Vision senses number directly

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We have recently suggested that numerosity is a primary sensory attribute, and shown that it is strongly susceptible to adaptation. Here we use the Method of Single Stimuli to show that observers can extract a running average of numerosity of a succession of stimuli to use as a standard of comparison for subsequent stimuli. On separate sessions observers judged whether the perceived numerosity or density of a particular trial was greater or less than the average of previous stimuli. Thresholds were as precise for this task as for explicit comparisons of test with standard stimuli. Importantly, we found no evidence that numerosity judgments are mediated by density. Under all conditions, judgements of numerosity were as precise as those of density. Thresholds in intermingled conditions, where numerosity varied unpredictably with density, were as precise as the blocked thresholds. Judgments in constant-density conditions were more precise thresholds than those in variable-density conditions, and numerosity judgements in conditions of constant-numerosity showed no tendency to follow density. We further report the novel finding that perceived numerosity increases with decreasing luminance, whereas texture density does not, further evidence for independent processing of the two attributes. All these measurements suggest that numerosity judgments can be, and are, made independently of judgments of the density of texture.

Introduction

In recent years many studies have shown that the number of objects (homogeneous or heterogeneous) in a field of view can be estimated without the opportunity to count. Approximate estimation of number has been demonstrated in humans (Whalen, Gallistel, & Gelman, 1999), in human infants (Xu & Spelke, 2000; Xu, Spelke, & Goddard, 2005), in cultural groups with no word for numbers much above two (Dehaene, Izard, Spelke, & Pica, 2008; Gordon, 2004), in monkeys (Hauser, Carey, & Hauser, 2000; Hauser, Tsao, Garcia, & Spelke, 2003; Sawamura, Shima, & Tanji, 2002) and other mammals (Galistel, 1990), in birds (Pepperberg, 2006) and even in bees (Dacke & Srinivasan, 2008). The ability to estimate number correlates strongly with mathematics achievement (Halberda, Mazzocco, & Feigenson, 2008).

A likely basis for this capability has been found in monkeys: neurons with overlapping log-normal tuning curves (analogous to neurons tuned for spatial frequency), each with a favored value at which its responses peaks (Nieder, 2005). Another type of neuron has been described in area LIP, which responds in a graded manner to number, some maximally to large numbers some to

small (Roitman, Brannon, & Platt, 2007). It is not unlikely that similar neurons are to be found in other species with highly evolved visual systems, underlying a capacity to estimate number. Certainly, fMRI and psychophysical studies point to the existence of neurons tuned to number in humans (Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999; Piazza, Mechelli, Price, & Butterworth, 2006; Piazza, Pinel, Le Bihan, & Dehaene, 2007).

Most physiological studies of number neurons have been careful to exclude, by suitable controls, the influence of spatial variables correlated with number, like dot density. A surprising fact is that neurons responsive to number also respond to numerals, that is symbols for numbers, in humans and monkeys who have learned them. This reinforces the conclusion that it is number and not some other property of a collection of objects, like the density of their distribution, which number-tuned neurons respond to.

Because there are neurons tuned for number, and because numerosity obeys Weber's law (Galistel, 1990; Jevons, 1871; Ross, 2003), Burr and Ross (2008) suggested it was a primary sensory attribute. If so, they argued, it should exhibit after-effects of adaptation, in line with many other sensory attributes such as color, motion, tilt and spatial frequency. Burr and Ross measured after-effects of

adaptation for perceived numerosity, finding them large and largely independent of element size, contrast or orientation.

Nevertheless it has been argued that the effects found by Burr and Ross are in fact after-effects of adaptation to texture and that number is derived from texture density, not sensed independently (Durgin, 1995, 2008). What complicates the issue is that disentangling texture from number is difficult. In this study we used two complementary approaches. In the first experiment we measured numerosity judgements of sparse dot patterns under conditions where density was not an informative cue to numerosity. Judgment of numerosity was not hampered under these conditions, suggesting that humans can sense numerosity without using density as a proxy. In the second study we addressed the issue of *texture,* and showed that a particular manipulation—changing average luminance levels—strongly affected perceived numerosity of sparse patterns but not apparent density of visual texture, showing a clear dissociation of the two attributes.

