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Number Adaptation Can Be Dissociated From Density Adaptation

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Abstract
Rapidly judging the number of objects in a scene is an important perceptual ability. Recent debates have centered on whether number perception is accomplished by dedicated mechanisms and, in particular, on whether number-adaptation aftereffects reflect adaptation of number per se or adaptation of related stimulus properties, such as density. Here, we report an adaptation experiment ($N = 8$) for which the predictions of number and density theories are diametrically opposed. We found that when a reference stimulus has higher density than an adaptation stimulus but contains fewer elements, adaptation reduces the perceived number of elements in the reference stimulus. This is consistent with number adaptation and inconsistent with density adaptation. Thus, number-adaptation aftereffects are more than a by-product of density adaptation: When density and number are dissociated, adaptation effects are in the direction predicted by adaptation to number, not density.

Keywords
psychophysics, number perception, adaptation

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People can rapidly judge the number of objects in a scene, even when there are too many to be counted serially at a glance (Dehaene, Dehaene-Lambertz, & Cohen, 1998; Jevons, 1871; Xu & Spelke, 2000). This *number sense* is important in many cognitive processes (Dehaene, 2011) and provides advantages such as the ability to evaluate resources from a distance. Compared with other fundamental abilities, such as color perception, relatively little is known about the neural computations that support number perception. Recent debates have addressed whether number perception depends on number-specific mechanisms (Anobile, Arrighi, Togoli, & Burr, 2016; Anobile, Cicchini, & Burr, 2014, 2016; Arrighi, Togoli, & Burr, 2014; Burr & Ross, 2008) or on mechanisms tuned to related properties, such as density (Dakin, Tiber, Greenwood, Kingdom, & Morgan, 2011; Durgin, 2008; Gebuis, Kadosh, & Gevers, 2016; Leibovich, Katzin, Harel, & Henik, 2017). This debate has broad theoretical significance, as it addresses the basic perceptual dimensions that are available for visual judgments.

One part of this debate concerns adaptation. After observers view several objects for 10 s to 20 s, the number of objects in other images can appear to change substantially. These aftereffects have been taken as evidence of dedicated number-processing mechanisms (Burr & Ross, 2008). However, adaptation occurs at several levels of visual processing (Hills, 2013; Kohn & Movshon, 2003), and other researchers have argued that number adaptation is instead a by-product of density adaptation (Dakin et al., 2011; Durgin, 2008).

Here, we report an experiment in which number- and density-adaptation hypotheses made opposite predictions. Adaptation typically causes percepts to shift away from the adapting stimulus—for example, after observers adapt to an intermediate spatial frequency, high spatial frequencies appear higher than when unadapted, and low spatial frequencies appear lower (Blakemore & Sutton, 1969). Our observers adapted to an array of elements and then judged the number of elements in a reference stimulus that had fewer elements but higher

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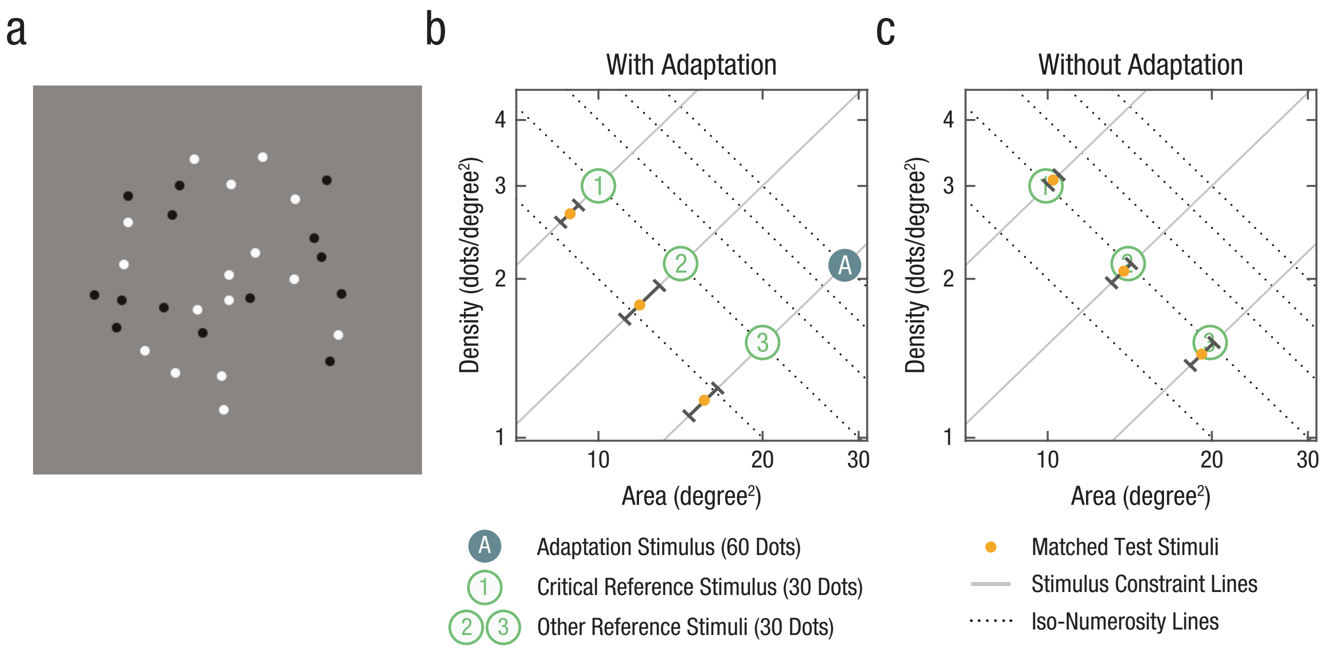

