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Citation: Zeljic, K., Morgan, M. J. & Solomon, J. (2026). No consistent bidirectional aftereffect from numerosity adaptation. *Vision Research*, 249, 108900. doi: 10.1016/j.visres.2026.108900

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No consistent bidirectional aftereffect from numerosity adaptation

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ARTICLE INFO

Keywords:

Aftereffects

Numerosity

ABSTRACT

Numerosity has been proposed as a primary visual attribute, akin to motion or colour, and has been reported to show bidirectional adaptation consistent with population coding by tuned mechanisms: after exposure to sparse or dense arrays, the perceived numerosity of an array with a moderate number of dots shifts away from the adaptor. However, recent studies argue against bidirectionality, claiming that adaptation to sparse arrays failed to increase perceived numerosity of a denser array. This suggests that previous accounts may reflect decisional rather than perceptual biases. To test this, we employed a comparison-of-comparisons paradigm using a four-quadrant display. Observers adapted to two spatially distinct dot clouds in upper quadrants of the visual field. Following adaptation, dot clouds were shown in all four quadrants. Observers judged which of the two bottom clouds appeared more different to the reference numerosity contained in each upper quadrant. Simple decisional biases such as a preference for selecting a previously adapted or unadapted stimulus cannot masquerade as perceptual bias in this paradigm. Across six observers, three adaptor numerosities (0, 25, 100) and three randomly interleaved reference numerosities (34, 50, 74), we found clear evidence for unidirectional aftereffects consistent with monotonic neuronal responses. Adapting to dense clouds (100 dots) produced the largest downward bias in perceived numerosity, with smaller reductions following 25-dot adaptors. No condition produced upward shifts, suggesting that previous reports of bidirectionality may reflect non-perceptual biases.

1. Introduction

Adaptation is the process by which prolonged exposure to a stimulus alters the sensory system, thereby briefly biasing the perception of subsequent stimuli (Mollon, 1974). In the domain of numerosity perception, a robust finding is that adapting to a dense array causes a subsequently viewed array with a moderate number of dots to appear less numerous (Aagten-Murphy & Burr, 2016; Burr & Ross, 2008; Durgin, 1995; Yousif, Clarke, & Brannon, 2024). A more surprising finding is that adapting to a sparse array can produce the opposite shift, making a moderate array appear more numerous, as first demonstrated by Burr and Ross (2008) and later by Ross and Burr (2010) and Aulet and Lourenco (2023). This phenomenon has been referred to as reverse adaptation (Yousif et al., 2024), while the presence of opposing shifts for sparse and dense adaptors is referred to as bidirectional adaptation.

It is surprising that numerosity, a prothetic dimension in which values can be ordered unequivocally as “more” or “less” (other examples

include luminance and weight; Stevens, 1957),¹ exhibits bidirectional adaptation, a pattern more typical of metathetic dimensions lacking ordinal structure, such as motion direction (Levinson & Sekuler, 1976) and orientation (Graham, 1989). In prothetic dimensions, adaptation effects are generally unidirectional, shifting perception toward lower magnitudes, consistent with monotonic neuronal responses. A classic example is contrast: prolonged viewing of a sine grating with 8% contrast made subsequently exposed sine gratings with 4% contrast appear to have just 1% contrast, as did prolonged viewing of sine gratings having just 2% contrast (Georgeson, 1985). In comparison, metathetic dimensions like orientation (Tolhurst & Thompson, 1975) show bidirectional aftereffects, explained by opponent-channel or population coding with localized tuning. Specifically, prolonged exposure reduces sensitivity in neurons tuned near the adaptor, so a subsequent target is represented disproportionately by non-adapted mechanisms, biasing perception toward their preferred values (Suzuki, 2005). In this light, numerosity's bidirectional adaptation suggests coding with locally tuned

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¹ Spatial and temporal frequency are typically considered prothetic dimensions, however high values in these dimensions correspond to low values in the similarly prothetic dimensions of spatial and temporal wavelength. Therefore, one stimulus cannot be considered unequivocally greater than another, just because it has a higher spatial frequency, and aftereffects in this dimension are indeed bidirectional (Blakemore & Sutton, 1969).

mechanisms (opponent or population) somewhere along the numerosity–density continuum, rather than a purely monotonic magnitude code.

A possible exception to the above is speed, *a priori* a prothetic continuum, where there is no doubt that adaptation reduces the apparent speed of test stimuli having equal or lower speed than the adaptor, but where reverse adaptation has also been claimed. Thompson (1981), however, found no evidence for this reverse adaptation and attributed previous reports to an artifact of adaptation's effect on apparent contrast and its influence on apparent speed. Stronger evidence for reverse adaptation comes from a recent study of apparent size (Meese & Baker, 2023, cf. Durgin & Martinez, 2024), indicating multiple channels selective for different size ranges.² The selectivity of these channels is thought to arise via subtractive inhibition between neurons with differently sized receptive fields. Without this subtractive inhibition, the neurons merely would be size sensitive; they might respond with greater vigour when stimuli were made larger, but they would never respond with greater vigour when otherwise-identical stimuli were made smaller.

In the field of numerosity perception, there seems to be a consensus that low-level visual mechanisms sensitive to texture density contribute to aftereffects of adapting to large, dense textures comprising around 100 items or more. Controversy has arisen, however, over how to explain the aftereffects of adapting to relatively sparse patterns, comprising relatively few items. One explanation, originally proposed by Burr and Ross (2008) and later defended by Burr, Anobile, and Arrighi (2025), is that perceived number is a primary visual property, analogous to colour or motion, and is encoded by specialised mechanisms early in visual processing rather than derived from other stimulus dimensions. In contrast, Paul, van Ackooij, Ten Cate, and Harvey (2022) argued against low-level, sensory coding of numerosity. Instead, their imaging experiment revealed numerosity-selective activity in association cortices–brain regions that are also implicated in attention and action planning. It is noteworthy that this activity was independent of stimulus retinotopy, making it hard to understand how such representations could mediate spatially specific aftereffects measured in a two-alternative forced-choice paradigm.

