A common visual metric for approximate number and density

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Abstract
There is considerable interest in how humans estimate the number of objects in a scene, in the context of an extensive literature on how we estimate the density (i.e. spacing) of objects. Here we show that our sense of number and density are intertwined. Presented with two patches, observers find it more difficult to spot differences in either density or numerosity when those patches were mismatched in overall size, and their errors were consistent with larger patches appearing both denser and more numerous. We propose that density is estimated using the relative response of mechanisms tuned to low and high spatial frequencies (SFs), since energy at high SFs is largely determined by the number of objects, while low SF energy depends more on the area occupied by elements. This measure is biased by overall stimulus size in the same way as human observers and by estimating number using the same measure scaled by relative stimulus-size we can explain all of our results. This model is a simple, biologically plausible common metric for perceptual number and density.

vision | psychophysics | number

Introduction
It has long been known that observers can judge the number of objects within a scene (1) but only recently has it been proposed that this ability is directly supported by low-level visual mechanisms. Specifically, Burr & Ross (2) report that prolonged viewing of a dense field of elements (adaptation) causes the number of elements in a subsequently viewed pattern to appear drastically reduced. The notion of “a visual sense of number” has generated considerable excitement, not least because, for example, children’s mathematical ability correlates with their ability to make approximate estimates of number (3). However, when one varies the number of elements within a fixed region one also varies the mutual separation or density of elements. Durgin (4) has reported that stronger adaptation is induced by a small-dense patch than by a large-sparse patch (that actually contains more elements). This is consistent with adaptation being determined by density and not number per se.

The notion that our sense of number might be linked to density is intuitive when one considers that there are only two ways to estimate number. The first is to explicitly count (item-by-item), a strategy ruled out by the finding that number estimation does not slow in proportion to number beyond around 7 elements (5). The second way is by comparing measurements whose product is dimensionless, e.g. density × area = number. If we only require relative number (i.e. “which is more numerous”, the judgement made in forced-choice experiments), then we can use a density estimate that need only scale with physical density (e.g. contrast). This is the approach adopted here: we sought to develop a computational model of approximate number estimation by identifying the measures used by the visual system to estimate density (and so encode approximate number).

A major constraint on any density-estimate is whether it is dependent of number. Can we determine experimentally if number and density estimation are independent? One approach is to show that manipulation of the notionally irrelevant dimension (say density) leaves estimation along the relevant dimension (say number) unaffected. For example, doubling element size (thereby doubling the ratio of occupied to unoccupied pixels in the pattern) has no effect on number-discrimination (2). However, if one defines density not as pixels per unit area but as elements per unit area – the latter being widely used (6) – then this result is not diagnostic.

The most direct way to decouple number and density is to mismatch the area over which elements are distributed within two stimuli. Several previous studies have reported that this manipulation does not greatly influence the precision of number discrimination (6-8). However, in addition to expressing the usual concern about negative results we note first that some studies have used relatively small numbers of elements (~30 (6,8)) which are less effective at engaging approximate number processing. Furthermore the study by Ross & Burr (7) required observers to make either number or density comparisons within different blocks of trials. In number-blocks (for example) either area or density were held constant so that on trials when the area of the stimulus matched the standard, observers could report density while on trials when the density was matched, they could report area; subjects never
perceptually matched to right, they show that for a small test patch to be perceptually matched to a variable-size reference the test's density must increase as the reference grows. Conversely, a large test paired with a small reference (leftmost blue point) can be sparser (i.e. fall below the dashed horizontal line) and still be perceptually matched. Essentially these data indicate that larger/more-numerous patches appear denser than they are and that perception of number and density is veridical (i.e. points fall on the dashed horizontal line) only when test and reference are matched in size.

Figure 2e indicates that number-matching across differences in patch-size is less biased than density-matching (the slopes of data in Figure 2e are shallower than 2c), but that observers still make systematic errors such that larger test patches appear more numerous (replicating (8)). Thresholds for the two tasks are shown in Figure 2d: observers require about 40% difference in number or density to make a reliable discrimination between a test and a reference-patch. This is somewhat higher than previous estimates of Weber fractions for number discrimination (~25% (2)) which we have identified (in control experiments) as being due to a combination of the larger element-size and parafoveal presentation employed here. We note that the largest size-mismatches substantially elevate thresholds (e.g. circled data point in Figure 2f).

