



ELSEVIER

Available online at www.sciencedirect.com

SCIENCE @ DIRECT®

Vision Research xxx (2005) xxx–xxx

**Vision
Research**

www.elsevier.com/locate/visres

The visual computation of 2-D area by human observers

M.J. Morgan *

*Henry Wellcome Vision Research Laboratories, Department of Optometry and Visual Science, City University, Northampton Sq,
London EC1V 0HB, United Kingdom*

Received 14 October 2004; received in revised form 5 April 2005

8 Abstract

9 Normal human observers compared either the width, height or area of two simultaneously-presented shapes (the standard and
10 the test), with a cue to indicate which decision had to be made. On ‘area’ trials, test width was a random variable, ensuring that
11 neither shape (aspect ratio), width nor height by themselves was a reliable signal. Weber fractions for width and height of both ellip-
12 ses and rectangles were in the range 5–10%, but for area they were higher (10–20%) than predicted from the combination of noisy
13 width and height decisions. With ellipses, observers were more likely to overestimate width or height when the other dimension dif-
14 fered from the standard in the same direction (e.g. both greater). We conclude that observers have no access to high-precision codes
15 for 2-D area, and that they base their decisions on a variety of heuristics derived from 1-D codes. A second experiment measured
16 acuity for changes in aspect ratio. For ellipses, accuracy for aspect ratio was higher than predicted by the combination of noisy
17 width and height signals; for rectangles it was worse, suggesting that 2-D curvature is a potent cue to shape.
18 © 2005 Published by Elsevier Ltd.

19 *Keywords:* Psychophysics; Shape; Weber fraction

21 1. Introduction

22 We can see that an elephant is larger than a mouse
23 even though the two animals have very different shapes.
24 This could mean that we perceive the linear dimensions
25 (such as the width and the height) of the elephant as lar-
26 ger; or we could have some special-purpose mechanism
27 for computing the 2-D area, or even the 3-D volume, of
28 an arbitrary shape. We consider here the simple case
29 where the area is computable from two linear measure-
30 ments, as is the case for conic sections like an ellipse.
31 Observers might compute the area of an ellipse by mul-
32 tiplying their independent estimates of the major and
33 minor axes, in which case the accuracy should be worse
34 than either linear estimation taken separately, since they
35 will be combining two sources of noise. If the two noise

sources are independent, their joint variance will be the 36
sum of their separate variances, according to the convo- 37
lution theorem (Bracewell, 1965). The purpose of this 38
paper is to see whether this is true. If accuracy for area 39
is better than predicted by addition of variances, we 40
shall be able to conclude that there is a specialised mech- 41
anism for 2-D area computation; if accuracy for area is 42
worse than predicted, several conclusions are possible, 43
as we shall see later in the paper. 44

The logic of the present approach is made clear by 45
Heeley and Buchanan-Smith (1996), who applied it to 46
the accuracy of angle estimation. They showed that an- 47
gle estimation is more accurate than we should predict 48
from the accuracy of estimating the angle of the compo- 49
nent lines, and that, therefore, there is a specialised 50
mechanism for angle computation. We are not aware 51
of any analogous investigations of area. Laursen and 52
Rasussen (1975) found that humans and monkeys can 53
detect 2–6% changes in the aspect ratio of ellipses. Since 54

* Tel.: +44 207 040 0183; fax: +44 207 040 0182.

E-mail address: m.morgan@city.ac.uk

55 the Weber fractions for line length changes are similar,
 56 we may be tempted to conclude that there is a special-
 57 ized mechanism for aspect ratio estimation, but without
 58 measurements of width and height accuracy in the same
 59 situation it is difficult to be certain. Using the method of
 60 single stimuli (a single rectangle elongated vertically vs
 61 elongated horizontally) Zanker and Quenzer (1999)
 62 found an accuracy of 1% when observers had to tell
 63 which of two ellipses was 'oriented more vertically',
 64 but this accuracy could have been based on height alone,
 65 since the area of the two shapes was the same. The same
 66 problem did not apply to Regan and Hamstra (1992)
 67 who randomly varied the relative area of the standard
 68 and comparison stimuli while requiring observers to
 69 compare aspect ratios. They found that accuracy was
 70 greatest when the reference shape was a perfect circle
 71 or square, falling off markedly with more extreme aspect
 72 ratios for the standard. They also measured independent
 73 width and height thresholds and found that these were
 74 'comparable with, but not better than, corresponding as-
 75 pect ratio near 1.4 and 0.7'. Although Regan and Hamstra
 76 did not make this comparison, the fact that thresholds for
 77 aspect were not worse implies that they were not derived
 78 from addition of independent noisy encoding of width
 79 and height. We return to this point in the discussion of
 80 our Experiment 2.