An alternative to sensory-based accounts of reverse adaptation is the possibility that this aftereffect reflects a task-related bias in the decision process (Yousif et al., 2024). Psychophysical dissection of sensory-based biases from non-perceptual biases may be impossible within the popular asymmetric matching paradigm. Within this paradigm, observers adapt to a visual stimulus in one part of the visual field. Following adaptation, test and reference stimuli are presented, only one of which occupies the same part of the visual field. A decisional bias for reporting this latter stimulus as more numerous and/or inclusion of any part of the adapting pattern in the comparison between test and reference could manifest as reverse adaptation.

Here, we adopt the comparison-of-comparisons approach (Ismail, Solomon, Hansard, & Mareschal, 2016; Morgan, Grant, Melmoth, & Solomon, 2015; Morgan, Melmoth, & Solomon, 2013; Morgan, Schreiber, & Solomon, 2016; Yarrow, Martin, Di Costa, Solomon, & Arnold, 2016) to investigate the directionality of adaptation to numerosity. This technique improves on Burr and Ross's (2008) asymmetric matching paradigm by ensuring that two stimuli in a comparison are subject to the same adaptation history. In the experiment described below, we opted to present these two stimuli in unadapted regions of the visual field. Observers were required to select whichever of these

candidate stimuli appeared least like stimuli appearing in adapted regions. Simple decisional biases such as a preference for selecting a previously adapted or unadapted stimulus cannot masquerade as perceptual bias in this paradigm. Analysis with signal-detection theory (Green & Swets, 1966) then allows for estimates of aftereffect magnitude that are resistant to directional response biases. Evidence for reverse aftereffects under these constraints would support accounts in which numerosity is encoded by opponent or population-based mechanisms.

2. Methods

2.1. Observers

Observers included three authors and three volunteers who were naïve with respect to the purpose of these experiments. They had normal or corrected-to-normal vision and reported no history of visual or vestibular disorders. Ethical approval was granted by the Optometry Proportionate Review Research Ethics Committee at City St George's, University of London.

2.2. Stimuli

The stimuli were arranged in four fixed visual-field quadrants, upper-left, upper-right, lower-left, and lower-right, each centred 10° from fixation and subtending 11.8° × 11.8°. Dot positions were pseudo-randomly distributed within each quadrant. Each individual 'dot' was a 2-D Gaussian blob with a space constant of 0.4°, random polarity, and maximum contrast. There was no explicit constraint on overlap.

Each trial began with an adaptation display in which a dot-cloud appeared in each of the two upper quadrants. Adaptation clouds contained either 0, 25, or 100 dots (densities: 0, 0.18, 0.72 dots/deg²), the same in each upper quadrant, though with differently sampled dot positions. After adaptation, a test display appeared containing four dot-clouds, one in each of the four quadrants. The two upper quadrants contained one of three reference numerosities: $n_r \in \{34, 50, 74\}$, selected on the basis of a pilot experiment to have approximately 1 just-noticeable difference (JND) between them. (For consistency with Weber's Law, differences are logarithmic: $\log 74 - \log 50 \approx \log 50 - \log 34$). Of the two lower quadrants, one matched this reference numerosity and the other contained one of 13 target numerosities: $n_t \in \{16, 19, 23, 28, 34, 41, 50, 61, 74, 90, 109, 133, 162\}$.

2.3. Procedure

Observers were encouraged to maintain fixation throughout adaptation and test phases. Observers judged which of the two bottom clouds appeared more different to the reference numerosity contained in each upper quadrant. They were instructed that "Although it may seem otherwise, three of the quadrants will contain the same number of dots. The odd-one-out will be one of the lower quadrants; it may have more dots or fewer dots."³

Each trial began with a 5-s adaptation period (reduced to 1 s when "adaptation clouds" contained 0 dots), followed by the test display, which was presented for 0.6 s (Fig. 1). Observers used the mouse to click anywhere in the quadrant containing the odd-one-out. Trials were blocked by adaptation numerosity, with reference and target values randomly interleaved within blocks. Observers completed either 15 (KZC, JCB, & JM), 18 (DV), 21 (MJM) or 42 (JAS) trials with each of 72 combinations of adapting, reference, and target numerosities. (Eight of

² Earlier reports of bi-directional size adaptation can be explained by effects of contour repulsion. The mechanism proposed by Pooremaeli, Arrighi, Biagi, and Morrone (2013) is indeed based on "inward" and "outward" shifts of V1's responses to stimulus contours, rather than size per se. The aftereffects reported by Yousif and Clarke (2024) similarly may have been based on contour repulsion.

³ Not reported here are the results of a pilot experiment, in which observers were asked to decide which of the lower dot clouds had the numerosity less similar to that in the upper clouds. Naïve observers produced extremely large JNDs in that experiment, suggesting its task demanded too much effort. Instructions couched in terms of an odd-one-out may have been less daunting.