Modelling We propose that shared effects on bias and precision arise from the use of a common metric for both number and density judgements. The coloured lines in Figure 2 are predictions from a model that estimates density and number using a pair of filters tuned to high and low spatial frequencies, specifically relying on the ratio of their responses to a full-wave rectified version of the stimulus. We predict density discrimination thresholds using these response-ratios corrupted by multiplicative noise. Discrimination of number requires this estimate be scaled in proportion to the relative area of stimuli: to this end, we simply multiply a given response-ratio by the ratio of the low SF filter responses (from the stimulus-pair). This number-estimate is corrupted by a second larger noise term (that we suppose originates from having to compare low SF response across space). Note that while number could be estimated directly from the output of high-spatial frequency filters, this would fail to produce the moderate bias evident in Fig. 2e. Given the small number of free parameters (one for density and one for number) the model does a remarkably good job of capturing our main effects including the strong and weak non-veridical matching of density and number, respectively, and Weber fractions for discrimination.

Results

Analysis For density discrimination, responses were first plotted (Figure 2a) as the proportion of times subjects said the test was denser than the reference, as a function of the ratio of the densities of the test and reference. Data were fit with cumulative Gaussian functions (grey lines in Fig. 2a) to derive (a) bias (offset: the proportion of test-density required to produce a subjective match between test and reference, i.e. so that the subject was 50% likely to say the test was denser than the reference) (b) threshold (the proportion of extra density required to raise performance from 50% to 82%). An analogous procedure was applied to number data (for the full dataset see Figure S1).

Average bias/thresholds Figure 2c shows how density-bias varies with patch-size mismatch. Consider the small red symbols; moving from left to right, they show that for a small test patch to be perceptually matched to a variable-size reference needed to judge number. Critically, when observers are forced to make an explicit comparison – as in the experiment of Tokita & Ishiguchi (8) – a strong effect of size is evident (albeit on the appearance rather than discriminability of the patches). Larger patches are perceived as being around 10% more numerous. Below we confirm this effect for number, find that it is magnified for judgements of density, and show how this is critical for understanding the mechanism supporting number and density judgements.

Figure 1(a,b) shows two patches containing 128 elements. The difference in patch-size makes this equivalence difficult to confirm, and below we will show that this interferes with observers' precision at discriminating number. Note that this is contrary to the notion of a sense of number that operates independently of stimulus size/density. Fig. 1c further illustrates that density-estimation is not immune to a similar manipulation of size/number. Figure 1c has the same physical density as Fig. 1a but appears considerably denser. Fig. 1d is a typical perceptual match for the density of Fig. 1a, and illustrates the results of our experiment below. We show that observers typically require around a factor of 1.4 reduction in density (100%/1.4 = 71%) to achieve a reliable perceptual match for density across this difference in number/size.

We experimentally quantified the impact of mismatching patch-size on observers’ ability to discriminate which member of a pair of stimuli (a test and a reference, the latter containing 128 elements) was either more numerous or more dense. We did this using a 3 X 3 design measuring observers’ performance with all possible pairings of patches with radii of 2.0, 2.8 or 4.0 degrees of visual angle.

Individual differences Individual differences in bias provide an independent source of evidence that
density and number employ a common perceptual metric. Fig. 2b plots observer-bias (percent of reference number or density required for a match, where 100% is veridical/unbiased performance) on the density versus the number task, for comparable size-mismatched conditions. Data from five observers indicate that these two biases are highly correlated (R=0.64, p=0.0001), but that the density bias is consistently higher than the number bias. The level of correlation and good agreement with the prediction of the model (olive-coloured line) again suggests that the two tasks are tapping into a common mechanism.