81 If we wish to measure how accurately observers can
 82 measure area or aspect ratio by eye, they must not be able
 83 to use either height or width separately, but must be
 84 forced to combine them. Therefore, like Regan and Ham-
 85 stra (1992) we required observers to compare the areas of
 86 two shapes with randomly-differing widths and heights.
 87 One shape, the standard, always had the same area, but
 88 its width (and concomitantly its height) was a random
 89 variable over trials. The other (the test) had a different
 90 (randomly-chosen) width from the standard but in addi-
 91 tion its area was different. The observer had to decide
 92 whether the test shape had a larger or smaller area than
 93 the standard. Randomly interleaved with 'area' trials were
 94 'width' and 'height' trials, where the non-relevant dimen-
 95 sion was randomly varied. An icon on the screen told the
 96 observer which kind of decision to make.

97 2. General methods

98 2.1. Apparatus and stimuli

99 The display (Mitsubishi DiamandPro colour moni-
 100 tor, with frame rate 100 Hz and background luminance
 101 halfway between the minimum and maximum of 0 and
 102 75 cd/m^2) was programmed in MATLAB and stimuli
 103 were generated by a Cambridge Research Systems
 104 VSG 2/3 graphics card. Linear luminance look-up tables
 105 were constructed with the CRS Optical system. The
 106 viewing distance was 57 cm at which the total viewing

area on the screen subtended $22.3^\circ \times 22.3^\circ$ and pixel size 107
 was 2.6 arcmin. The stimuli were white-filled figures 108
 (75 cd/m^2) on a grey background (37.5 cd/m^2), rather 109
 than outlines because it was felt that this was more like 110
 natural objects. No anti-aliasing was employed, but the 111
 minimum size change of 1 pixel (1% of standard width) 112
 was well below the thresholds we found. 113

2.2. Procedure 114

The shape of the fixation point on each trial indicated 115
 to the observer the decision (width, height or area) to be 116
 made. A horizontally-oriented rectangle (22×5.5 arc- 117
 min) indicated width, a vertically-oriented rectangle 118
 indicated height, and a square rectangle (25×25 arcmin) 119
 indicated area. One second after the fixation point ap- 120
 peared the stimulus array was presented, and remained 121
 visible for one second before being replaced by a mean 122
 luminance screen. 123

On each trial the width of the standard stimulus was 124
 randomly chosen from a uniform distribution in the 125
 range standard width $\pm 50\%$. The standard width was 126
 4.53° . The height of the standard stimulus was then cho- 127
 sen so that the area was constant and equivalent to the 128
 area of a rectangle of $4.53^\circ \times 4.53^\circ$. 129

The standard was always presented to the right of the 130
 fixation point and the test to the left, but the exact posi- 131
 tions were jittered over trials to prevent the observer 132
 using alignment cues. The mean distance of the centres 133
 of the two stimuli were 5.7° from the fixation point, 134
 and the jitter was drawn from a rectangular distribution 135
 with limits \pm standard width/4. 136

The procedure for generating the test stimulus de- 137
 pended on which condition was in operation on that 138
 trial: 139

Width trials. The width of the test stimulus was that 140
 of the standard, plus or minus a percentage change 141
 determined by the APE psychometric procedure (see be- 142
 low). For convenience, the percentage change will be re- 143
 ferred to in future as 'the increment', although it is 144
 equally often a decrement. The height was randomly 145
 chosen in the range standard height $\pm 50\%$. 146