Methods

Stimuli

For the first experiment the stimuli comprised N dots of 14 arcmin diameter, half white and half black (see Figure 1A) spread randomly over an area A, with dot density D defined as $D = N/A$. The average area was 50 deg^2, a 10 cm diameter circle viewed from 71 cm. Mean luminance of the gray background was 20 cd/m^2 and dot Michelson contrast 95%.

To study separately the discrimination of numerosity and density, we manipulated these parameters independently, and on separate occasions asked subjects to make judgments about apparent numerosity or density. We used three separate conditions where one of the three parameters was kept constant, and the other two (yoked) parameters varied randomly over a 0.4 log-unit range. In the constant-area condition, the area was kept constant at 50 deg^2 while numerosity, and hence density, were chosen randomly over a 0.4 log-unit range centered at 50 dots and 1 dot/ deg^2. In the constant-density condition, density was kept constant at 1 dot/ deg^2 and area and numerosity varied randomly around the average of 50 deg^2 and 50 dots. In the constant-numerosity condition the numerosity was constant at 50 dots, while both area and density varied around 50 deg^2 and 1 dot/deg^2.

In order to study the extent to which numerosity judgments depended on density information, we ran all the experiments separately with the conditions blocked into separate session, and intermingled. In the blocked sessions, all trials were taken from only one condition: constant-area, constant-density or constant-numerosity. Subjects were informed of the condition, and could therefore knew, for example, that in the constant-area condition density co-varied with numerosity and this could be used as an effective cue. In the intermingled sessions, trials were chosen at random from the three separate conditions (with responses stored separately for each condition). In these intermingled sessions, subjects
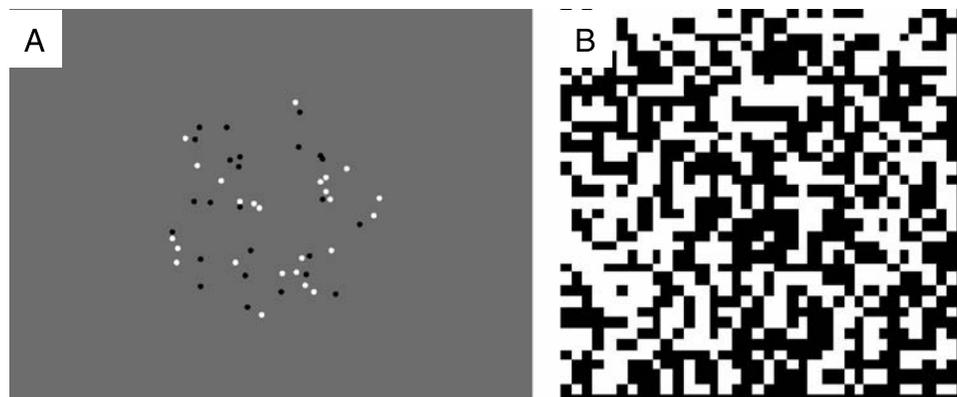

Figure 1. Example of the stimuli used in this experiment. **A** Stimuli comprised N dots (average 50) of 14 arcmin diameter, half white half black, confined to a virtual circle of A deg^2 (10 cm diameter for the average area of 50 deg^2, viewed from 71 cm). Mean luminance was 20 cd/m^2 and contrast 95%. For the various conditions, either area, density or numerosity were kept constant at their average, while the other two parameters varied over a 0.4 log-unit range around there geometric mean. Note that the perimetry of the dots does not form a precise circle of constant radius, that could be readily used to judge area. **B** The stimulus used to measure the effects of luminance on texture density. M rectangles, randomly assigned as black or white, were confined to an 8 × 8 degree square, where M defines the density of the texture. The height and width of the rectangles varied randomly over a two-fold uniform range around a mean size of 8/M deg. Luminance of the bright rectangles (and dots in the dot stimuli) varied over a 3 log-unit range, from 0.04 to 45 cd/m^2, by varying the monitor intensity (calibrated by photometer). The luminance of the black rectangles or background was always 0.01 cd/m^{-2}.

could not know what condition a particular trial belonged to, so density was a far less effective proxy for numerosity. The blocked sessions were 90 trials long, the intermingled 130 (the first 10 trials were discarded). The order of testing was randomly chosen from 2 constant-area sessions, 2 constant-density sessions, 2 constant-numerosity sessions and 4 intermingled sessions, leading to a total of 160 trials per condition. For all three conditions (constant area, density and numerosity), both blocked and intermingled separate sessions were run with subjects asked to judge either numerosity or density ($3 \times 2 \times 2 = 12$ conditions in all).