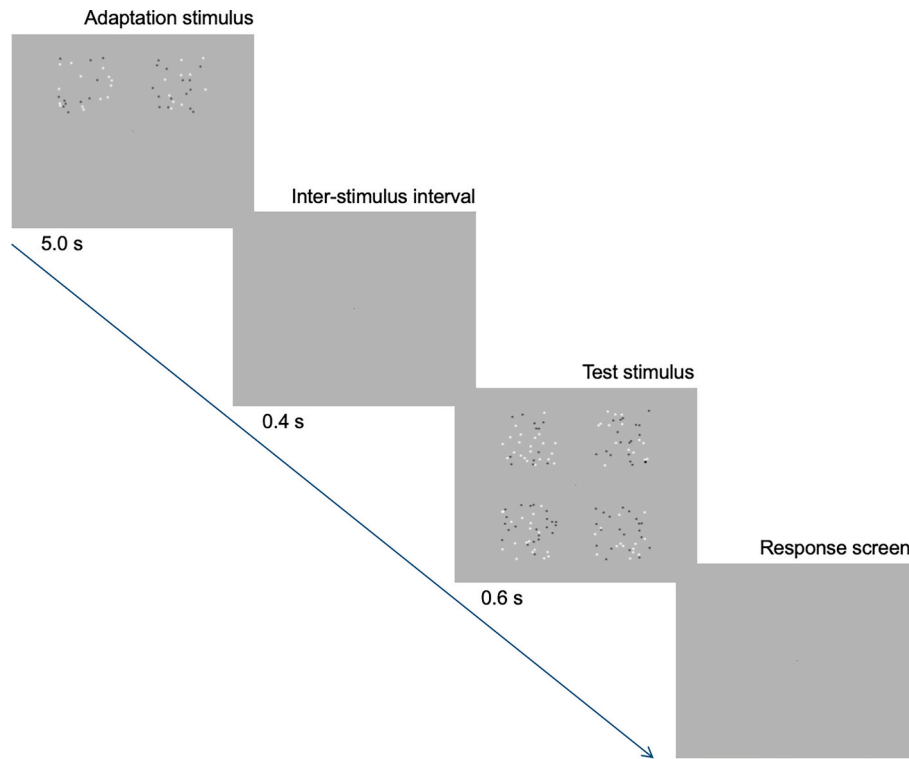


Fig. 1. Stimulus sequence for the task.

the 13 target numerosities were used for each combination of adapting and reference numerosity. These excluded the 4 largest when the reference was smallest, the 4 smallest when the reference was largest, and the 2 largest and 2 smallest when the reference numerosity was 50. Also excluded was the target numerosity equal to the reference numerosity.)

Note that the stimulus geometry (12° square dot clouds, centred 10° from fixation), adaptation duration, and one particular combination of adaptation and reference numerosities (25 and 50, respectively) were recently considered optimal for producing reverse adaptation (R. Arrighi, personal communication, Apr. 13, 2024).

A folder containing MATLAB code for running the experiment plus a Mathematica notebook with all data and analyses is available at <http://www.staff.city.ac.uk/~solomon/NumerosityAdaptation.zip>.

2.4. Analysis

Psychophysical response data were analysed using signal-detection theory (SDT; Green & Swets, 1966). This framework assumes that the signal elicited by each lower quadrant is normally and independently distributed around an intensity that is proportional to its log numerosity. Thus, the elicited signals are $R \sim \mathcal{N}(\log n_r, \sigma^2/2)$ and $T \sim \mathcal{N}(\log n_t, \sigma^2/2)$. Model observers select the target's quadrant with probability $1 - \lambda$ if and only if $|R - (\log n_r - \mu)| < |T - (\log n_t - \mu)|$. Note that λ defines the lapse (or “finger error”) rate, σ can be considered the JND, $-\mu$ can be considered the bias, and $n_r 10^{-\mu}$ can be considered the point of subjective equality (PSE). This model degenerates into the ideal observer in the limit, as σ approaches 0 and $\mu = \lambda = 0$.

While a dependence of the lapse rate on the adapting numerosity is plausible, a dependence on the reference numerosity is not, given that the reference value was randomly sampled on each trial. For computational convenience, we decided to fix the lapse rate at a single value for all of the 9 combinations of adapting and reference numerosity. This value was determined separately for each observer by averaging together the maximum-likelihood estimates from separate fits to the

data from each of the 9 combinations. Estimates ranged from 0.002 (for JAS) to 0.087 (for JM).

Having fixed the lapse rate, the data from each combination of adapting and reference numerosities were fit twice: once allowing the remaining two parameters (μ and σ) to vary across the 9 combinations of adaptor and reference, and again after eliminating bias by fixing $\mu = 0$. Nonparametric bootstrap resampling (Efron, 1987) was employed to calculate 95% (BC α) confidence intervals for each of the parameter estimates (μ and σ), as well as their ratio (μ/σ), which has been considered a measure of conspicuousness in units of JND (Ismail et al., 2016).

Note that each 2-parameter (μ and σ) fit is guaranteed to have a likelihood greater than or equal to that of the corresponding 1-parameter (σ) fit. An even greater likelihood (specifically, a likelihood of 1) is guaranteed for a model containing one free parameter for each combination of reference and target numerosities. Since there were eight such combinations, the Akaike Information Criterion (AIC) for this “saturated” model is -16 . Consequently, we consider any fit having an AIC > -16 to be a good fit.⁴ Fits that did and did not satisfy this criterion are noted along with results from individual observers in the Appendix.

3. Results

Of the 18 (6 observers $\times$ 3 reference numerosities) psychometric functions obtained with 100-dot adapting stimuli, 13 of them were satisfactorily fit by the 2-parameter SDT model (see Fig. 2a–c for examples), whereas only 2 of them were satisfactorily fit by the “bias-free” 1-parameter model (see Fig. 2d–f). In all 18 cases, the bias was downward, meaning that responses were consistent with the upper (adapted) test quadrants appearing to have fewer dots than the reference cloud in the lower half of the display.

Of the 18 psychometric functions obtained with the 0-dot adapting

⁴ This is a somewhat arbitrary criterion. Consequently, we did not bother adjusting it for the fact that the saturated model's parameters were (arguably unfairly) allowed to exceed $1 - \lambda$.