Element type/arrangement In order to test the wider relevance of the model we examined its ability to predict psychophysical discrimination of stimuli composed of different elements. Starting with a smaller number (32) of random contrast polarity Gaussian elements, as used above, we compared performance with a random spatial arrangement (Fig. 3a) versus one that minimised element overlaps (Fig. 3b). We also tested single contrast-polarity elements (Fig. 3c), as well as SF narrowband Gabor elements (Fig. 3d-f) with either a small envelope (Fig. 3d) a large envelope (Fig. 3e), or a medium envelope with carrier SF jittered (σ=0.5 octaves; Fig. 3f). We compared this to performance with another class of contrast-defined element (with an isotropic noise-carrier; Fig. 3g) or animal-silhouettes either presented against a uniform grey (Fig. 3h) or a fractal noise background (Fig. 3i). These conditions challenge the model by manipulating: element-arrangement, cue-type (contrast or luminance), element-shape, surrounding context, and feature density within elements. Results from the experiment are presented alongside predictions from the response-ratio model in the righthand part of Figure 3. Removing element overlap improves performance considerably, while thresholds are remarkably stable across variation in contrast polarity, envelope-size and envelope-shape. This is captured well by the density-estimate from the response-ratio model using the same filters as before, with only a single (multiplicative-noise) parameter varying (being set once for each of the three classes of stimuli). We note here that the connectedness of elements can also influence numerosity judgements (9, 10); in Figure S2 we show that the response-ratio model also predicts performance with such stimuli.

Discussion
We have shown that observers’ difficulty in matching and discriminating both number and density across differences in stimulus-size and element-type is consistent with their using a simple perceptual metric based on the relative response of a pair of spatial-frequency tuned filters. We note that our approach has something in common with Allik’s “occupancy” model of numerosity (11), a major difference being that our model operates not on abstracted object locations but on raw images. That our model knows nothing of objects is critical since it predicts that systematic mismatching of element-size should affect both number and density judgements, whereas contrast (and contrast polarity) should not (since response-ratios don’t change with overall contrast-level). These predictions are broadly supported by existing literature; substantial differences in element-size disrupt numerosity judgements (12, 13), while contrast manipulations do not (2, 13).

The predictions for density discrimination are based directly on noisy response-ratios while for number discrimination these values were scaled by the ratio of low SF outputs, in order to compensate for the effect of difference in region-size on response-ratio. We do not suggest that this means density estimation can never compensate for size, merely that this task did not promote such a strategy. It may be that, for density, a more natural compensation is for element-size (which would give a scale-invariant representation of density, i.e. one that does not change with viewing distance). We suggest that such a computation could be achieved using the ratio of responses from a different (intermediate SF) filter-pair. Because our experiment did not alter element size, it may not have revealed the behavioural consequences of such a computation.

Why then should judgements of number and density be so biased by stimulus size? Consider a comparison to the visual coding of luminance. For humans it is luminance-difference (contrast) and not absolute-luminance that drives our visually guided behaviour. A predominantly contrast-based code might sacrifice veridical representation of luminance – e.g. through a centre-surround RF organisation - in order to detect image structure under wild fluctuations in overall luminance. The price we pay is that our judgement of absolute luminance can be biased by context, a fact that is exploited by a variety of impressive brightness illusions. In analogy to luminance, we suggest that the visual system makes a similar sacrifice of accuracy for absolute number/density in order to preserve our sensitivity to relative-number and relative-density under fluctuation in absolute levels of these visual attributes. Producing estimates of number/density that are biased by overall size may be the price the visual system pays to preserve discriminability of visual attributes that are likely more functionally important.

Our work broadly fits with several recent suggestions that the representation of number is linked to other visual attributes (e.g. coding of duration, (14)). It is inconsistent with the notion of a dedicated visual mechanism for approximate
number (independent of density) as has been claimed e.g. based on psychophysical evidence from adaptation (2). In terms of physiological mechanisms we note that the great majority of studies have employed low numbers of elements (typically 1-7, never higher than 32). Although it is assumed that such mechanisms could deal with larger numbers, this has not been explicitly demonstrated. In terms of modelling the details of number-channels - i.e. how one moves from images to predicted behaviour - have yet to be described. That neural mechanisms tuned for small-numbers have been located in parietal cortex (15-18) suggests that they may rely on resources such as attentional pointers. This in turn is consistent with low-number discrimination (subitizing) placing a heavier attentional load on observers than estimation of larger numbers suggesting that different mechanisms exist for both (19, 20). This squares with earlier adaptation findings that the critical switch at higher numbers is towards a more density-dependent measure (21). The general idea is that statistical mechanisms like the response ratio are always available but that at lower numbers they may be unreliable compared to strategies that engage more attentional resources (like pointers).

