin & Huk, 1997; Durgin & Proffitt, 1996), and average numerosity (Burr & Ross, 2008). As previous authors have argued, adaptation provides evidence for the existence of visual mechanisms that explicitly encode a particular attribute along a single dimension (e.g., Campbell & Robson, 1968). Furthermore, our findings support proposals like those by Ariely (2001) and Chong and Treisman (2005) that mean size is extracted automatically, possibly by a specialized process used to represent sets of objects in a more efficient manner than the more resource-intensive mechanisms responsible for representing individual objects (cf. Myczek & Simons, 2008).

The question of the physiology underlying the observed adaptation to mean size remains open. As our results in Experiments 2 and 3 show, the mechanisms responsible cannot be based simply on pooling the responses of retinal ganglion or striate cells tuned to density or spatial frequency. If either of these explanations were the case, we should not have observed a consistent aftereffect when controlling for density and spatial frequency over the adapting and test displays in Experiments 2 and 3. However, a specific neural correlate of mean size representation has yet to be identified. Perhaps the most likely candidates are individual retinal neurons found to adapt rapidly to the spatial scale of images (e.g., Smirnakis, Berry, Warland, Bialek, & Meister, 1997). Similar mechanisms might hold beyond the retina as well. For example, perceived size appears to be represented in early visual cortex (Arnold, Birt, & Wallis, 2008; Murray, Boyaci, & Kersten, 2006), and population coding of object size could also give rise to ensemble coding of average size. Along these lines, Im and Chong (2009) reported that the mean sizes of sets of target circles embedded in rings of smaller or larger surrounding circles were perceived as a function of the Ebbinghaus illusion induced by the surrounding circles, and not based on the physical sizes of the target circles. This type of coding for perceived ensemble size might be useful for calculating textures and quickly recovering depth across scenes. The capacity to encode the mean size of a collection of objects may also help to further our understanding of the mechanism(s) presumed to underlie rapid perception of scene "gist" (e.g., Potter, 1976).

Overall, our results demonstrate an aftereffect of mean size adaptation. This effect was persistent, even when we controlled for differences in the densities and spatial frequencies of the adapting and test stimuli, and the magnitude of the effect decreased as the variance in the diameters of the individual dots comprising the adapting displays increased. Based on the premise that basic visual dimensions are adaptable, this consistent differential aftereffect indicates that mean size is explicitly encoded as a basic dimension of visual scenes, like other dimensions such as texture density and numerosity.

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