Fig. 1. Example stimulus (a) and results for a typical observer (b, c). Each stimulus was an array of black and white dots. The graphs show the stimulus space for the adaptation condition and the unadapted condition. The orange data points indicate matched test stimuli, which the observer judged to have the same number of dots as the corresponding reference stimuli (green circles). Iso-numerosity lines show points where stimuli have the same number of dots. Stimulus-constraint lines indicate points where test stimuli were sampled, and these lines were orthogonal to the iso-numerosity lines. The three reference stimuli were the same in both conditions. Error bars show 95% confidence intervals.

density. If observers adapt to number, the reference stimulus should have appeared to have fewer elements after adaptation, and if they adapt to density, it should have appeared to have more elements. Thus, the direction of aftereffects provided a direct test of these two theories.[1]

Method

Observers

There were eight observers. Two were authors (M. Kim and R. F. Murray); the others were unaware of the purpose of the study. All reported normal or corrected-to-normal vision and provided written informed consent. We chose eight observers because adaptation effects can be upward or downward, and under the null hypothesis that the adaptation direction for each observer is random, eight observers showing adaptation effects in the same direction would be highly unlikely ($1/2^8 < 0.01$). All procedures were approved by the York University Office of Research Ethics.

Stimuli

Each stimulus was an array of black and white dots (Fig. 1a; for a demonstration of the adaptation aftereffects, see the stimulus movies posted on OSF at https://doi.org/10.17605/OSF.IO/QG5YM). The Weber contrast of each dot was randomly set to ±90%, and dots were displayed on a gray background (50 cd/m^2); thus, mean luminance was not a cue to number. Each dot had radius of 0.07° of visual angle, and dots were randomly placed inside an invisible circle with the constraint that dot centers were separated by at least three dot radii. The number of dots and the radius of the bounding circle are described in the Procedure section. Stimuli were shown on an LCD monitor with a resolution of 1,920 × 1,080 pixels, a pixel size of 0.250 mm, and a nominal refresh rate of 60 Hz. Head position was stabilized using a chin rest positioned 84 cm from the monitor.

Experimental design

Figure 1b illustrates the experimental design in a stimulus space; log area is given on the *x*-axis and log density on the *y*-axis. The adaptation stimulus (dot A) had 60 dots and an intermediate density (2.12 dots/degree^2; radius = 3.00°).[2] The critical reference stimulus (Green Circle 1) had fewer dots (30) and a higher density (3.01 dots/degree^2; radius = 1.78°) than the adaptation stimulus. After adaptation, we measured the perceived number of dots in the reference stimulus by finding which unadapted test stimulus along a diagonal line in stimulus space (solid line through Green Circle 1; details below) appeared to have the same number of dots as the adapted reference stimulus. To provide a point of comparison for the size of any adaptation effects we found, we ran the same procedure with two other reference stimuli (Fig. 1b, Green Circles 2 and 3) in which density and number were not in conflict; the second reference stimulus had 30 dots and the same density as the adaptation stimulus (2.12 dots/degree^2; radius = 2.12°), and the third had 30 dots and a lower density (1.50 dots/degree^2; radius = 2.52°). Figure S1 in the Supplemental Material shows the adaptation and reference stimuli. To factor out simple biases, such as a bias to choose the left-hand stimulus, we measured the perceived number of dots in each reference stimulus with adaptation (Fig. 1b) and without adaptation (Fig. 1c) and took the adaptation effect to be the difference in the perceived number of dots with and without adaptation.