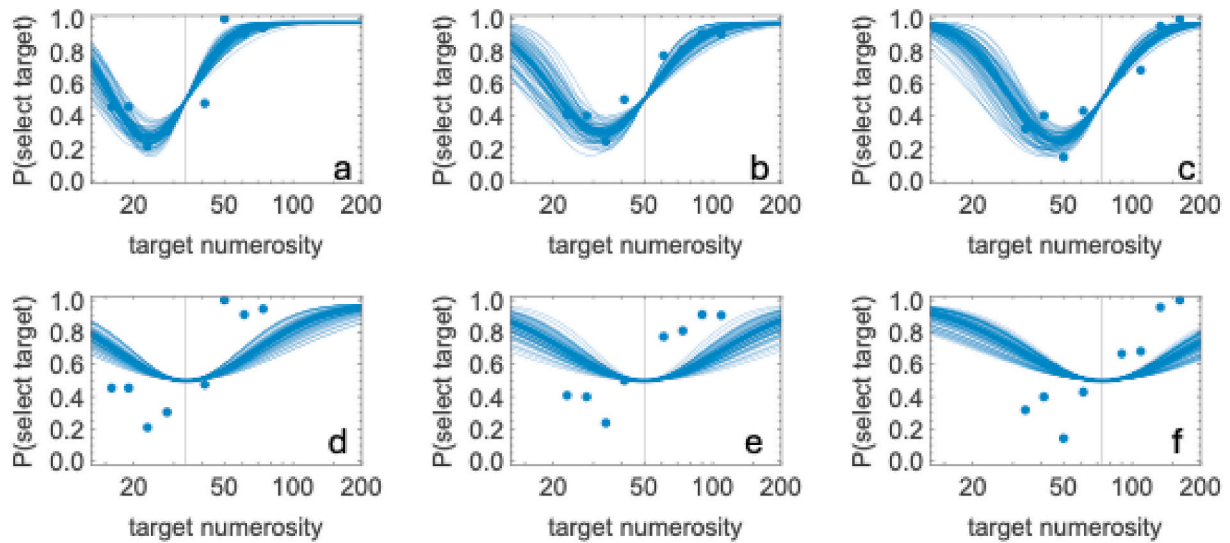


Fig. 2. Psychometric functions for a typical observer's target selection after adapting to dense (100-dot) stimuli and testing with reference stimuli having numerosities of (a, d) 34, (b, e) 50, and (c, f) 74. For this observer (MJM), each data point represents 21 trials. Note that panels a and d show the same data, as do panels b and e, and panels c and f. Thick curves in panels a–c illustrate the best-fitting, 2-parameter model from signal-detection theory. Each panel also contains 100 thin curves representing the bootstrap distribution of fits. Model comparison with the Akaike Information Criterion indicates that a saturated model having one free parameter for each data point can achieve a significantly better fit only to the data in panel a, not the data in panels b or c. In each panel, the minima of all curves are achieved with target numerosities smaller than the reference numerosity illustrated by the thin vertical line. This negative bias indicates repulsion downward: responses were consistent with the upper (adapted) test quadrants appearing to have fewer dots than the reference cloud in the lower half of the display. Curves in panels d–f illustrate fits of the 1-parameter model, in which bias is fixed at 0.

