Undercounting features and missing features: evidence for a high-level deficit in strabismic amblyopia

Vineeta Sharma[1,2], Dennis M. Levi[1] and Stanley A. Klein[3]

[1] University of Houston, College of Optometry, 4901 Calhoun Blvd., Houston, Texas 77204-6052, USA

[2] Current address: Alcon Laboratories, 6201 South Freeway, Fort Worth, Texas 76134-2099, USA

[3] University of California at Berkeley, School of Optometry, Berkeley, California 94720-2020, USA

Correspondence should be addressed to D.M.L. (dlevi@uh.edu)

Abnormal visual development in strabismic amblyopia drastically affects visual perception and properties of neurons in primary visual cortex (V1). To test the notion that amblyopia also has consequences for higher visual areas, we asked humans with amblyopia to count briefly presented features. Using the amblyopic eye, strabismic amblyopes counted inaccurately, markedly underestimating the number of features. This inaccuracy was not due to low-level considerations (blur, visibility, crowding, undersampling or topographical jitter), as they also underestimated the number of features missing from a uniform grid. Rather, counting deficits in strabismic amblyopes reflected a higher-level limitation in the number of features the amblyopic visual system can individuate.

Abnormal visual experience during early visual development results in dramatic deficits in the properties of neurons in cortical area V1 (refs. 1–3) and in visual perception[4,5]. For example, if one eye is turned (strabismus) during early childhood, the resulting amblyopia (from the Greek *amblos*, blunt, and *opia*, vision) leads to a loss of visual acuity, contrast sensitivity and position acuity[5–7]. It is thought that the main site of the abnormal developmental changes in amblyopia is V1, where there is a dramatic loss of binocular neurons, and neurons driven by the amblyopic eye have lower contrast sensitivity and may sample the image sparsely[1–3].

However, strabismic amblyopes show losses that may reflect processing at stages beyond V1. For example, the physiological losses in V1 underestimate the behavioral losses in monkeys with amblyopia[3]. Moreover, strabismic amblyopes require more samples than normals for position discrimination[8] and for pattern perception[9], even when the samples are highly visible, suggesting that the samples are not used efficiently by the amblyopic visual system.

To use each sample, the visual system must attend to and individuate each sample[10,11]. Here, by having observers count the number of features in a brief presentation, we tested the hypothesis that strabismic amblyopes are unable to attend to and individuate multiple stimulus samples.

RESULTS
Experiment 1: counting features
We asked observers to count highly visible, resolvable features (small Gaussian or Gabor patches) that varied in number (**Fig. 1a**). The non-amblyopic eyes of amblyopes showed near-perfect performance (percentage of correct responses) for up to four or five patches (**Fig. 2a**, open symbols), consistent with earlier studies in normals[12,13]. Performance of amblyopic observers

was dramatically worse with the amblyopic eye (**Fig. 2a**, filled symbols). We obtained a counting 'threshold' by fitting a function to a plot of the percentage correct. Thresholds for amblyopic eyes (**Fig. 2b**, ordinate) of the seven strabismic amblyopes were much lower than those for the fellow non-amblyopic eyes (abscissa). Compared with the average counting thresholds of normals (~7.3), the average threshold of the non-amblyopic eyes was slightly lower (~5.6) and that of the amblyopic eyes was three-fold lower (only ~2.2).

If the reduced performance of the amblyopic eyes were due to a limit in the amount of information that the amblyopic visual system can attend to and individuate, then one might expect that amblyopes would systematically underestimate the number of features. This is precisely what we found. Compared to normals (**Fig. 3a**), the amblyopic observers often slightly overestimated the number of patches presented to their amblyopic eye for $N < 5$ and greatly underestimated the number of patches presented to their amblyopic eye for $N > 5$ (**Fig. 3b–d**). At high values of N, the amblyopic eyes underestimated the number by approximately half.

One possible explanation for the errors in counting by the amblyopic eyes is that the stimuli presented to the amblyopic eye had low visibility[14–16]. To test this, we measured contrast detection thresholds of each eye for single patches and equated the visibility of the stimuli (in multiples of the contrast detection threshold) for the two eyes. Lowering the contrast in the non-amblyopic eye (to match the stimulus visibility of the amblyopic eye) did not result in an underestimate of the number of samples by the non-amblyopic eye (**Fig. 3c**). Thus we conclude that low visibility could not explain the underestimation.