We started out by pointing out several flaws in earlier studies of the influence of relative size on number/density judgement. Although the behavioral evidence relating to numerical cognition is frequently contentious we believe our findings will generalise. First, we note that since we are reporting a positive effect of our manipulation we cannot have made a Type II error. Second, since conducting these experiments, we have measured larger biases on both number and density discrimination under conditions of higher uncertainty and have further evidence for a close correspondence between these tasks under a wide range of manipulations (including variable attentional load, contrast-manipulation, element-size manipulation (22)). Finally we have shown that the model can predict performance with other classes of stimuli (Figure 3).

Inspecting Figure 1, one could argue that it should come as no surprise that number and density are supported by a common mechanism since both code the degree to which space is "occupied". What is striking about our findings is that our sense of density (or feature-spacing) is inconsistent with an explicit code for spatial position, beyond the influence that feature arrangement has on the spatial frequency structure of an image. We must be surprisingly poor at judging average feature spacing (which would unambiguously code density in our experiment) for us to rely on a measure that was so vulnerable to a simple manipulation of overall size! The idea that feature density might always be derived from filter activities - in a manner that is more akin to the processing of e.g. contrast - runs contrary to the notion that an explicit code for "token-position" - the corner stone of the "primal sketch" (23, 24) - is preserved throughout visual processing. Instead either token-positions are pooled or undersampled within clusters (25) in a manner consistent with some form of local spatial compression, or the tokens didn’t exist in the first place. The latter view would be consistent with our sense of relative-spatial position of features being illusory, manufactured after the fact based on the spatial frequency structure of the scene.

The model we have described computes a response-ratio estimate at every location and then pools over the entire image. We now briefly consider the advantages of an explicit representation of local response-ratio. We have already shown that element clustering increases overlaps and leads to poorer performance (Fig. 3) but it is also known that clustering reduces perceived number and/or density (26). Figure 4a,b shows an example of this phenomenon; note that more regularly spaced elements (Fig. 4b) appear more numerous, despite having the same number as the clustered stimulus (Fig. 4a). Below each image (Fig. 4e,f) are "response-ratio-maps" based on the (Gaussian smoothed) local filter-ratios. Note that the "warmer/denser" response to the more evenly-spaced pattern predicts about an 8% elevation in perceived number (in line with psychophysical estimates (26)).

It is known that the visual system has access to statistical-attributes such as mean element-orientation (27) and element-size (28), and while there is a candidate neural mechanism for orientation averaging (a population code based on the response of V1 neurons) the mechanism for size-averaging is currently unclear. Fig. 4c shows a typical stimulus containing size-varying elements and 4g shows how the corresponding response-ratio map reflects local feature-density. A pooled response-ratio for this image could be used as a reliable proxy for mean-size estimation. We have noted that a curious feature of size-averaging is that performance seems to depend on neither the diameter nor the area of stimuli, but on a measure closer to $R^{-1/4}$ (29). We propose that this arises from observers relying on a cue from response-ratio that rises slower than density with increasing stimulus-diameter (Fig. 5c).

Finally, it is known that element-size/density is a useful cue to surface shape. Fig. 4d and 4h show, respectively, a textured figure and a version of the same that has been labelled using local response-ratio to indicate local surface density. Note how element colour now reflects size/density of elements and that "hotspots" indicate regions of surface discontinuity.
In summary, our psychophysical evidence indicates that the ability to judge number and density are both influenced by the size of stimuli in a manner that suggests they rely on a common visual mechanism. This, we propose, is based on the relative response of spatial filters tuned to high and low spatial frequencies. Such a simple mechanism may prove useful in uncovering the operation of a variety of additional tasks including size averaging and texture processing. Furthermore, we speculate that ratios of filter responses are the “common currency” of visual magnitude estimation (14). For example duration estimation could similarly be based on the ratio of responses from a transient and sustained filter-mechanism, a notion that squares with recent suggestions that our visual “clock” continuously compares the output of magnocellular and parvocellular channels (30) or is sensitive to the second-order temporal statistics of natural visual stimuli (31).