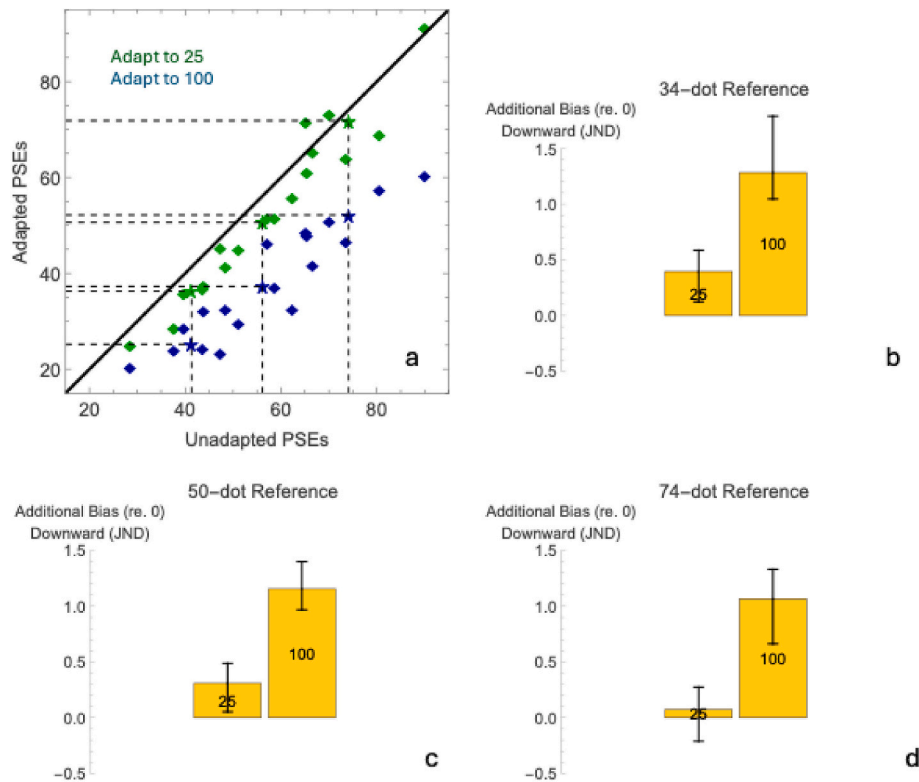


Fig. 3. No evidence of bidirectional adaptation. Panel a illustrates all (9 conditions $\times$ 6 observers) 45 estimates of PSE. Dashed lines indicate group mean values, both for the ‘unadapted’ condition, in which the adapting stimuli contained 0 dots, as well as the conditions in which the adapting dot clouds contained 25 dots (green stars) and 100 dots (blue stars). Points falling below the equality line indicate additional biases downward (i.e. when compared with the unadapted PSEs). In panels b–d, each amber bar illustrates a mean difference between maximum-likelihood estimates of conspicuousness $\bar{c} \equiv (\mu_i/\sigma_i)_i$ across observers ($i = 1, 2, \dots, 6$) in two conditions: one in which the adapting stimuli contained dot clouds and one in which the adapting stimuli contained 0 dots. The number of dots in each adapting dot cloud is indicated within each amber bar. Each error bar contains the interval $(\bar{c} - \sqrt{\sum_i \delta_{i1}^2}/6, \bar{c} + \sqrt{\sum_i \delta_{i2}^2}/6)$, where δ_{i1} and δ_{i2} denote the differences between the maximum likelihood of conspicuousness for observer i and the minimum and maximum (respectively) of the corresponding 95% confidence interval. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

stimuli, 16 were satisfactorily fit by the 2-parameter model and 10 were satisfactorily fit with the 1-parameter model. Like the biases inferred from trials with 100-dot adapting stimuli, on average, the biases inferred from these “unadapted” trials were downward. To minimize any non-perceptual component of the former biases, we quantify the aftereffect of adapting to dense patterns by the difference between its conspicuousness and that of adapting to 0-dot patterns. A resumé of these differences is illustrated for the three reference numerosities in Fig. 3.

Of the 18 psychometric functions obtained with the 25-dot adapting stimuli, 13 were satisfactorily fit by the 2-parameter model and 6 were satisfactorily fit with the 1-parameter model. Like the biases inferred from trials with 100-dot adapting stimuli, on average, these biases were downward, and of greater magnitude than the biases inferred from trials without adapting clouds (see Fig. 3). Thus, our data certainly contain no compelling evidence for repulsion upward (i.e., ‘reverse adaptation’). On the other hand, we did find compelling evidence for repulsion downward.

The comparison-of-comparisons task has relatively low sensitivity in the sense that its data suggest relatively large JNDs (mean = 0.17, SD = 0.04; the mean corresponds to a Weber fraction of $-1 + 10^{0.17} = 0.49$).⁵ One consequence of this low sensitivity is that individual estimates of bias are relatively imprecise. This imprecision is manifest in the wide error bars of Fig. A1. Nonetheless, despite this imprecision, our data allow us to reject the possibility of reverse adaptation (i.e. an upward net bias, after adapting to 25-dot clouds) in the 34-dot and 50-dot reference stimuli with 95% confidence at the group level. This confidence has been illustrated with error bars in Fig. 3. Note that our confidence against reverse adaptation does not extend to our results with 74-dot reference stimuli. However, as suggested by the error bars in Fig. 3d, we can be 95% confident that any such reverse adaptation in those stimuli must be small, having a conspicuousness less than 0.25 JNDs.

Our Fig. 3 suggests similar repulsions downward from 100 dots, when those repulsions are quantified in terms of conspicuousness. When quantified in terms of log numerosity, the downward repulsion scales with the ratio between adaptor and reference numerosities (Fig. 4, amber symbols). That scaling may even extend to the downward repulsions from 25-dot adaptors (Fig. 4, blue symbols).

4. Discussion

We obtained compelling evidence for unidirectional aftereffects of numerosity adaptation. Across all conditions, adaptation consistently reduced perceived numerosity rather than producing bidirectional shifts. This challenges interpretations of bidirectionality reported in earlier work, which may reflect intrusion of non-perceptual biases, the confounds that the comparison-of-comparisons paradigm was designed to minimize. By eliminating these biases, our findings clarify that the dominant effect of numerosity adaptation is a downward shift.

Note that our results are consistent with those reported by Burr and Ross (2008), in the sense that we found a monotonic relationship between the average (across observers) downward bias and the ratio between adapting and adapted numerosities (see Fig. 4). The critical difference between our results seems to be the fact that none of our average downward biases were negative. In other words, none of our average biases were upwards.

Importantly, Burr (2025) suggests that some failures to find reverse adaptation (e.g. Yousif et al., 2024) might stem from using very high numerosities (160–240 dots), which fall into the density regime rather than the numerosity regime (Anobile, Cicchini, & Burr, 2014, 2016). Our stimuli (adaptors: 25, 100 dots; references: 34, 50, 74) sit within the numerosity range, so the consistent downward bias we observed reflects adaptation of a numerosity mechanism as defined by Burr and

colleagues.

A report (Benedetto, Anobile, Arrighi, Casavecchia, & Burr, 2026) published after our work was first submitted indicates a rightward shift of 0.9 dots in the aggregate psychometric function mapping test numerosity to the probability with which that test was judged more numerous than a 12-dot reference stimulus appearing in the same portion of the visual field as a 6-dot adapting stimulus. Importantly, this rightward shift of PSE was accompanied by a rightward shift in the functions mapping test numerosity to average confidence rating and average response time, suggesting that this aftereffect has a truly perceptual basis, rather than a decisional bias (Maldonado Moscoso, Cicchini, Arrighi, & Burr, 2020; Gallagher, Suddendorf, & Arnold, 2021). Our Fig. 3a has been formatted in the style of their Fig. 3a to facilitate an easy comparison of PSE estimates.