Other control experiments showed that the underestimate was not a consequence of temporal integration of the stimulus elements with those of the mask or of the brief duration of the
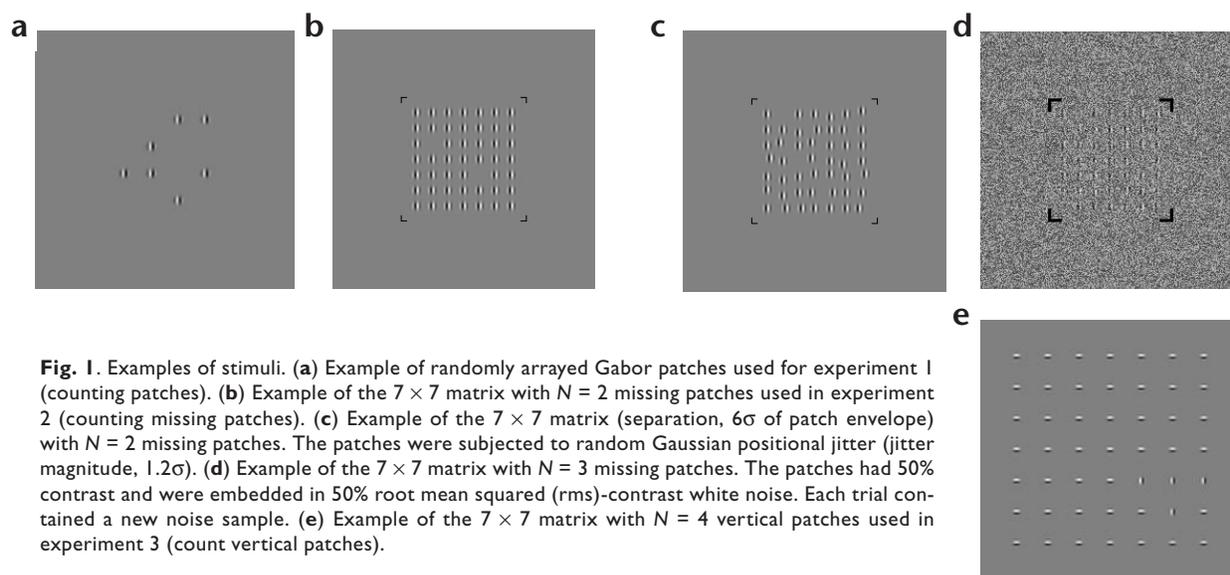
Fig. 1. Examples of stimuli. (**a**) Example of randomly arrayed Gabor patches used for experiment 1 (counting patches). (**b**) Example of the 7 × 7 matrix with *N* = 2 missing patches used in experiment 2 (counting missing patches). (**c**) Example of the 7 × 7 matrix (separation, 6σ of patch envelope) with *N* = 2 missing patches. The patches were subjected to random Gaussian positional jitter (jitter magnitude, 1.2σ). (**d**) Example of the 7 × 7 matrix with *N* = 3 missing patches. The patches had 50% contrast and were embedded in 50% root mean squared (rms)-contrast white noise. Each trial contained a new noise sample. (**e**) Example of the 7 × 7 matrix with *N* = 4 vertical patches used in experiment 3 (count vertical patches).

stimulus presentation. Neither removing the mask nor increasing the stimulus duration (**Fig. 3d**) significantly altered the underestimates of number using the amblyopic eyes. These results imply that the counting errors in the amblyopic eyes were not due to temporal integration or abnormalities of temporal processing[17,18].

### Experiment 2: low-level versus high-level deficits

Why can't strabismic amblyopes count accurately? One possible explanation is that these errors were due to low-level abnormalities, such as undersampling of receptive fields in V1 (refs. 1, 7) or poor stimulus visibility, even though the individual patches were highly visible and resolvable. An alternative hypothesis is that the errors reflected a higher-level limitation. To test between these two hypotheses, we conducted an experiment in which we asked amblyopes to estimate the number of patches missing from a briefly presented uniform grid of forty-nine patches (7 × 7 grid of Gabor patches; **Fig. 1b**). A low-level explanation (such as undersampling or poor stimulus visibility) predicts that an amblyope would see fewer patches with the amblyopic eye and would there-

fore overestimate the number of missing patches. On the other hand, given that the missing patches are the features to be counted, a high-level limitation predicts that they would underestimate the number of missing patches.