Height trials. As for Width trials, but the increment 147
 was added to the height, and width was randomly 148
 varied. 149

Area trials. The width was randomly chosen from a 150
 uniform distribution in the range [standard width ± 0.5 151
 standard width], as the standard had been. The area 152
 was the same as the standard, plus or minus a percent- 153
 age change determined by the APE psychometric proce- 154
 dure (see below). The height was therefore determined as 155
 area/width. An example of the stimuli on an 'Area' trial 156
 is shown in Fig. 1. 157

Aspect ratio trials. In Experiment 2 observers com- 158
 pared the aspect ratio of the standard and comparison 159
 stimulus, instead of the area. The dimensions of the 160

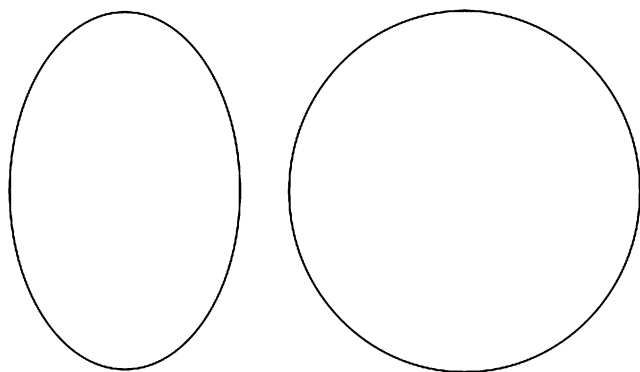


Fig. 1. Schematic representation of the stimuli on an 'Area' trial. In this case, the ellipse on the right has the greater area. If this were a 'Width' trial the correct choice would be the left-hand ellipse; if it were a 'Height' trial, the correct choice would be 'right'.

161 standard were determined as in Experiment 1. The
162 dimensions of the comparison were then scaled by a ran-
163 dom variable, before adding a percentage increment/
164 decrement to the width. To help the observer to com-
165 pare aspect ratios the mnemonic was suggested of think-
166 ing of the shapes as persons, and deciding which shape
167 belonged to the 'thinner' person.

168 After each stimulus presentation the observer pressed
169 the left of two buttons to indicate a 'smaller' decision
170 and the right to indicate 'greater.'

171 2.3. Threshold determination

172 Thresholds (Weber fractions) were determined by the
173 adaptive APE procedure (Watt & Andrews, 1981),
174 which optimises the range and central values of the
175 increment/decrement selected on each trial by a maxi-
176 mum likelihood fit of the data collected up to that trial
177 to a cumulative Gaussian function having two parame-
178 ters, σ representing the slope of the function and μ its
179 central value or bias. The increment/decrement under
180 control of APE was in the form of a Weber Fraction,
181 that is, a proportion of the standard width/height/area
182 on the trial in question.

183 Three independent APE-controlled sequences, each
184 of 64 trials, were run in each block, corresponding to
185 each of the three conditions (Width, Height, Area).
186 The three sequences were randomly interleaved.

187 For the first 16 trials of each sequence, stimuli were se-
188 lected in the range ± 0.08 (Weber Fraction) as if the Meth-
189 od of Constant Stimuli were in operation, in order to give
190 the observer clear examples of the stimuli. Following this
191 initial run, stimuli were free to vary with a grain size of
192 0.01. Each block consisted of 192 (3×64) trials, and at
193 least 4 blocks were run in each condition. Blocks with
194 rectangles and ellipses were randomly interleaved.