Materials and Methods
Stimulus and task. We presented pairs of stimuli (±6.0 deg left/right of central fixation) – a test and a reference patch – for 250ms. Observers reported which patch was either more numerous or more dense (in separate blocks). No feedback was given. Patches were composed of a variable number of small 2D Gaussian patches (σ = 3.8 arc min; 50% contrast, random contrast-polarity) falling within a circular region. We used a 3 X 3 design independently varying the size of the test and reference patches (radii: 2.0, 2.8 or 4.0 deg). The (variable-size) reference always contained 128 elements (e.g. Figure 1a is the smallest reference). The density or number of the (variable-size) test (e.g. Figure 1b is the largest test patch) was set using a method of constant stimuli, and varied over a range of 50% to 200% in 7 steps (centred on 100% i.e. a physical match to the density or number of the reference, according to run). Thus for “number” runs, tests contained 64, 81, 102, 128, 162, 203 or 256 elements. For “density” runs, tests were 50, 63, 79, 100, 126, 159 or 200% of reference density (2.5, 5.2 or 10.4 elements/deg² depending on reference size). Each run consisted of 112 trials (16 trials at 7 stimulus levels) and five observers (two naïve, all experienced in psychophysics, with normal or corrected-to-normal vision) performed 1-2 runs of each judgement type (number or density discrimination).

Modelling. To reliably discriminate number (N) and density (D=N/A; where A is area) the visual system requires estimates (n and d) such that n ~ N and d ~ D. We propose that the responses of known visual mechanisms - spatial frequency (SF) band-pass filters – are combined to make these estimates. Specifically we convolve stimuli with Laplacian-of-Gaussian - “centre-surround” filters - constructed from the combination of a Gaussian filter and a second-derivative:

\[ \nabla^2 G_{\sigma}(x,y) = \frac{1}{\pi s^4} \left(1 - \frac{x^2 + y^2}{s^2}\right) \exp \left( -\frac{x^2 + y^2}{s^2} \right) \]

(1)

to estimate the filter-response to a rectified version of a given image* (I_{n}) pooled across all image locations:

\[ R_{n} = \sum_{x,y} |\nabla^2 G_{\sigma} \otimes I_{n}| \]

(2)

Figure 5 illustrates the logic of using this filter-response to estimate density and number. The first row presents stimuli similar to those used in our experiment and looks at the effects of number, density and radius by fixing one of these parameters (in a,b,c respectively) and allowing the other two to co-vary. The example stimuli are from the extremes of the range tested and beneath each is the result of filtering a rectified version of it at two different scales. The graphs in the bottom row plot the response from the high and low frequency filters (purple and blue symbols, respectively), averaged across all pixels in 32 image-examples. For the purpose of illustration (and since we are interested in discrimination) we have normalised responses relative to the response to the mid-range stimulus. Solid green and red lines show the ideal (normalised) responses of a mechanism tuned for density and number respectively. Note that the purple symbols (high frequency response) closely follow the pure number prediction (solid red line). That \( R_{n} \propto N \) should be unsurprising since small filters generate isolated responses to individual elements. Looking at blue symbols (low frequency response) we note that although this measure rises as a function of (b,c) number it also rises as a function of (a) patch radius when number is fixed. That \( R_{n} \propto A \) is a consequence of large filters responding to clusters of elements and their response ultimately being limited by the patch size elements fall within. Based on this observation we propose that the ratio of two filter responses might be a useful correlate of density and number:

\[ C = 2^{\gamma} \frac{R_{hi}}{R_{lo}} \]

(3)

* This non-linear transform of the image confers subsequent filtering with sensitivity to “second-order”, or contrast-defined, image structure.
a measure we call response-ratio (where \( \gamma \) is Gaussian random noise, so that \( 2^{\gamma} \) is a multiplicative noise term). Response-ratio is plotted as the green dashed line in Figure 5. The slope of straight-line fits to response-ratio are around (a) -0.30 and (c) +0.4 when density changes (with either fixed number or radius) but only (b) +0.08 when density is fixed. We selected the filters to use in this and following simulations by averaging the magnitude of the slopes of the functions in (a) and c) for all possible pairings of filter spatial frequencies, selecting the filter-pair that maximised the slope of the functions (i.e. maximising sensitivity to density change). We then ran Monte Carlo simulations of our experimental procedure generating stimulus image pairs (a and b) the same way as in the real experiment and then computed an estimate of relative-density as:

\[
D_{a,b} = \frac{C_a}{C_b}
\]

The denser stimulus was selected based on whether \( D_{a,b} \) was less than or greater than 1.0, and this selection used to derive psychometric functions. Because filter sizes had been set by the earlier simulation this model has only one free parameter (the multiplicative noise level in Equation 3 which was set to \( \sigma = 0.1 \)).