Although our results are inconsistent with 25-dot adaptors repelling the perception of more numerous dot clouds, it remains a logical possibility that the comparison-of-comparisons paradigm would produce evidence for repulsion upwards from 6-dot adaptors. The technique of using minimum confidence as a surrogate for perceptual bias holds promise. It should be noted, however, that confidence ratings are not free from non-perceptual sources of bias. Indeed, one study (Locke, Gaffin-Cahn, Hosseinizadeh, Mamassian, & Landy, 2020) found a group of observers whose confidence ratings shifted with the reward structure (payoff matrix) of their perceptual task.

Holding arguably even more promise is the technique of using choice reaction time to disentangle perceptual sources of bias from non-perceptual sources. The diffusion model (e.g. Ratcliff & Rouder, 1998) is a popular framework for understanding choice reaction time. Within this model, bias can be incorporated in several ways, including different drift rates for adapted and unadapted stimuli and/or a starting point for diffusion that is uncentred between response boundaries. As yet, it remains unclear which (if either) of these features would be most appropriate for perceptual (and/or non-perceptual) sources of bias. Theoretical work may prove necessary to sort this out. Prior to that, a comparison with the data from Benedetto et al. (2026) seems premature.

Aftereffects of adaptation are often understood to reflect gain-control processes, which relieve repeatedly stimulated mechanisms from having to respond with undiminished vigour. The mechanisms responsible for the aftereffects reported in this paper may perform a variety of computations. For example, their output (the eponymous signal of SDT) may vary monotonically with contrast energy at fine spatial scales, such as the texture processor proposed by Morgan, Raphael, Tibber, and Dakin (2014). More complicated computations of texture density have also been proposed (e.g. Dakin et al., 2011).

Regardless how they are computed, texture density and numerosity are regional statistics. Any mechanism responsible for computing these statistics must have a receptive field with an extent greater than a few minutes of arc. This requirement seems to exclude retinal neurons. It does not exclude neurons in primary visual cortex, where many visual neurons respond better to moderate levels of contrast energy than they do to low levels of contrast energy. However, relatively few (< 4% in V1 and V2; Peirce, 2007) of these neurons have (“supersaturating”) response functions with a degree of nonmonotonicity that seems required for shifting population responses toward greater levels of contrast energy.

Recent high-field functional magnetic resonance imaging evidence shows that numerosity adaptation selectively suppresses early visual cortex responses (V1–V3, hV4, LO1–LO2, V3A/B), with suppression effects growing progressively stronger along the visual hierarchy (Zhang et al., 2025). These findings support our conclusion that perceptual numerosity underestimation arises from adaptation-driven gain reduction in early, monotonic visual responses rather than tuned mechanisms. Zhang et al. reported that parietally tuned neural numerosity preferences are also affected by adaptation, with increases in perceived numerosity after low numerosity adaptation being far weaker than decreases after high numerosity adaptation (Aulet & Lorenzo, 2023; Yousif

⁵ JNDs in this range are not unprecedented (e.g. Morgan et al., 2014).

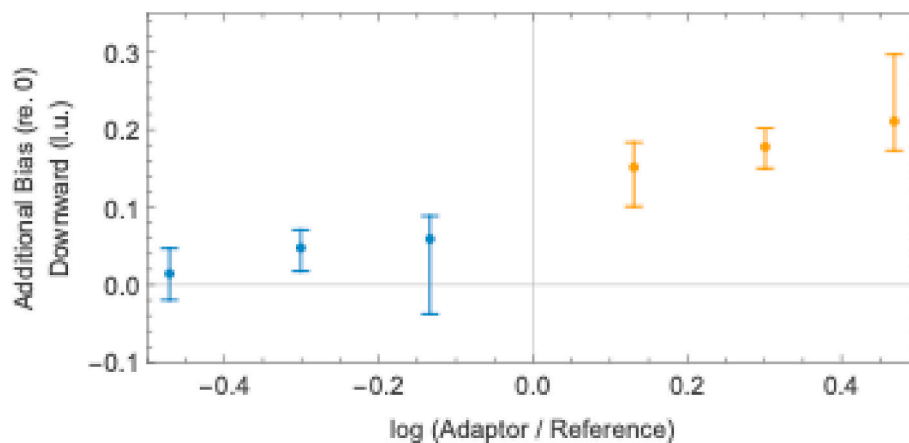


Fig. 4. Mean biases quantified in terms of log numerosity. Amber symbols represent net downward biases, after adapting to 100-dot clouds. Blue symbols represent net downward biases, after adapting to 25-dot clouds. The formula for error bars is identical to that of Fig. 3, with the following re-definition: $\bar{c} \equiv \langle \mu_i \rangle_i$, which excludes the JND σ_i . (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

& Clarke, 2024). Although our data do not show this effect, we agree it remains a possible contribution, with the asymmetry likely reflecting additional adaptation at the monotonic response stage for high numerosity displays.

Yousif et al. (2024) did not appeal to gain control for their explanation of aftereffects. Instead, they appeal to Block (2022) and his critics, Phillips and Firestone (2023), who seem to consider perception a form of “news” about changes in an organism’s environment. In this view, previously encountered positions become “old news,” so judgments emphasize novelty relative to recent input. This is similar to Morgan and Solomon’s (2019, 2020, 2021) local novelty account, where adaptation enhances the salience of changed and previously absent items. These items appear to have a property that is not shared by unchanged and previously present items. Locating a single changed item proved to be much easier than locating a single unchanged item. Morgan and Solomon (2020) demonstrated that relative novelty was neither greater apparent contrast, earlier apparent onset, nor greater apparent speed, although the changed item might have some of these properties also. Contrary to texture density, news and relative novelty might be computed by neurons with very small receptive fields. Dots presented in or very near to previously presented dots would not be expected to elicit

news or relative novelty signals. Consequently, adaptation to any dot cloud would be expected to reduce the number of news or novelty signals elicited by dot clouds subsequently presented to the same part of the visual field, and this attenuation would be expected to scale with the numerosity or density of the adapting dot cloud.