The second experiment attempted to disentangle numerosity from *texture,* using two different types of stimuli. One was like that of the first: a sparse pattern of *N* distinct dots of 14 arcmin diameter, all white on a black background, confined to a circle of 8 degree diameter, viewed from 71 cm. The other was a 8 by 8 degree dense visual *texture* comprising *M* rectangles, randomly assigned as black or white ([Figure 1B](#)), where *M* defined the texture density. The height and width of the rectangles varied randomly over a two-fold uniform range. For both types of stimuli the luminance of the bright dots or rectangles was varied over a 3 log-unit range, from 0.04 to 45 cd/m^2, by varying the monitor intensity (calibrated by photometer). The luminance of the black rectangles or background was always 0.01 cd/m^2. Here each session comprised 130 trials (first 10 discarded), repeated 4 times (randomizing order of numerosity and texture-density sessions), yielding 120 trials per condition. Each session lasted about 10 minutes, and subjects could take breaks between sessions.

Procedure and data analysis

All experiments used the method of single stimuli (MSS: Morgan, Watamaniuk, & McKee, [2000](#)) where observers were asked, on separate occasions, to judge whether the perceived numerosity or the density of a specific stimulus was greater or less than the running average of all stimuli they had seen in that session. The first 10 trials were discarded. Depending on condition, the numerosity or the density or the area was chosen randomly over a uniform logarithm range of 0.4 log-units centered at a particular value. Observer response was plotted as a function of log-numerosity, log-density or log-area, and fitted with a cumulative Gaussian function (like those of [Figure 2](#)). The mean of the function gives an estimate of point of subjective equality (PSE) of the relevant parameter, and the standard deviation an estimate of the just noticeable difference (JND) or precision of the judgment.

Standard errors and statistics were calculated by bootstrap (Efron & Tibshirani, [1993](#)). To calculate the standard errors of individual subjects (e.g. [Figure 5](#)), the standard
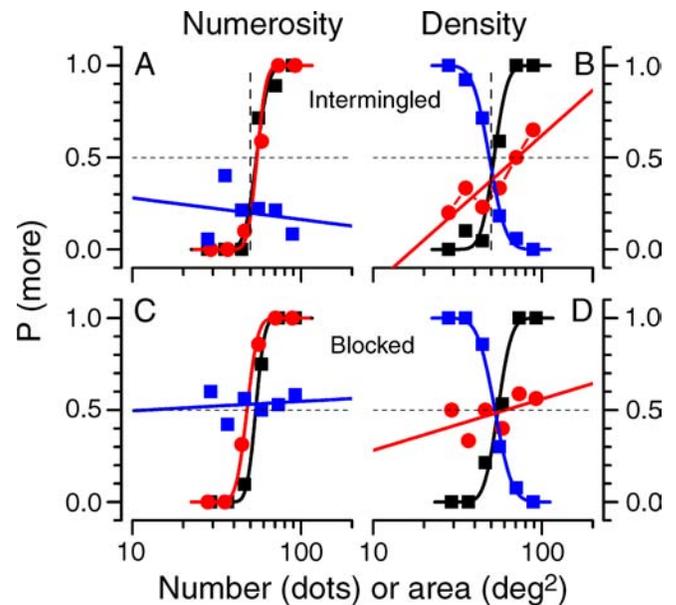

Figure 2. Example psychometric functions for naïve observer JED for the numerosity task (A & C) and density task (B & D), showing the proportion of trials judged to be more numerous than average of what has preceded them (the first 10 responses in any session were ignored). Figures A & B show results for intermingled trials, C & D for blocked conditions. Results are plotted as a function of dot number (for constant-area and constant-density conditions) and/or area (for constant-number and constant-density conditions). Black symbols refer to constant-area, red to constant-density, blue to constant-numerosity. The curves are best-fitting cumulative Gaussian curves constrained to asymptote at 0 and 1, except where the variable to be discriminated (numerosity or density) was constant. These curves are fitted by linear regression.

bootstrap technique was used: *N* random samples (with replacement) were drawn from the data of a particular condition (where *N* is the number of trials of that condition), and this sampled data fit with a cumulative Gaussian distribution to yield estimates of PSE and JND. This procedure was repeated 500 times, and the standard error of both parameters taken as the standard deviation of the estimates of the samples.