Our results (**Fig. 4**) show that estimating the number of missing features is difficult—even normal observers were a little 'amblyopic' when counting missing features; that is, they underestimated when *N* was greater than four (**Fig. 4a**); however, strabismic amblyopes underestimated to a much greater degree with their amblyopic eyes (**Fig. 4b**). Thus, for example, when ten patches were missing, normal observers estimated six missing patches on average, but between two and four were estimated by amblyopes using amblyopic eyes. The underestimation was more or less independent of patch separation, so it was not a simple crowding effect. Moreover, it could not be mimicked using normal eyes either by lowering the stimulus contrast (and thus visibility) or by jittering the positions of the patches so that they did not form a uniform grid (**Figs. 1c** and **4a**). Thus our missing-patch experiments ruled out a number of potential low-level explanations (including undersampling, crowding and topographical jitter)[4,6,7].

Fig. 2. Experiment 1: counting patches. (**a**) The percentage of times observers reported the number of elements accurately is plotted as a function of the number of Gabor patches. Open symbols, non-amblyopic eye; filled symbols, amblyopic eye. Circles, triangles and squares represent data for Gabor carrier frequencies of 6, 10 and 14 cycles per degree, respectively. Note that observer DS's amblyopic eye has little or no loss of contrast sensitivity for isolated patches at the two lower spatial frequencies (filled circles and triangles). Each datum represents the mean of four to five blocks, and error bars represent ± s.e. Solid curves represent Weibull functions fit to the data. (**b**) Counting thresholds obtained from the Weibull fits for the amblyopic eyes (ordinate) are plot-

ted against the thresholds for the non-amblyopic eyes (abscissa) of all seven amblyopes for the Gaussian (solid diamonds) and Gabor (gray circles) stimuli. The counting thresholds of four normal observers are shown by the small open diamonds plotted on the diagonal.

articles
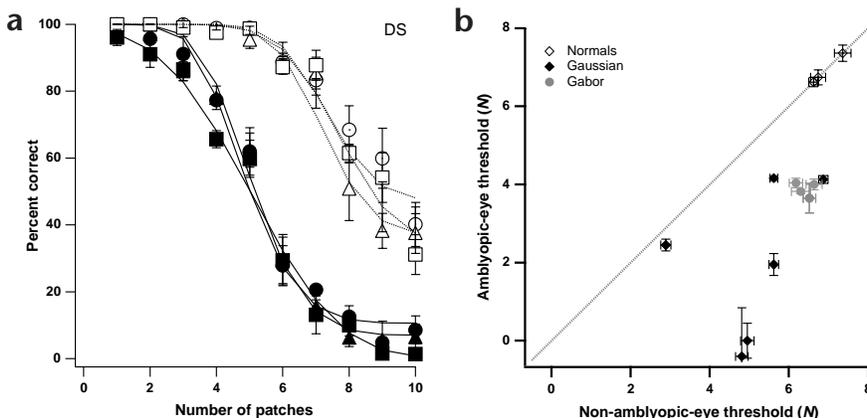
A simple model of cortical undersampling would result in missing whole features. However, some low-level losses, including retinal undersampling or increased noise, might result in a uniformly poorer representation of the display. In this case, observers might be unsure about which features were missing and, consequently, report only the missing patches of which they were certain, resulting in a severe underestimate. To test this possibility, we lowered the target contrast and added random noise to degrade the display (**Fig. 1d**). Degrading the display by lowering the contrast and adding noise in normal observers increased the error rate to levels comparable to those for amblyopes; however, unlike errors made using the amblyopic eyes, the errors were random, with no change in the mean estimates (**Fig. 4a**). Similarly, the jitter control also increased the error rate. However, large amounts of positional jitter (1.2σ) resulted in an overestimate of the number of missing features at $N < 4$ (**Fig. 4a**), because the large amount of jitter created apparent 'holes'. However, none of our control experiments in normal eyes resulted in the severe underestimates made by amblyopic eyes when $N > 4$.

It is well known that blindspots (including the physiological blindspot) are 'filled-in' so we are unaware of them. However, a 'filling-in' explanation of undercounting of missing patches in experiment 2 would have difficulty in accounting for the undercounting of patches in experiment 1. Therefore, we conclude that low-level explanations involving simple image degradations are unlikely to account for the underestimation of both features (experiment 1) and missing features (experiment 2).

Experiment 3: cueing the target location

Attention is often considered to be a resource that must be shifted, like a spotlight, or focused, like a zoom lens[19–21]. Our experiments suggested that strabismic amblyopes showed surprising deficits in counting that seemed to occur at a stage beyond the primary visual cortex. Perhaps there was a loss in counting because the amblyopic visual system was unable to

switch attention to the appropriate region of the visual display. One way to test attention switching is to use cueing. In normal vision, cueing the location of a target can improve performance. Therefore, in a third experiment, we tested whether amblyopes undercounted when the location of the target was cued. Specifically, we asked observers to estimate the number of test Gabors (with vertical carrier orientation) presented among distractor Gabors (with horizontal carrier orientation). The test and distractor Gabors were arranged in a 7×7 square array. One to four test Gabors (N) were presented in a random manner in one of five quadrants within the array (top left, top right, bottom right, bottom left and center; **Fig. 1e**). The observers were cued (see Methods) to the quadrant where the test Gabors would appear, with a 0.8 probability of the cue being correct. We also made measurements without cueing.