Procedure

Each observer participated in two 210-trial sessions. The first was the baseline session (Fig. 1c), and the second was the adaptation session (Fig. 1b).

In the adaptation session, each trial began with an adaptation stimulus of 60 dots in a circle of radius 3.00°, centered 3.50° to the left of fixation for half the observers and to the right for the other half. A small fixation dot was shown continuously at the center of the screen. The adaptation stimulus was shown for 30 s on the first trial and 3 s on subsequent trials. The adaptation stimulus was followed by a blank screen (with a fixation dot) for 0.5 s. The reference and test stimuli were then shown together for 0.5 s. The reference stimulus was a random dot array with 30 dots, centered 3.5° to the same side of fixation as the adaptation stimulus. There were three reference stimuli on different trials, subtending circular regions with radii 1.78°, 2.12°, and 2.52° (areas 10.0, 14.1, and 20.3 degrees^2, respectively), and the radius was chosen randomly on each trial. The test stimulus was a random-dot stimulus centered 3.5° on the other side of fixation. The number of dots in the test stimulus was chosen using a separate one-up, one-down staircase for each reference-stimulus radius. When the staircase indicated that the test stimulus should have n dots, the actual number of dots was chosen randomly between $n - 5$ and $n + 5$, to sample the psychometric function more broadly. When the test stimulus had n dots, it had radius $(n/30)^{1/4} r_{\text{ref}}$, where r_{ref} is the radius of the associated reference stimulus; as a result, the test stimuli were chosen along the diagonal solid constraint lines shown in Figures 1b and 1c. After the reference and test stimuli disappeared, the observer pressed one of two keys to indicate which stimulus contained more dots. No feedback was given, and the next trial began after a short pause. To find the point of subjective equality (PSE), we made a maximum likelihood fit of a normal cumulative distribution function to the empirical psychometric function for each reference stimulus. The PSE was the number of test dots for which the fitted response probability was 0.5.

The baseline session was the same as the adaptation session, except that no adaptation stimulus was shown at the beginning of each trial. We ran the baseline session before the adaptation session so lingering adaptation effects would be avoided.

Trial-by-trial data for all observers are available on OSF (https://doi.org/10.17605/OSF.IO/QG5YM).

Results

Figures 1b and 1c show results for a typical observer. After adaptation (Fig. 1b), all three reference stimuli, including the critical reference stimulus (Green Circle 1), appeared to have fewer dots, which is consistent with number adaptation and not with density adaptation.[3] Without adaptation (Fig. 1c), the observer perceived approximately the same number of dots in the reference stimulus as in the test stimulus that actually had the same number of dots; thus, any response biases were small.

This adaptation effect was consistent across observers (Fig. 2; individual observers' data are shown in Fig. S2 in the Supplemental Material). Observers perceived all reference stimuli, including the critical reference stimulus, as having fewer dots after adaptation, and the adaptation effect was about as large for the critical reference stimulus as for the other two reference stimuli. For all three reference stimuli, the reduction in the mean perceived number of elements was statistically significant—two-tailed repeated measures t tests, $t(7)$s = −8.0, −5.4, −3.7; all ps < .01; Cohen's d = −1.4, −1.9, −2.7.

For some observers, the adaptation effect was larger for the large-area, low-density reference stimulus (Fig. 1, Green Circle 3) than for the critical reference stimulus (Green Circle 1), and the average adaptation effect across observers also showed a trend in that direction (Fig. 2). This suggests that area or density may modulate the strength of number adaptation. However, this tendency was not consistent across observers, and it was not significant in the average results, so we cannot draw strong conclusions on this point.