For the group means of [Figure 3](#), raw data was not pooled, but sampled separately for each subject to yield three estimates of JND, which were averaged (geometric mean). The procedure was repeated 500 times, to estimate standard error of the mean (shown as errors bars) from the standard deviation of these estimates from the samples.

The bootstrap sign-test used a similar procedure. The conditions to be compared were sampled separately for each subject and condition, then averaged (geometrically) to yield 10,000 averages for each condition to be compared. Each pair of samples for the two conditions was compared, and the proportion of times condition A was higher than
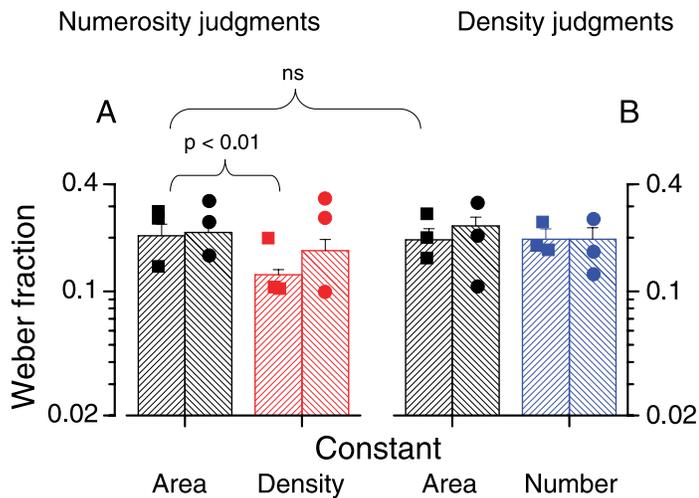
Figure 3. The bar graphs report the geometric means of Weber fractions of the three observers (taken from Figure 3) for the numerosity (A) and density judgments (B). Forward-sloping hatching (at left) refers to intermingled conditions, back-sloping to blocked. Standard errors are obtained by bootstrap, calculating thresholds separately for all observers before averaging. The square and circle symbols show the individual means for the 3 observers.

condition B was calculated. The lower of these two numbers (two-tailed test) was taken as the probability that the two conditions were equal. The comparisons made were: numerosity judgments against density judgments (only constant-area, but pooling intermingled and blocked, as intermixing clearly had little effect); and for numerosity judgments the constant-area against the constant-density (again pooling intermingled and blocked).

Observers

Three observers participated in the study, the two authors and one well experienced in psychophysical experiments but naïve as to the goals of the current study.

Results

Experiment 1: Effect of instructions, numerosity and density

In separate session, observers were asked to judge the numerosity or density of dot stimuli, density or numerosity being held constant (at 50 dots, 1 dot/deg^2 or 50 deg^2), while the other two yoked parameters varied around this average. Figures 2A and 2B show example

psychometric functions for the naïve observers' judgements of perceived numerosity and density. The upper panels (A & B) show sessions where the three conditions were intermingled randomly throughout each session, the lower panels symbols (C & D) where a particular condition (e.g. constant-area) was "blocked" within each session.

The first thing to note is that psychometric functions were orderly and steep for all conditions, except for constant-numerosity for numerosity judgments and constant-density for density judgments (where there was no useful information). This shows that observers were able to do the task well, keeping running averages of both numerosity and density, as has been shown for a range of other tasks (Morgan et al., 2000). Indeed the JNDs for this task are well within the range obtained using other techniques that employ explicit standards (e.g. Ross, 2003).