As in the previous experiments, amblyopes using their amblyopic eyes made large underestimates of the number of test patches presented among distractors (**Fig. 5**). Although the mean estimates for normal observers (and non-amblyopic eyes) were veridical, their performance was not error free when N was three or four (**Fig. 6**). For example, with $N = 4$, normal observers had error rates of approximately 9% and 20% for valid and invalid cues. (Uncued performance fell about midway between the two.) Whereas the non-amblyopic eyes often had higher error rates, and the amblyopic eyes' error rates were higher yet, we found a substantial benefit from cueing in both normal and amblyopic observers. The invalid cue increased the error rate (relative to the valid cue) on average by 8.5 ± 1.7% for the normal observers, 8.4 ± 1.2% for the non-amblyopic eyes of amblyopes and 7.6 ± 1.6% for the amblyopic eyes. This effect on the error rate was consistent with work suggesting that peripheral cues also have an additive effect in normal observers[22]. Thus, although there was consider-

Fig. 3. Number reported versus number of features for experiment 1. The average of the subjective estimates of the number seen is plotted as a function of the number of Gaussian or Gabor patches actually present. The dotted gray line (1:1) represents correct estimates. (**a**) Data for four normal observers. (**b**) Data for six amblyopic observers; open symbols represent the mean data for the non-amblyopic eyes, and filled symbols represent individual data for the amblyopic eyes. (**c**) Effect of visibility on the non-amblyopic eyes of observers RH (circles) and DS (triangles). Filled symbols, data for the amblyopic eye; open symbols, non-amblyopic eye when visibility (in contrast-threshold units) was equated to that for the amblyopic eye. (Stimulus contrasts for the non-amblyopic and amblyopic eyes were set at equal multiples of their respective detection thresholds.) (**d**) Effects of duration and eliminating the mask (0.2-s duration without mask, small symbols; 1-s duration, large symbols) for each eye of observers DS (circles) and AJ (triangles).
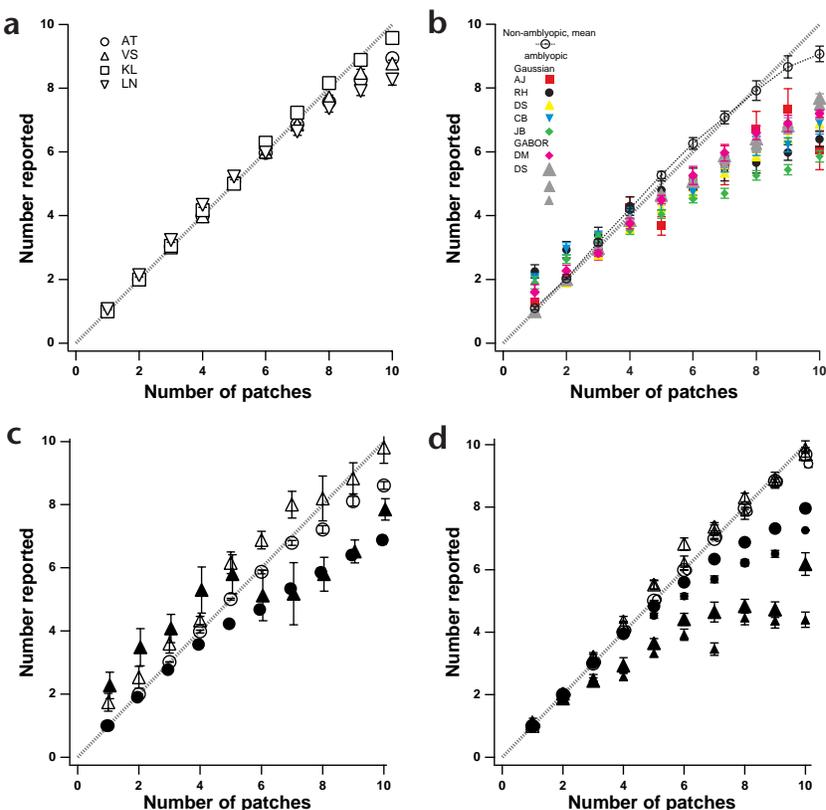
Fig. 4. Experiment 2: counting 'missing features'. The average of the subjective estimates of the number of missing patches is plotted as a function of the number of Gabor patches that were actually missing from the 7×7 array. (**a**) Gray circles show data for normal observers at several different separations. Red circles show the effects of 2-dimensional Gaussian jitter of patch envelope; small) or 1.2σ (large). Blue squares show results at lower contrast levels (small, 30%; large, 50%) than the standard (100%). Green diamonds show the effect of lowering the patch contrast to 50% and adding random noise with contrasts of 5%, 25% or 50% (small, medium or large green diamonds) to the display. (**b**) Data for 3 amblyopic observers (RH, DM and QM) at each of 3 separations (4σ, 6σ or 9σ, denoted by small, medium or large symbols, respectively). Open purple diamonds, mean data for the non-amblyopic eyes at each separation. Open gray circles, mean estimates of the normal observers.
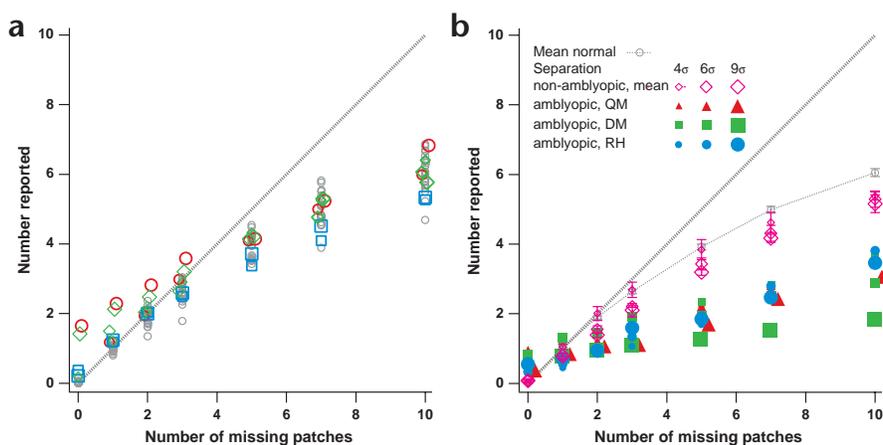
able individual variation, cueing was effective in modulating the error rates of normal and amblyopic eyes.