195 When all the data had been collected for all condi-
196 tions they were subjected to a single overall analysis to

find the maximum likelihood fit to a Gaussian distribu- 197
tion with asymptotic probabilities for a 'larger' response 198
of 0.01 and 0.99 to allow for the occasionally mistaken 199
'finger error'. Note that the full psychometric functions 200
were fit, not just the thresholds. Two analyses were com- 201
pared. In the first each condition width, height and area 202
decisions had separate means and variances, giving rise 203
to a six-parameter fit; in the second, the variance of 204
the area decisions was calculated from the summed vari- 205
ances of the width and height estimates, giving rise to a 206
five-parameter model. χ^2 for the difference between these 207
two models was derived from twice the difference in their 208
log likelihood, distributed with 1 (i.e. 6–5) degrees of 209
freedom. 210

211 2.4. Observers

The observers in Experiment 1 were the author and 212
one female undergraduate Optometry student (KS) na- 213
ïve as to the purposes of the experiment. In Experiment 214
2 KS was replaced by DM, a male postdoctoral fellow in 215
the Department of Optometry, who was an experienced 216
psychophysical observer. 217

218 3. Experiment 1

Width, height and area trials were interleaved as de- 219
scribed above. The object was to see whether area 220
thresholds could be predicted by the addition of vari- 221
ances from width and heights thresholds. 222

223 3.1. Results

Weber fractions for the three kinds of decision 224
(width, height and area) are shown in Fig. 2. Note that 225
the error bars represent 95% confidence limits, not stan- 226
dard errors. Weber fractions for area were high, in the 227
10–20% region, much higher than those for width and 228
height. The prediction for area is based on the notion 229
that area is computed from independent measures of 230
width and height with their own independent noise, in 231
which case the threshold for area should be the square 232
root of the sum of the squared thresholds for width 233
and height (cf Ahumada & Watson, 1985; Burgess, 234
Wagner, Jennings, & Barlow, 1981; Morgan, Hole, & 235
Ward, 1990). Clearly, the actual thresholds for area 236
are higher than those predicted by the addition of vari- 237
ances, so the independence model is rejected. We com- 238
pared two models of the data by maximum likelihood 239
as described in the Methods section. The χ^2 values for 240
the difference in likelihood of the six- and five-parameter 241
models were (for MM) 6.4 and 23.24 for ellipses and 242
rectangles, respectively The equivalent values for KS 243
were 6.64 and 14.42 All these values are significant 244
(for $df = 1$) at the 0.05 level, leading to rejection of the 245

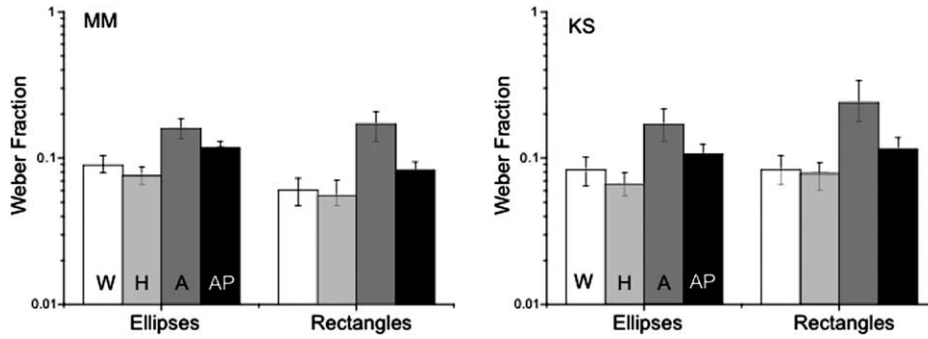


Fig. 2. Thresholds for width (W), height (H) and area (A) tasks for two observers and for two different reference shapes (ellipses and rectangles). Error bars represent 95% confidence limits, estimated from psychometric functions by a bootstrap procedure. The area prediction (AP) is based on the additivity of variances from independently-noisy width and height measurements. For details see the text.

246 addition of variances model. Note that the failure of the
247 model is more extreme for rectangles than for ellipses, as
248 Fig. 2 seems to indicate.