The bar plot of Figure 3 shows the average (geometric mean) of the Weber fractions (JNDs normalized by mean) of numerosity and density judgements in the various conditions, together with the individual means and the overall standard errors (calculated by bootstrap). Density judgments at constant-density and numerosity judgements at constant-numerosity are not shown, as in no case did these conditions produce monotonic psychometric functions.

The data show no evidence to support the suggestion that numerosity judgments are mediated by density. Under all conditions, numerosity judgements were as precise as density judgements, obvious from the bar graphs of Figure 3. A bootstrap sign-test (see Methods) between density and numerosity judgements (in conditions of constant-area) revealed no significant difference ($p = 0.40$). Secondly, numerosity judgments under conditions of constant-density were no worse than those of constant-area, as may be expected if density were a proxy to numerosity. Admittedly subjects could still be estimating *both* density and area, but one would expect an additional cost in this calculation, which would be reflected in higher JNDs. Indeed, the numerosity judgments at constant-density were significantly *more* precise than the constant-area ($p = 0.007$, bootstrap sign-test). Thirdly, the thresholds in the intermingled condition, where density could not be so readily used as a proxy for numerosity, were as precise as the blocked thresholds ($p = 0.40$, bootstrap sign-test for mixed versus blocked numerosity, excluding constant-numerosity trials). And fourthly, numerosity judgements in the constant-numerosity condition showed no tendency at all to be influenced by density or area, which were both varying (and an imperfect calculation of numerosity from density and area may lead to a bias). This was true even in the intermingled condition where constant-numerosity trials were impossible to identify (although there was a slight tendency for density judgments to be influenced by numerosity). All these measurements suggest that numerosity judgments can be made independently of density judgments.
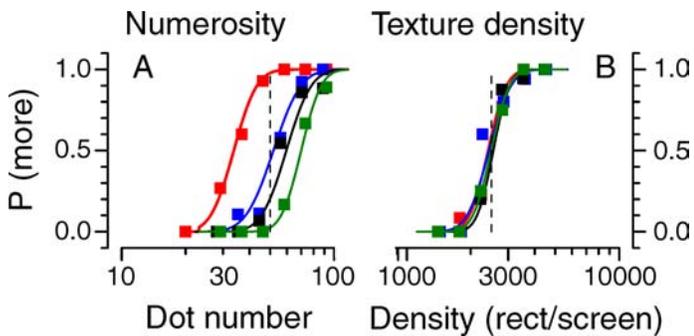
Figure 4. Example psychometric functions for observer JED for numerosity (A) and texture density judgments (B) at various luminances—red: 0.04 cd/m², blue: 0.08 cd/m², black: 7 cd/m², green: 45 cd/m². Luminance had a clear effect on perceived numerosity, systematically displacing the curves at the four luminances, while texture density was virtually unaffected. The numerosity curves are displaced leftward at low luminances, yielding lower PSEs, showing that at low luminance fewer dots are needed to be perceived as more than the running average of all conditions than at high luminance. The lower the PSE in a condition, the higher its perceived luminosity.

Experiment II: Effects of luminance on perceived numerosity and texture-density

There was very little evidence in the previous experiment to suggest that numerosity perception may depend on element density in sparse arrays. In this experiment, we study the relationship between visual *texture* (where the elements are not clearly distinguishable from each other) as it has been suggested that numerosity may be mediated by texture judgments (Durgin, 2008).

Many visual properties are affected by luminance, such as apparent color (Boynton & Gordon, 1965) and apparent speed (Hammett, Champion, Thompson, & Morland, 2007; Vaziri-Pashkam & Cavanagh, 2008). We investigated the effects of luminance on perception of numerosity and texture density, to see if they were similar. The stimuli for numerosity were like the previous ones, except that all dots were bright against a dark (0.01 cd/m²) background, with dot luminance varying from 0.04 to 45 cd/m². To study texture density we devised patterns like Figure 1B comprising randomly chosen black or white rectangles whose width and height varied randomly by a factor of two around a specific mean size (which defined the density). Again the black rectangles were fixed at 0.01 cd/m², while the white varied over the same three log-unit range as the white dots. Again the method of single stimuli was used, with all luminance conditions randomly interleaved (separately for numerosity and density).