DISCUSSION

It has been known for over a century that normal observers can count up to four briefly presented items without error[12,13]. When the number of items exceeds four, normal observers make errors. Here we showed that strabismic amblyopes were substantially worse than normals at correctly estimating the number of fea-

tures. In particular, strabismic amblyopes markedly underestimated the number of features (experiment 1), missing features (experiment 2) and different features (experiment 3) with the amblyopic eye, even when cued to the target location. We argue that this inability to count features (or missing features) accurately was not due to the well established limitations of low-level processing in the amblyopic visual system[1–7], as our experiments allowed us to rule out factors such as feature visibility, crowding, positional jitter or abnormal temporal integration. Moreover, the use of band-limited Gabor patches reduced the likelihood that the stimuli were analyzed by large (low spatial frequency) filters in the early stages of processing in the amblyopic cortex[23] (in linear V1 filters).

The neural mechanisms involved in counting are not fully understood; however, when the number of features to be enumerated is small ($N < 5$) and briefly presented, rapid, error-free performance is achieved through a process known as subitizing, which is thought to be 'pre-attentive'. When the number of features to be enumerated is large ($N > 4$), performance is slow and subject to error[10,11] (but see also ref. 24). Neural imaging suggests that subitizing ($N = 1–4$) and counting ($N > 4$) may activate different brain regions[25]. Specifically, subitizing activates regions in the occipital extrastriate cortex, whereas counting activates a large number of regions, including regions of the parietal cortex thought to be involved in visual attention. Thus, individuation of $N > 4$ features seems to depend on the function of the higher visual pathways, in particular the parietal cortex[25].