How then to estimate number? The first possibility is that the visual system directly accesses \( R_{hi} \) (useful since \( R_{hi} \propto N \)). This is unlikely for two reasons: first, if this information were available then mismatching region-size would have little or no effect on performance (which it demonstrably does). For example, the red symbols in Figure 5a would indicate that density/radius have no effect of perceived number whereas our own bias data indicate that they do. Second it would predict that observers' estimate of number would increase with increasing contrast; if anything the opposite is true. Instead we propose that number is derived from response-ratio and that an explicit weighting for degree of size-mismatch is applied in order to "recover" the high spatial frequency component. Because low spatial frequency is used as a proxy for area in computing density, the scaling is based on the ratio of the low SF response from the two stimuli:

\[
n_{a,b} = \left( 2^{\gamma_a a R_{hi}} \right) \left( 2^{\gamma} \right) D_{a,b}
\]

which includes a second noise term (\( \gamma = 1.9 \) in the simulations). In Figure 5 the dashed red lines plot estimated number \( n \) and show that (Figure 5a) the estimate is essentially flat when number is unchanging, and increases with number at about the same rate when density is fixed (Fig. 5b) or increases (Fig. 5c), closely mirroring the predictions from high SF energy. Given that the slope of these functions indicates discriminability it is interesting to note that re-weighting of the response-ratio estimates leads to similar slopes with either pure-number change or when number changes with density. Ross & Burr (3) took their finding that subjects could discriminate number equally well under both of these conditions as an indicator that number could not be mediated by density. This simulation shows that such performance does not rule out reliance on a common mechanism (based on neither number nor density but on a simple statistic based on the SF-structure of the image).

Figure 51 plots individual psychometric functions from the five observers for both tasks (red=density, green=number) alongside the predictions of the model described above (solid lines) fit to the mean psychometric function.

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References
Figure legends

Figure 1. Our sense of number and sense of density (element-spacing) are entangled. (a) The small reference patch contains 128 elements. (b) Doubling the radius of the patch makes it difficult to tell that (a) and (b) contain the same numbers of elements. The size change disrupts our “sense” of number. (c) This patch has the same physical density as (a) but the elements typically appear more closely spaced. (d) is perceptually matched to the density of (a) but has a much lower physical density - it contains 365 elements i.e. 147 fewer than the physical match (c). Size-change disrupts our “sense” of both density and number.

Figure 2. (a) Psychometric functions for number and density discrimination. Symbols plot average proportion of times observers categorised a test as denser (green) or more numerous (red) than the reference as a function of the number of elements in the test compared to the reference. Grey lines are the best-fitting cumulative Gaussian functions, with the stimulus levels producing a perceptual match (bias) or a just noticeable difference (threshold) overlaid for the density task. Dashed coloured lines are the predictions of the model using the relative activity (response-ratio) of two filters tuned to low and high spatial frequencies. (b) Individual observers' bias on number- versus density-discrimination on comparable size-mismatched conditions. Note that bias is greater for density judgements and is correlated with bias on the number judgements in a manner predicted by the model (olive line). (c,e) Matching and (d,f) discrimination performance for (c,d) density and (e,f) number. Biases indicate that subjects see larger objects as (c) denser and (e) more numerous. (d,f) Discrimination is broadly similar for both tasks (observers can spot a difference of ~40% (i.e. x140%) in either number or density), with both tasks being compromised by mismatching stimuli-sizes. Solid lines are the predictions of the response-ratio model.

Figure 3. Manipulation of element-type and configuration. (a-c) Gaussian elements of either (a,b) mixed or (c) single contrast polarity positioned either (a,c) randomly or (b) to avoid overlaps. (d-f) Gabor elements with (d) small, (e) large or (f) medium envelopes and a (d,e) fixed or (f) variable carrier spatial frequency. (g-i) complex elements made up of (g) patches of isotropic noise or (h-i) animal silhouettes in (h) isolation of (i) embedded in fractal noise. (j) Psychophysical discrimination performance (coloured symbols) for the nine conditions compared to predictions of the simple filter model (solid line) described above.