The MSS experiment with four luminance conditions intermingled yields four different psychometric functions,

one for each of the four luminance levels. If lowering luminance increases perceived numerosity then the psychometric functions for the different luminance levels will separate out on the abscissa. Figure 4 shows sample psychometric curves for the naïve observer JED for one numerosity (average 50) and one density (average 250 rectangles/screen) condition. The effects of luminance on the psychometric curves are obvious. For numerosity, the curves shift systematically with luminance, towards lower numerosities at lower levels of luminance. The shift towards lower luminosities means that lower numbers in the low-luminance condition are perceived as more numerous than the overall average. This leads to a lower PSE, implying greater perceived numerosity at lower luminances. For texture density, however, luminance had no effect at all, the curves all superimpose each other.

Figure 5 plots points of subjective equality (PSEs) for perceived numerosity and density against luminance for two subjects, at three levels of average numerosity or
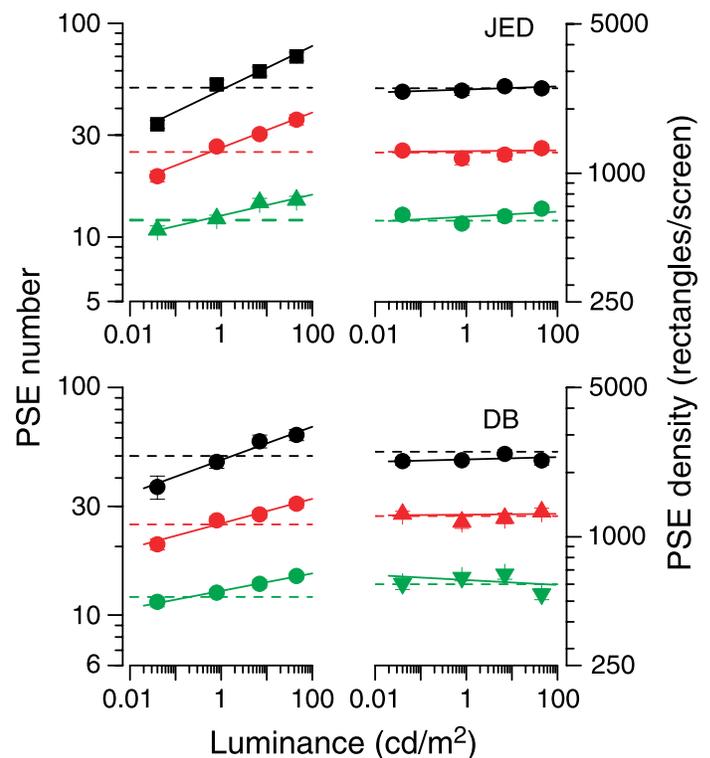

Figure 5. The effect of luminance on perceived numerosity (left) and perceived texture density (right). The data show points of subjective equality between the particular luminance condition (given by the median of psychometric functions like those of Figure 5) and the perceived running average of all conditions: lower PSE means higher perceived numerosity. Error bars show standard error of the mean, calculated by bootstrap. The continuous curves are best fitting linear regressions (on log coordinates, weighting data by standard error), with the numbers giving the slope of the regression curve. Dashed lines indicate the physical number or density.
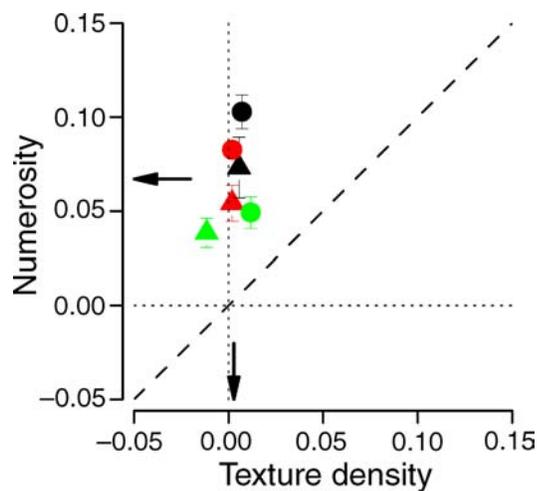
Figure 6. Luminance dependency (given by the slopes of the curves of Figure 6) for numerosity judgments plotted against texture density. The bars refer to ±1 s.e.m. for the regression fit. The arrows near the axes represent means. Black symbols refer to average numerosity 50 and average texture density 2500, red to 25 and 1250, green to 12 and 600.