When several features are presented together, perception of the spatial details of an individual element depends on the ability of the attentional mechanisms to isolate each element[11]. Indeed, there are reports that certain people with damage to the parietal cortex (for instance, Balint's syndrome) lack the ability to individuate objects and, as a consequence, are unable to estimate the number of spatial objects[26,27].
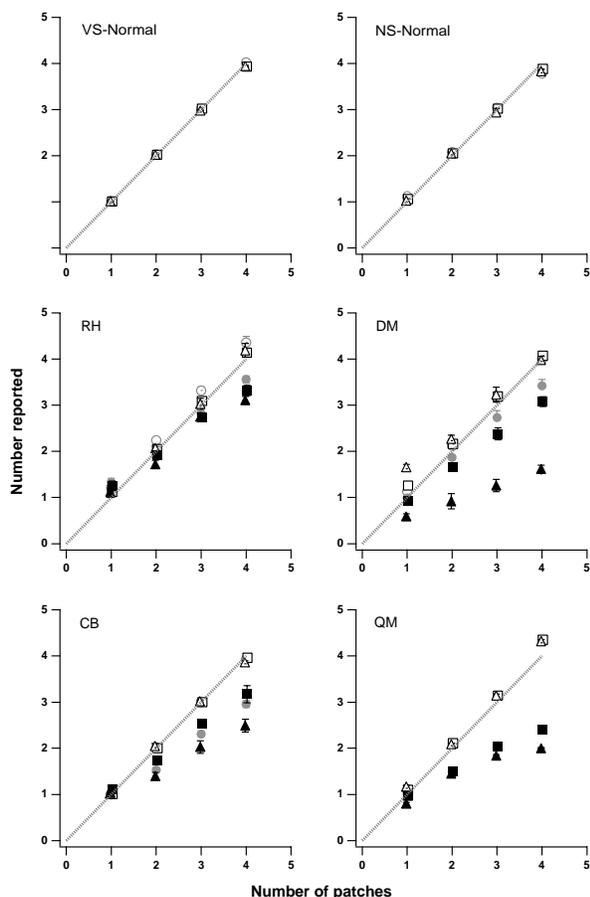
Fig. 5. Experiment 2: counting 'vertical features'. Each panel shows the mean subjective estimates of the number of vertical test Gabor patches plotted as a function of the number of vertical test patches among horizontal distractors. Squares and triangles, performance with valid and invalid cues, respectively. Circles, performance with no cueing. Top two panels are for two normal observers; others are for amblyopic observers (open symbols, non-amblyopic eye; filled symbols, amblyopic eye).
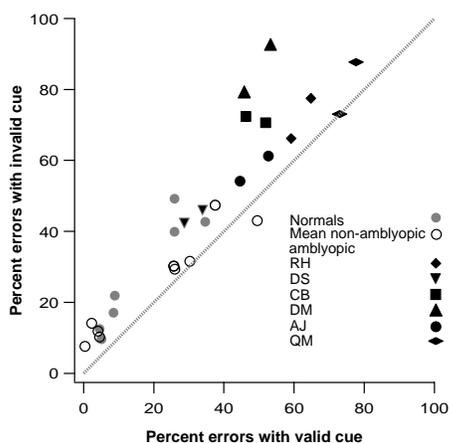
articles

Fig. 6. Effect of cueing on attention. Mean percentages of errors when cues were invalid (ordinate) against the errors when cues were valid for $N = 3$ and $N = 4$ for normal observers (gray symbols) and for non-amblyopic eyes of amblyopes (open circles). Individual error percentages are given for amblyopic eyes of each amblyope (filled black symbols); left and right symbols of each pair represent the error rate for $N = 3$ and $N = 4$, respectively, for each observer. Dotted line represents 1:1. Most of the data fall above the line, showing that the error rate was higher (by ~8%, on average) when the cue was invalid than when it was valid.

Although there are no physiological data on the effects of strabismus on higher cortical function in primates, there is physiological evidence that monkeys reared with both eyelids sewn shut have severe loss of neuronal function in parietal cortex[28]. There is also neuroimaging evidence to suggest that the neural alterations with amblyopia get progressively worse for higher visual areas[29]. However, our results are the first to show directly how these deficits at higher levels of visual processing are reflected in the perception of strabismic amblyopes. This high-level deficit in strabismic amblyopia may be similar to normal peripheral vision, where unreliable signals from small stimuli are grouped rather than individuated[30,31]. We speculate that the high-level deficit in strabismic amblyopia may reflect unreliable signals emanating from the representation of the amblyopic fovea in V1 as a consequence of abnormal binocular visual experience[2].

METHODS

Nine normal observers and seven strabismic amblyopes participated in this study. Not all observers participated in every experiment. Ages ranged from 23 to 42 years. Viewing was monocular, with appropriate optical correction. All experiments were performed in compliance with the relevant laws and institutional guidelines and were approved by the University of Houston committee for the protection of human subjects.

Small circular Gaussian or Gabor patches were generated using a Cambridge Research Systems VSG/2 graphics card (Cambridge, U.K.) and presented on a Mitsubishi Diamond Scan monitor with a P4 phosphor (Mitsubishi, USA; mean luminance of 50 cd per m²) and a frame rate of 120 Hz. The bandwidth of the Gabor patches ranged from 0.5 octaves to 1.2 octaves in different experiments and, except for control experiments, patches had 100% contrast.