249 Some insight into the failure of additivity can be
250 gained by a separate analysis of trials when the width
251 and height vary in the same direction, as opposed to
252 varying in opposite directions (Fig. 3). Accuracy tends
253 to be higher in the 'same' direction (significant for both
254 observers with ellipses, and for MM with rectangles). In
255 other words, if both the height and width of the compar-
256 ison stimulus are greater (or smaller) than that of the
257 reference, observers tend to be more accurate in classifying
258 it. The same tendency is seen for the width and
259 height tasks themselves in the case of ellipses (significant
260 for both width and height in MM; and for width in KS).
261 These data suggest that observers cannot treat the vari-
262 ables of width and height independently. An analysis of
263 biases (μ in the psychometric function, see Methods)
264 supports this conclusion (Fig. 4). On 'width' trials when
265 the test stimulus had a greater height than the standard,
266 the observer was more likely to respond 'larger' than on
267 trials when the height was smaller. Interpretation of
268 these biases is complicated by an overall response bias
269 towards 'smaller' responses (particularly in MM). How-
270 ever, the difference between the two kinds of trial is sig-

271 nificant for both MM and KS in the case of the ellipse-
272 width task and for the height task in MM.

273 To see if separate analysis of 'same' and 'different' tri-
274 als significantly improved fit to the data, the likelihood
275 of two-parameter fits to all the data were compared to
276 those with four-parameter fits that had different values
277 of μ , σ for the 'same' and 'different' trials. The results
278 are shown in Table 1. In all cases, the values of χ^2 were
279 significant at least the $p = 0.05$ level ($df = 2$).

280 We wondered whether our results might have been
281 influenced by using solid rather than outline shapes.
282 Author MM therefore repeated the Ellipse experiment
283 described above, but with an outline rather than a filled
284 figure. Results were very similar, and once again, thresh-
285 olds for area were significantly higher than predicted
286 from width and height by addition of independent noisy
287 codes ($\chi^2 = 9.0$; $df = 1$; $p < 0.01$).

4. Experiment 2

288
289 As noted in the Introduction, several studies have
290 claimed high accuracy for aspect-ratio discrimination,
291 suggesting a high-precision mechanism for computing
292 the ratio of width to length. However, only one of these

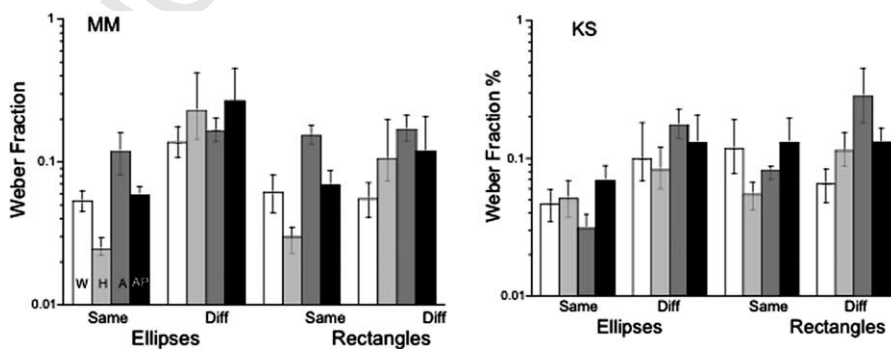


Fig. 3. Separate analysis of trials on which width and height co-varied in the same direction relative to the standard, vs. trials when they co-varied in opposite directions. For further explanation see the text.

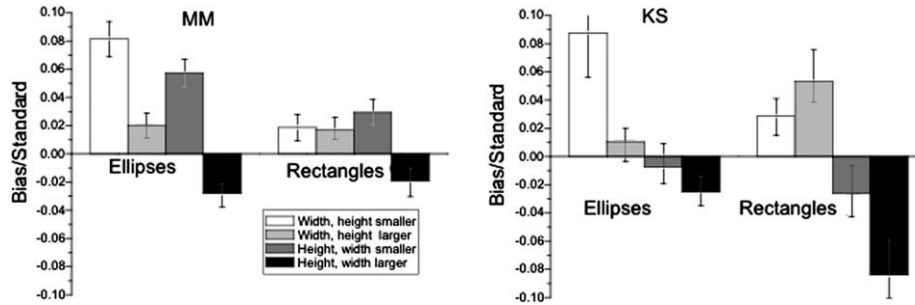


Fig. 4. Biases (μ of the psychometric function) in sub-sets of the trials in the experiment. Positive bias indicate a tendency to respond 'smaller' when the reference and test stimuli are physically equal. For further explanation see the text.