density. In all cases luminance had a clear effect on perceived numerosity of dot patterns (which increased with decreasing luminance), but no systematic effect on perceived texture density, which remained constant across all luminances. The data were fit by linear regression (on logarithmic coordinates). For perceived numerosity, the best fits ranged from 0.04 to 0.1 log-number/log-luminance, while for density the slopes were never above 0.005, and sometimes negative. This is brought out more clearly in Figure 6, which plots the slopes of the perceived numerosity against the perceived density dependency. Clearly the density slopes cluster around 0, while the numerosity indexes are all positive, on average 0.067 (averages indicated by arrows).

Discussion

This study provides strong evidence that numerosity can be estimated without passing through an intermediate stage, such as texture density: judgements of numerosity were as precise as those of density; holding density constant does not impede, but actually enhances numerosity discrimination; numerosity judgements in blocked conditions where the relationship with density is fixed are no better than in random conditions; and when numerosity is fixed, there is no tendency for judgements to be determined by density or area. Of course it remains possible that the visual system calculates area effortlessly and combines this with density to estimate numerosity, but it seems unlikely that there would be no cost what-soever in estimating area (exacerbated by the ragged

edges of the stimulus), and also in the calculation involving a multiplication with density.

Perhaps the strongest evidence for independent mech-anisms for sensing numerosity and texture (at least dense texture) was that while numerosity estimates showed a strong dependency on luminance, decreasing systemati-cally with luminance over a three log-unit range, texture density was completely independent of luminance over this range.

These results all suggest that perceived numerosity is not simply a by-product of perceived density, but is calculated independently, probably by separate mecha-nisms. Certainly, the two attributes may share common neural mechanisms (from the photoreceptors onwards), but there is clearly a good deal of independent processing. Physiological studies point to area LIP as a likely candidate for at least an initial stage of numerosity processing, the most probably site of the adaptation to numerosity. There the neurons have clearly defined receptive fields, permitting spatially selective adaptation, and respond in a graded way to numerosity (Roitman et al., 2007).

These results sit well with many other recent results that distinguish numerosity from density. For example, within a single view, observes can estimate the numerosity of objects featurally distinct from others (for example different color) as efficiently as when there were no other objects present (Halberda, Sires, & Feigenson, 2006). Number estimation under these conditions can occur only after object classification, presumably at higher areas than those that Durgin (1995) claims to be involved in judging texture density. Similarly, grouping pairs of objects into a single object by connecting them causes dramatic decreases in apparent numerosity, even though the density of individual items remains unchanged (Franconeri, Bemis, & Alvarez, 2009; He, Zhang, Zhou, & Chen, 2009).

The method of constant stimuli (MSS) requires observers to keep a running average of previous presentations (Morgan et al., 2000). That observers can work so easily with MSS implies that vision can not only sense numerosity independently of area and density, but can also remember it and compute a running average. We presume this is done by analog means, without the use of symbols or multiplication, possibly by accumulating the residue of noisy representations of stimulus magnitudes along a sensory continuum. Vision may also be capable of computing other image statistics, including variance (Morgan, Chubb, & Solomon, 2008) and others, like kurtosis, based on even higher than second-order moments (Kingdom, Hayes, & Field, 2001) or higher-order image statistics (Julesz, 1984). Given the feats of calculation necessary for seemingly effortless tasks, like size con-stancy, or the extrapolation of trajectories, it should not be surprising that the visual system can sense number and compute averages.

We recently claimed that vision senses numerosity directly, presenting it to consciousness as a visual quality

like shape or color, enabling rough estimates of number to be made without the intervention of counting or other cognitive mechanisms (Burr & Ross, 2008). In that study we showed that, like other visual attributes, perceived numerosity is strongly susceptible to adaptation. The results we report here strengthen the case that it is an independent sensory attribute, not derived from others like texture density, which are also susceptible to adaptation (Durgin, 1995, 2008; MacKay, 1973).

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