In the first experiment (counting patches; **Fig. 1a**), the stimulus was a randomly arranged group of from one to ten high-contrast, bright-centered, Gaussian or Gabor patches. To generate the random spatial arrangement, a square grid with dimensions $\sqrt{2M} \times \sqrt{2M}$ was created, where M represented the maximum number of stimulus elements ($M = 10$, in this case). The grid positions were then shuffled and the first N positions were selected for presenting the patches. (N represents the

number of stimulus elements presented in that given trial.) The observers' task was to record the number of patches seen in that trial. Observers were not instructed as to the range of the number of stimuli and were not given feedback.

To eliminate eye movements, the patches were presented briefly (for 200 ms) and were immediately followed by a mask that consisted of a much larger number of similar patches. The mask was presented for 400 ms. Both the stimulus and the mask were presented with abrupt onsets and offsets. The mask eliminated the use of after-images. To eliminate density cues, the separation between the patches was varied between trials. The minimum center–center separation between the test patches was $3\sigma–6\sigma$ (where σ represents s.d. of the Gaussian envelope of the patch).

Observers performed the experiments in blocks of 200 trials, and 4–5 separate blocks were accumulated for each condition. The error bars represent ± s.e. Performance at each N was determined by calculating the percentage of correct responses (as in **Fig. 2**) and the mean of all the responses (as in **Fig. 3**). Plots of percent correct as a function of N were fit using a Weibull function, where the reported counting threshold was midway between the upper and lower asymptote (estimated by the fit).

In the second experiment (missing patches), the stimulus was a 7×7 square array of high-contrast (100% contrast) Gabor patches presented for 200 ms, followed by a blank screen of the same mean luminance (**Fig. 1b**). On each trial, N patches were randomly removed from the array (where $N = 0, 1, 2, 3, 5, 7$ or 10), and observers recorded the number of 'missing' patches. Patch separation was $4\sigma–9\sigma$. In control experiments, we varied the patch contrast, subjected the patches to random Gaussian positional jitter (**Fig. 1c**) or added Gaussian random noise (**Fig. 1d**); each 1.2-arcmin pixel contained an independent noise sample, which varied from trial to trial.

In the third experiment, observers were asked to estimate the number of test Gabors (with vertical carrier orientation) presented among distractor Gabors (with horizontal carrier orientation). The test and distractor Gabors with 100% contrast were arranged in a 7×7 square array. The center–center separation between the Gabors was fixed at 9σ (large enough to minimize crowding, as shown in pilot experiments). One to four test Gabors (N) were presented randomly in one of five (top left, top right, bottom right, bottom left and center) three-by-three quadrants within the array (**Fig. 1e**). The observers were cued to the quadrant where the test Gabors would appear; cues had an 80% probability of being correct. In separate runs, observers were also tested with no cueing.

Each trial began with the appearance of a central fixation spot (diameter, 0.05°; 600 ms) and a cue (an outline of a square) indicating the quadrant in which the test patches were most likely to appear. The cue appeared for 100 ms. Observers were instructed not to move their eyes toward the cue, but to fixate the fixation spot. Next, the stimulus containing the test and distractor Gabors was presented for 200 ms, followed by a blank screen at mean luminance. The observers then recorded the perceived number of test Gabors. Results were based on the mean of at least 5 blocks of 250 trials per block.

1. Weisel, T. N. Postnatal development of the visual cortex and the influence of environment. *Nature* **299**, 583–591 (1982).
2. Smith, E. L. III *et al.* Residual binocular interactions in the striate cortex of monkeys reared with abnormal binocular vision. *J. Neurophysiol.* **78**, 1353–1362 (1997).
3. Kiorpes, L., Kiper, D. C., O'Keefe, L. P., Cavanaugh, J. R. & Movshon, J. A. Neuronal correlates of amblyopia in the visual cortex of macaque monkeys with experimental strabismus and anisometropia. *J. Neurosci.* **18**, 6411–6424 (1998).
4. Hess, R. F. Developmental sensory impairment: amblyopia or tarachopia. *Hum. Neurobiol.* **1**, 17–29 (1982).