Figure 4. (a-d) Original images and (e-h) “heat maps” of local response-ratio (blue=low response-ratio, red=high response-ratio). (a,b) Both images contain similar numbers of elements but lack of “clustering” in (b) increases it's perceived number by ~8%. (e,f) local response-ratio reflects this difference. (c,d) Response-ratio can also be mapped onto images as an estimate of (c,g) local size and (d,h) local surface gradient.

Figure 5. Stimuli with one parameter fixed - (a) number, (b) density or (c) radius - and the other two allowed to co-vary. (Top row) example stimuli and (second row) high-SF and (third row) low-SF filtered versions of rectified versions of the stimuli. (Bottom row) graphs plot pooled energy from the high (purple-disks) and low (blue-disks) filters under conditions of fixed number, density and radius, along with the estimated density (green dashed lines) and number (red dashed lines) based on response-ratio. Units are a proportion relative to the value derived from the mid-value stimulus (so all lines pass through 1.0). An ideal estimate of number and density is shown as the solid red and green lines respectively.
Figure 1
(a) Typical psychometric functions

(b) Density versus numerosity bias

(c) Density bias

(d) Density threshold

(e) Number bias

(f) Number threshold

Figure 2
Figure 3

Figure 4
Figure 5
Supporting Information

**Figure S1** shows the full data set for the experiment examining the effect of size-mismatch on number and density judgements. Shown are the raw data that were fit with cumulative Gaussian psychometric functions to derive the summary Figure 2c-f. Now the model predictions (solid lines) are proportions of responses for which the test was judged more numerous or more dense than the reference as a function of the difference (in number or density) between the test and reference stimuli. The fit is generally good.

He et al (1) showed that connecting pairs of elements within a pattern reduces its perceived numerosity. In a matching task they had observers judge if a reference (12 elements, 4 lines, 0 pairs connected) or a test (9-15 elements, 4 lines, 0-2 pairs connected) was more numerous. When the lines connected at least one pair of elements within the test pattern, the test needed to contain more than 12 elements to perceptually match the 12-element reference pattern. The inset of Figure S2 shows typical stimuli from this experiment (all containing 12 elements) and the reduction in perceived numerosity as one connects elements (from left to right) is clear. The main section of Figure S2 replots psychophysical data from this experiment (symbols). We ran a Monte Carlo simulation of the experiment applying the response-ratio model to a set of stimuli generated in a similar way. No noise was added to the model output and filter parameters (\(\mu_1\) in Eqn. 1) were set to 2 and 23 pixels for the high and low spatial frequency filters, respectively. The good fit of the model prediction (solid lines) we obtain indicates that the response-ratio model is able to capture the influence of connecting elements on perceived numerosity without recourse to any notion of “segmentation” (2).

References


**Figure legends**

**Figure S1.** Full data-sets for the nine conditions of the main experiment, showing the five observers’ performance on density or number judgements (green or red symbols, respectively) alongside predictions from the response-ratio model (solid lines) fit to the mean performance level. Grey disks (inset) indicate schematically the size of reference (R) and test (T) stimuli. Blue lines show the point at which stimuli were physically matched (for number or density): shifts of the psychometric functions away from this point indicate bias. The boxed percentage values quantify bias (\(\mu_d\) and \(\mu_x\)) and threshold (\(\sigma_d\) and \(\sigma_x\)) - using the mean parameters from the cumulative Gaussian functions that best fit the individuals’ raw data.

**Figure S2.** Solid symbols are data re-plotted from He et al (2009) indicating the number of times an observer reported that a test pattern (containing a variable number of discs) was more numerous than a reference containing 12 discs. All test stimuli contained four lines that could join (red) no pairs, (green) one pair or (blue) two pairs of discs (example stimuli are given at the top left). We generated stimuli using a similar method to the original study [10] and used the density measure (Equation 4) to generate predicted performance (solid lines). The model provides an excellent fit to the data.
Figure S1
Figure S2