Discussion

These findings show that number adaptation is not reducible to density adaptation. One possible concern is that the adaptation stimulus was larger than the reference stimuli, and if number adaptation is highly spatially

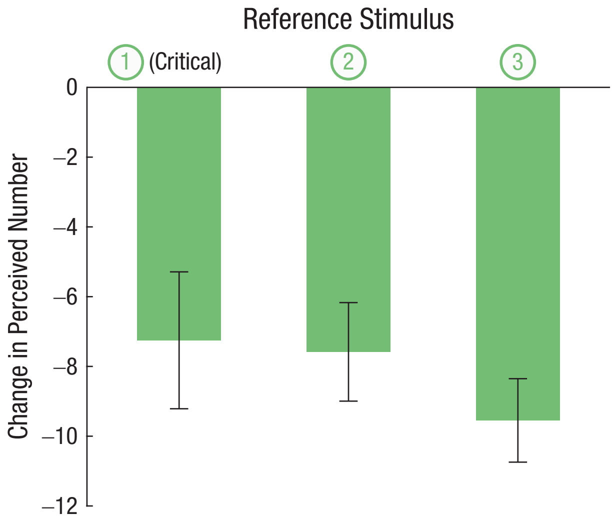

Fig. 2. Mean change in the perceived number of dots after adaptation, separately for each reference stimulus. Reference Stimulus 1 (Green Circle 1 in Figs. 1b and 1c) is the critical reference stimulus, and Reference Stimuli 2 and 3 (Green Circles 2 and 3 in Figs. 1b and 1c) are the comparison reference stimuli. Error bars show standard errors of the mean.

specific, then only a subset of adaptation dots (21 dots) adapt the reference stimulus. However, this view predicts an increase in the perceived number of dots in the reference stimulus (which has 30 dots), indicating that this is not a viable model. The downward adaptation effects suggest that number adaptation depends on receptive fields larger than the stimuli used here (radii = 1.78°–3.00°), consistent with neuroimaging evidence that locates numerosity-sensitive neurons in frontoparietal and occipitotemporal regions (Harvey & Dumoulin, 2017), where population receptive fields typically span quadrants or hemifields (Amano, Wandell, & Dumoulin, 2009; Mackey, Winawer, & Curtis, 2017).

A related point is the possibility that the adaptation aftereffects are based on area. Here, we aimed to test number and density theories of adaptation,[4] and our data could not rule out this third alternative, although previous studies have provided some evidence that number judgments are not based on a simple combination of area and density (Cicchini, Anobile, & Burr, 2016; Zimmerman & Fink, 2016). Furthermore, our interpretation of the present experiments relies on several assumptions about adaptation (e.g., the degree of spatial specificity and the direction of aftereffects) that we did not test directly. Additional studies should more rigorously test these assumptions by exploring the stimulus space more thoroughly—for example, by using adaptation stimuli that are predicted to cause an increase in the perceived number instead of a decrease, and by searching for an effect of area on adaptation aftereffects. Such experiments would help to develop a robust and consistent theory of number perception and adaptation that is valid over a broad range of stimuli and tasks.

Transparency

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Author Contributions
R. F. Murray developed the study concept. All authors contributed to the experimental design. K. DeSimone and R. F. Murray programmed the experiment. K. DeSimone and M. Kim ran the experiment. K. DeSimone and R. F. Murray analyzed the data. All authors contributed to creating the figures and writing the manuscript, and all authors approved the final version for submission.
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Open Practices
Data, stimulus movies, and supplementary material for this study have been made publicly available on OSF and can be accessed at https://doi.org/10.17605/OSF.IO/QG5YM. The design and analysis plans were not preregistered. More information about the Open Practices badges can be found at http://www.psychologicalscience.org/publications/badges.

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Supplemental Material

Additional supporting information can be found at http://journals.sagepub.com/doi/suppl/10.1177/0956797620956986

Notes

1. Alternatively, if density adapts downward only, then density alone cannot mediate number adaptation, which adapts in both directions.
2. Previous studies have indicated that dots/degree^2 is the relevant density measure and that factors such as dot size play little role in number perception (Burr & Ross, 2008).
3. All adaptation effects found here were in the same direction, which is a limitation of the present study (see the Discussion section).
4. Durgin (2008) also aimed to dissociate number and density theories of adaptation; see the caption of Figure S3 in the Supplemental Material for a discussion.

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