CRediT authorship contribution statement

Kristina Zeljić: Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Investigation. **Michael J. Morgan:** Writing – review & editing, Investigation, Conceptualization. **Joshua A. Solomon:** Writing – review & editing, Validation, Supervision, Software, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Appendix

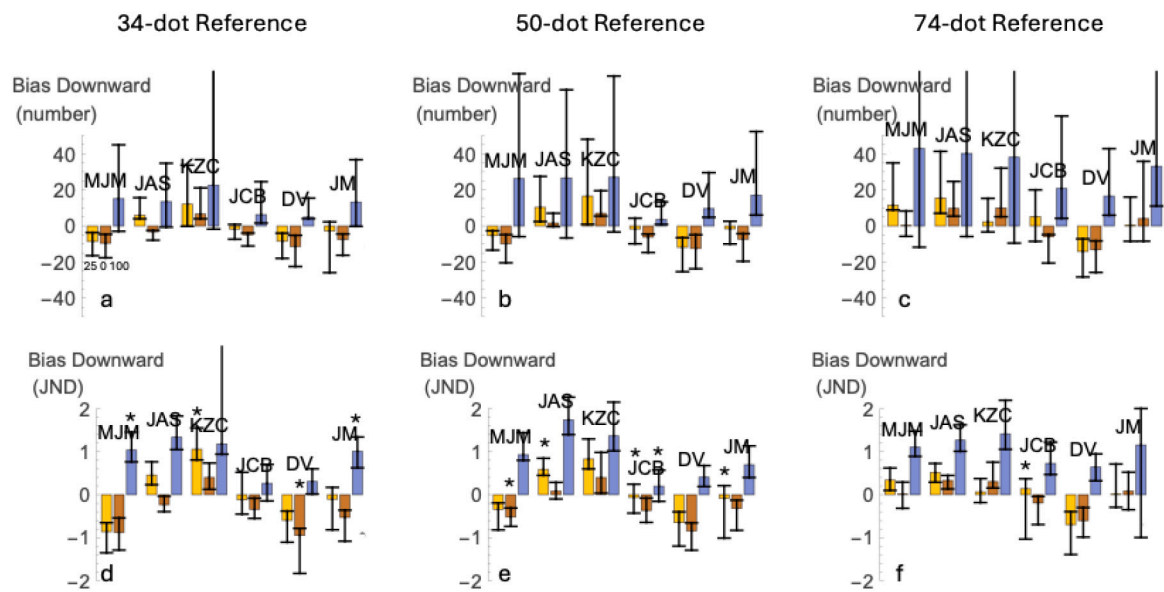


Fig. A1. Estimates of bias for every combination of observer, adaptor, and reference numerosity. Bar colour corresponds to the number of dots in each adapting quadrant: amber, 25; brown, 0; blue, 100 (see panel a). Bar height represents maximum-likelihood fit of the 2-parameter (bias, JND) SDT model. Error bars contain BCa Bootstrapped 95% confidence intervals. In panels a–c, bias is quantified in terms of number. In panels d–f, it's quantified as a proportion of the just-noticeable difference, a.k.a. conspicuousness. Asterisks (there are 12 of them) indicate fits with lower AIC than the 8-parameter saturated model. Bias downward with 0-dot adaptors was smaller than bias downward with 100-dot adaptors in all 18 cases (6 observers $\times$ 3 references), with an average conspicuousness of 1.17 JNDs. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