Table 1
Likelihood for two- and four-parameter fits to the data, and χ^2 values for the likelihood ratios

	Ellipses			Rectangles		
	Width	Height	Area	Width	Height	Area
MM 2 par	-394.32	-409.47	-431.59	-220.32	-211.78	-240.37
MM 4par	-346.39	-343.47	-426.05	-189.72	-194.78	-234.37
Chi-squared	-95.86	-132	-11.08	-61.2	-34	-12

For further explanation see text.

293 studies (Regan & Hamstra, 1992) required observers to
 294 compare figures of different overall size, so the decision
 295 could have been based on one dimension (width or
 296 height) alone. No study, as far as we are aware, has mea-
 297 sured width, height and aspect-ratio thresholds concu-
 298 rrently in the same block of trials, to see if thresholds
 299 for the latter are predicted from separate noisy estimates
 300 of width and height. We therefore adapted the methods
 301 of Experiment 1 to measure thresholds for aspect ratio
 302 instead of area. The standard stimulus was generated
 303 as before and the tasks of width and height were the
 304 same. On 'aspect trials' the comparison stimulus was
 305 generated by scaling the overall size of the standard,
 306 to produce an invariant shape, and by then adding a
 307 percentage increment/decrement to the width. Thus,
 308 the best performance could be obtained only by examin-
 309 ing the relative shape of the standard and comparison.

5. Results

The results are shown in Fig. 5. Qualitatively they
 were similar for the two observers. For ellipses, aspect
 ratio thresholds were better than those predicted from
 the summed variances of noisy width and height tasks;
 for rectangles they were worse. To assess significance
 of these differences, likelihood of independent (six-
 parameter) vs. dependent (five-parameter) fits to all the
 data were computed (see Experiment 1). For MM the
 χ^2 values derived from the likelihood ratios were 5.46
 and 8.74 respectively, leading to rejection of the null
 hypothesis at the $p = 0.01$ level in both cases ($df = 1$).
 However, for observers DM the null hypothesis could
 not be rejected ($\chi^2 = 0.65$ in both cases). This means that
 DM could have been combining independent noisy esti-
 mates of width and height, although qualitatively his re-
 sults go in the same direction as that of MM

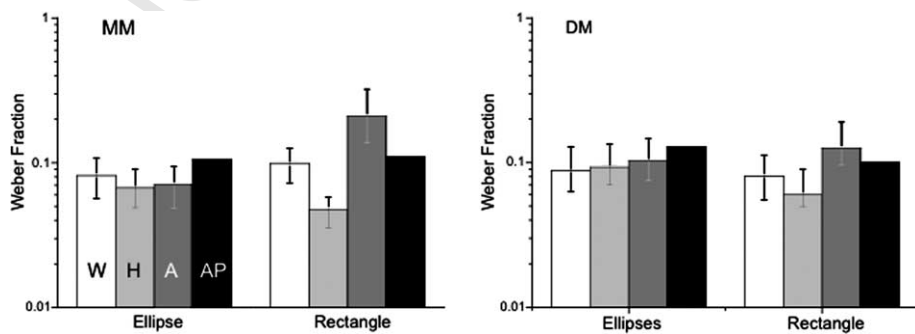


Fig. 5. Thresholds for width, height and aspect ratio tasks in Experiment 2. Apart from the label 'A' referring to aspect ratio rather than area, conventions are the same as in Fig. 2

327 6. General discussion

328 6.1. Aspect ratios

329 We found no evidence in the case of rectangles that
 330 observers did any better at comparing aspect ratios than
 331 they would have by combining independent noisy codes
 332 for width and height. One observer (MM) did even
 333 worse. Only in the case of ellipses, and only for one ob-
 334 server (MM) was there evidence for a higher-precision
 335 mechanism. The most likely candidate for the special-
 336 purpose mechanism is curvature discrimination, which
 337 has been shown to be a high-precision mechanism (Dob-
 338 bins, Zucker, & Cynader, 1987; Fahle & Braitenberg,
 339 1983; Koenderink & Richards, 1988; Watt & Andrews,
 340 1982; Wilson, 1985). Of course, curvature discrimination
 341 is no use for rectangular shapes.