5. Levi, D. M. in *Vision and Visual Dysfunction*. Vol. 10B (ed. Cronly-Dillon, J.) 212–238 (Macmillan, New York, 1991).
6. Levi, D. M. & Klein, S. A. Vernier acuity, crowding and amblyopia. *Vision Res.* **25**, 979–991 (1985).
7. Levi, D. M. & Klein, S. A. Sampling in spatial vision. *Nature* **320**, 360–362 (1986).
8. Wang, H., Levi, D. M. & Klein, S. A. Spatial uncertainty and sampling efficiency in amblyopic position acuity. *Vision Res.* **38**, 1239–1251 (1998).
9. Levi, D. M., Klein, S. A. & Sharma, V. Position jitter and undersampling in pattern perception. *Vision Res.* **39**, 445–465 (1999).
10. Pylyshyn, Z. *et al.* Multiple parallel access in visual attention. *Can. J. Exp. Psychol.* **48**, 260–283 (1994).
11. Trick, L. M. & Pylyshyn, Z. W. Why are small and large numbers enumerated differently? A limited-capacity preattentive stage in vision. *Psychol. Rev.* **101**, 80–102 (1994).
12. Jevons, W. S. The power of numerical discrimination. *Nature* **3**, 281–282 (1871).
13. Atkinson, J., Campbell, F. W. & Francis, M. R. The magic number 4±0: A new look at visual numerosity judgments. *Perception* **5**, 327–334 (1976).
14. Levi, D. M. & Harwerth, R. S. Spatiotemporal interactions in anisometropic and strabismic amblyopia. *Invest. Ophthalmol. Vis. Sci.* **16**, 90–95 (1977).
15. Hess, R. F. & Howell, E. R. The threshold contrast sensitivity function in strabismic amblyopia: Evidence for a two-type classification. *Vision Res.* **17**, 1049–1055 (1977).
16. Bradley, A. & Freeman, R. D. Contrast sensitivity in anisometropic amblyopia. *Invest. Ophthalmol. Vis. Sci.* **21**, 467–476 (1981).
17. Chino, Y. M., Smith, E. L. 3rd, Yoshida, K., Cheng, H. & Hamamoto, J. Binocular interactions in striate cortical neurons of cats reared with discordant visual inputs. *J. Neurosci.* **14**, 5050–5067 (1994).
18. Roelfsema, P. R., Konig, P., Engel, A. K., Sireteanu, R. & Singer, W. Reduced synchronization in the visual cortex of cats with strabismic amblyopia. *Eur. J. Neurosci.* **6**, 1645–1655 (1994).

19. Posner, M. I. Orienting of attention. *Q. J. Exp. Psychol.* **32**, 3–26 (1980).
20. Eriksen, C. W. & Murphy, T. D. Movement of attentional focus across the visual field: A critical look at the evidence. *Percept. Psychophys.* **42**, 299–305 (1987).
21. Nakayama, K. in *Visual Coding and Efficiency* (ed. Blakemore, C.) 411–422 (Cambridge Univ. Press, Cambridge, 1990).
22. Lu, Z. L. & Dosher, B. A. External noise distinguishes attention mechanisms. *Vision. Res.* **38**, 1183–1198 (1998).
23. Levi, D. M., Waugh, S. J. & Beard, B. L Spatial scale shifts in amblyopia. *Vision Res.* **34**, 3315–3334 (1994).
24. Balakrishnan, J. D. & Ashby, F. G. Subitizing: magical numbers or mere superstition? *Psychol. Res.* **54**, 80–90 (1992).
25. Sathian, K. *et al.* Neural evidence linking visual object enumeration and attention. *J. Cogn. Neurosci.* **11**, 36–51 (1999).
26. Treisman, A. M. Feature binding, attention and object perception. *Phil. Trans. R. Soc. Lond. B Biol. Sci.* **353**, 1295–1206 (1998).
27. Vuilleumier, P. & Rafal, R. "Both" means more than "two": localizing and counting in patients with visuospatial neglect. *Nat. Neurosci.* **2**, 783–784 (1999).
28. Hyvarinen, J., Hyvarinen, L. & Linnankoski, I. Modification of parietal association cortex and functional blindness after binocular deprivation in young monkeys. *Exp. Brain Res.* **42**, 1–8 (1981).
29. Imamura, K. *et al.* Reduced activity in the extrastriate visual cortex of individuals with strabismic amblyopia. *Neurosci. Lett.* **225**, 173–176 (1997).
30. Kooi, F. L., Toet, A., Tripathy, S. P. & Levi, D. M. The effect of similarity and duration on spatial interaction in peripheral vision. *Spat. Vis.* **8**, 255–279 (1994).
31. He, S., Cavanagh, P. & Intriligator, J. Attentional resolution and the locus of visual awareness. *Nature* **383**, 334–337 (1996).
32. Watson, A. B. Probability summation over time. *Vision Res.* **19**, 515–522 (1979).