References

- Aagten-Murphy, D., & Burr, D. (2016). Adaptation to numerosity requires only brief exposures, and is determined by number of events, not exposure duration. *Journal of Vision*, 16(10), 22.
- Anobile, G., Cicchini, G. M., & Burr, D. C. (2014). Separate mechanisms for perception of numerosity and density. *Psychological Science*, 25(1), 265–270.
- Anobile, G., Cicchini, G. M., & Burr, D. C. (2016). Number as a primary perceptual attribute: A review. *Perception*, 45(1–2), 5–31.
- Aulet, L. S., & Lourenco, S. F. (2023). Visual adaptation reveals multichannel coding for numerosity. *Frontiers in Psychology*, 14, 1125925.
- Benedetto, A., Anobile, G., Arrighi, R., Casavecchia, E., & Burr, D. C. (2026). Adaptation acts directly on the sensory representation of numerosity. *Scientific Reports*, 16, 4892.
- Blakemore, C., & Sutton, P. (1969). Size adaptation: A new aftereffect. *Science*, 166, 245–247.
- Block, N. (2022). *The border between seeing and thinking*. Oxford University Press.
- Burr, D., Anobile, G., & Arrighi, R. (2025). Number adaptation: Reply. *Cognition*, 254, Article 105870.
- Burr, D., & Ross, J. (2008). A visual sense of number. *Current Biology*, 18, 425–428.
- Dakin, S. C., Tibber, M. S., Greenwood, J. A., Kingdom, F. A. A., & Morgan, M. J. (2011). A common visual metric for approximate number and density. *Proceedings of the National Academy of Sciences*, 108, 19552–19557.
- Durgin, F. H. (1995). Texture density adaptation and the perceived numerosity and distribution of texture. *Journal of Experimental Psychology: Human Perception and Performance*, 21(1), 149.
- Durgin, F. J., & Martinez, Z. (2024). Relative numerosity is constructed from size and density information: Evidence from adaptation. *Journal of Vision*, 24(7), 4.
- Efron, B. (1987). Better bootstrap confidence intervals. *Journal of the American Statistical Association*, 82, 171–185.
- Gallagher, R. M., Suddendorf, T., & Arnold, D. H. (2021). The implied motion aftereffect changes decisions, but not confidence. *Attention, Perception & Psychophysics*, 83, 3047–3055.
- Georgeson, M. A. (1985). The effect of spatial adaptation on perceived contrast. *Spatial Vision*, 1, 103–112.
- Graham, N. V. S. (1989). *Visual pattern analyzers*. Oxford University Press.
- Green, D. M., & Swets, J. A. (1966). *Signal detection theory and psychophysics*. New York: Wiley.
- Ismail, A. M. H., Solomon, J. A., Hansard, M., & Mareschal, I. (2016). A tilt after-effect for images of buildings: Evidence of selectivity for the orientation of everyday scenes. *Royal Society Open Science*, 3, Article 160551.
- Levinson, E., & Sekuler, R. (1976). Adaptation alters perceived direction of motion. *Vision Research*, 16, 779–781.
- Locke, S. M., Gaffin-Cahn, E., Hosseinzadeh, N., Mamassian, P., & Landy, M. S. (2020). Priors and payoffs in confidence judgments. *Attention, Perception, & Psychophysics*, 82, 3158–3175.
- Maldonado Moscoso, P. A., Cicchini, G. M., Arrighi, R., & Burr, D. C. (2020). Adaptation to hand-tapping affects sensory processing of numerosity directly: Evidence from reaction times and confidence. *Proc. Roy. Soc. B*, 287, 20200801.
- Meese, T. S., & Baker, D. H. (2023). Object image size is a fundamental coding dimension in human. *Neuroscience*, 514, 79–91.
- Mollon, J. D. (1974). After-effects and the brain. *New Scientist*, 61, 479–482.
- Morgan, M. J., Grant, S., Melmoth, D., & Solomon, J. A. (2015). Tilted frames of reference have similar effects on the perception of gravitational vertical and the planning of vertical saccadic eye movements. *Experimental Brain Research*, 233, 2115–2125.
- Morgan, M. J., Melmoth, D., & Solomon, J. A. (2013). Linking hypotheses underlying class A and class B methods. *Visual Neuroscience*, 30, 197–206.
- Morgan, M. J., Raphael, S., Tibber, M. S., & Dakin, S. C. (2014). A texture-processing model of the 'visual sense of number'. *Proceedings of the Royal Society B: Biological Sciences*, 281(1790), 20141137.
- Morgan, M. J., Schreiber, K., & Solomon, J. A. (2016). Low-level mediation of directionally specific motion aftereffects: Motion perception is not necessary. *Attention, Perception, & Psychophysics*, 78, 2621–2632.
- Morgan, M. J., & Solomon, J. A. (2019). Attention and the motion aftereffect. *Quarterly Journal of Experimental Psychology*, 72, 2848–2964.
- Morgan, M. J., & Solomon, J. A. (2020). A visual search asymmetry for novelty in the visual field based on sensory adaptation. *Attention, Perception & Psychophysics*, 82, 938–943.
- Morgan, M. J., & Solomon, J. A. (2021). Adaptation facilitates change detection even when attention is directed elsewhere. *Attention, Perception & Psychophysics*, 83, 97–102.
- Paul, J. M., van Ackooij, M., Ten Cate, T. C., & Harvey, B. M. (2022). Numerosity tuning in human association cortices and local image contrast representations in early visual cortex. *Nature Communications*, 13(1), 1340.
- Peirce, J. W. (2007). The potential importance of saturating and supersaturating contrast response functions in visual cortex. *Journal of Vision*, 7(6), 13.
- Phillips, I., & Firestone, C. (2023). Visual adaptation and the purpose of perception. *Analysis*, 83, 555–575.
- Pooresmaeili, A., Arrighi, R., Biagi, L., & Morrone, M. C. (2013). Blood oxygen level-dependent activation of the primary visual cortex predicts size adaptation illusion. *Journal of Neuroscience*, 33, 15999–16008.
- Ratcliff, R., & Rouder, J. N. (1998). Modeling response times for two-choice decisions. *Psychological Science*, 9, 347–356.
- Ross, J., & Burr, D. C. (2010). Vision senses number directly. *Journal of vision*, 10(2), 10–10.
- Stevens, S. S. (1957). On the psychophysical law. *Psychological Review*, 64(3), 153.
- Suzuki, S. (2005). High-level pattern coding revealed by brief shape aftereffects. In C. Clifford, & G. Rhodes (Eds.), *Vol. 2. Fitting the Mind to the World: Adaptation and After effects in High-Level Vision. Advances in visual cognition series* (pp. 138–172). Oxford, UK: Oxford University Press.

- Thompson, P. G. (1981). Velocity [sic] after-effects: The effects of adaptation to moving stimuli on the perception of subsequently seen moving stimuli. *Vision Research*, 21, 337–345.
- Tolhurst, D. J., & Thompson, P. G. (1975). Orientation illusions and aftereffects: Inhibition between channels. *Vision Research*, 15, 967–972.
- Yarrow, K., Martin, S. E., Di Costa, S., Solomon, J. A., & Arnold, D. H. (2016). A roving dual-presentation simultaneity judgment task to estimate the point of subjective simultaneity. *Frontiers in Psychology*, 7(416), 1–19.
- Yousif, S. R., & Clarke, S. (2024). Size adaptation: Do you know it when you see it? *Attention, Perception, & Psychophysics*, 86, 1923–1937.
- Yousif, S. R., Clarke, S., & Brannon, E. M. (2024). Number adaptation: A critical look. *Cognition*, 249, Article 105813.
- Zhang, L., Hendrikx, E., Wang, Y., Gayet, S., Dumoulin, S. O., & Harvey, B. M. (2025). Numerosity adaptation suppresses early visual responses. *Communications Biology*, 8 (1), 1655.