342 Our results for rectangles appear to contradict Regan
 343 and Hamstra (1992) who argued for a special-purpose
 344 mechanism. The discrepancy probably arises because
 345 we randomly varied the aspect ratio of our standard
 346 as well as its area. For extreme aspect ratios of the stan-
 347 dard Regan and Hamstra found Weber fractions
 348 approaching 0.1, comparable to ours. It should also be
 349 noted that our Thresholds are based on the 18–82%
 350 points on the psychometric function rather than on the
 351 25–75% points that were used by Regan and Hamstra.
 352 We have no reason to doubt Regan and Hamstra's con-
 353 clusion that aspect-ratio thresholds for near-perfect
 354 ellipses and rectangles are better than predicted from
 355 separate width and height accuracy. As they point out,
 356 for squares observers could use the angle of intersection
 357 of imaginary lines joining opposite corners; for circles
 358 they could use curvature.

359 6.2. Area

360 First, we note that keeping the standard always on the
 361 same side, as we did in this experiment, means that this
 362 was the 'Method of Constant Stimuli' in the correct his-
 363 torical sense of that term (Morgan, Watamaniuk, &
 364 McKee, 2000) rather than two-alternative forced choice
 365 (2AFC). A potential problem with the Method of Con-
 366 stant Stimuli is that the observer can internalize the stan-
 367 dard and need only look at the variable stimulus to make
 368 a decision, making the task equivalent to the Method of
 369 Single Stimuli (MSS). However, this was not true in this
 370 experiment, because width and height were random vari-
 371 ables for the standard, so the observer was forced to com-
 372 pare the standard and comparison stimuli. Only on 'area'
 373 trials could the observer have ignored the standard with-
 374 out loss of accuracy, since the area of the standard was
 375 constant. However, the prediction of Signal Detection
 376 Theory is that ignoring the standard should decrease
 377 threshold by $\sqrt{2}$ (Morgan et al., 2000). The fact that the
 378 area of the standard was constant is thus unlikely to ex-

plain our finding that area thresholds are *higher* than
 those predicted from width and height.

We found that the accuracy of measuring the area of
 a shape by eye is not limited only by the accuracy of
 measuring its width and its height. The Weber fractions
 for area are amongst the highest ever reported, and it is
 likely that they would have been even higher for irregu-
 lar polygons with unequal numbers of sides. If observers
 estimate the area of an ellipse by multiplying their esti-
 mates of length and width, there must be considerable
 noise following the multiplication stage itself. Our find-
 ings (Fig. 3) suggest that observers use a variety of heu-
 ristics for combining width and height estimates into an
 estimate of area. One such might be to classify the test
 shape as larger than the standard if both its width and
 height are greater. This condition produces greater accu-
 racy than the cases where the two dimensions vary in
 different directions. If the width is greater but the height
 smaller, a decision could be reached by deciding which
 difference from the standard is greater. This amount to
 estimating the quantity:

$$\Phi = (\omega_1 - \omega_2) - (\eta_1 - \eta_2) \quad (1)$$

where ω and η are random variates corresponding to the
 widths and heights of the two stimuli. This makes iden-
 tical predictions to the multiplication model we have al-
 ready rejected. The implication is that there is further
 noise in the representation of the height difference and
 the width difference. For example, the observer might
 have to attend to the width and height dimension
 sequentially and store the intermediate results in a noisy
 memory. What is certain is that early in the encoding of
 width and height is not the only source of noise limiting
 area computation.

The finding that width decisions are influenced by
 height and vice versa could be explained by a cognitive
 confusion between the two dimensions (tending to say
 that a stimulus is less wide when it is in fact less high)
 or by geometrical effects. If an ellipse is flattened in
 height, its ends begin to resemble the ingoing arrows
 of a Muller-Lyer figure, possibly leading to underesti-
 mation of its width. Individual differences and differ-
 ences between ellipses and rectangles in the bias data
 (Fig. 4) suggest that both cognitive and geometrical fac-
 tors may be operating.

It may initially seem puzzling that there is not a high-
 precision, special-purpose mechanism for computing 2-
 D area. After all, the visual system has no difficulty in
 carrying out signal multiplication when it is useful, as
 the example of the Reichardt detector shows (Morgan
 & Chubb, 1999). The ecological answer may be the rar-
 ity of occasions where it is valuable to compare different
 shapes by their area. To see that an elephant is larger
 than a mouse is easy and useful because it is larger in
 all its dimensions; to decide whether an elephant has a
 larger 2-D area than a giraffe is more difficult and of

379
380
381
382
383
384
385
386
387
388
389
390
391
392
393
394
395
396
397
398
399
401
402
403
404
405
406
407
408
409
410
411
412
413
414
415
416
417
418
419
420
421
422
423
424
425
426
427
428
429
430
431
432
433
434

435 more doubtful utility. We suggest that the encoding of 3-
 436 D shape attributes, such as volume, is derived directly
 437 from 1-D measurements using a variety of heuristics,
 438 without involving an explicit 2-D intermediate.

439 7. Uncited reference

440 [Regan, Hadjir, and Hong \(1996\).](#)

441 References

- 442 Ahumada, A. J., Jr., & Watson, A. B. (1985). Equivalent noise model
 443 for contrast detection and discrimination. *Journal of the Optical*
 444 *Society of America A*, 2(7), 1133–1139.
- 445 Bracewell, R. (1965). *The Fourier transform and its applications*. NY:
 446 McGraw-Hill.
- 447 Burgess, A. E., Wagner, R. F., Jennings, R. J., & Barlow, H. B. (1981).
 448 Efficiency of human visual signal discrimination. *Science*, 214,
 449 93–94.
- 450 Dobbins, A., Zucker, S. W., & Cynader, M. S. (1987). Endstopped
 451 neurons in the cortex as a substrate for calculating curvature.
 452 *Nature*, 329, 438–441.
- 453 Fahle, M., & Braitenberg, V. (1983). Curvature detection in the central
 454 and peripheral visual field of human subjects. *Neuroscience Letters*
 455 *Supplement*, 14, 108.
- 456 Heeley, D. W., & Buchanan-Smith, H. M. (1996). Mechanisms
 457 specialized for the perception of image geometry. *Vision Research*,
 458 36(22), 3607–3627.

- Koenderink, J. J., & Richards, W. (1988). Two-dimensional curvature
 operators. *Journal of Optical Society of America*, 5, 1136–1141. 459
- Laursen, A. M., & Rasussen, J. B. (1975). Circle–ellipse discrimination
 in man and monkey. *Vision Research*, 15, 173. 460
- Morgan, M., & Chubb, C. (1999). Contrast facilitation in motion
 detection: Evidence for a Reichardt detector in human vision. 461
Vision Research, 39, 4217–4231. 462
- Morgan, M. J., Hole, G. J., & Ward, R. M. (1990). Evidence for
 positional coding in hyperacuity. *Journal of Optical Society of*
America A, 7, 297–304. 463
- Morgan, M. J., Watamaniuk, S. N. J., & McKee, S. P. (2000). The use
 of an implicit standard for measuring discrimination thresholds. 464
Vision Research, 40, 2341–2349. 465
- Regan, D. M., Hadjir, L. V., & Hong, X. H. (1996). Two-dimensional
 aspect ratio discrimination for shape defined by orientation texture. 466
Vision Research, 36, 3695–3701. 467
- Regan, D. M., & Hamstra, S. (1992). Shape Discrimination and the
 judgement of perfect symmetry: Dissociation of shape from size. 468
Vision Research, 32, 1845–1864. 469
- Watt, R. J., & Andrews, D. P. (1981). APE: Adaptive probit
 estimation of a psychometric function. *Current Psychological*
Review, 1, 205–214. 470
- Watt, R., & Andrews, D. (1982). Contour curvature analysis:
 Hyperacuties in the discrimination of detailed shape. *Vision*
Research, 22, 449–460. 471
- Wilson, H. R. (1985). Discrimination of contour curvature: Data and
 theory. *Journal of Optical Society of America A*, 2(7), 1191–1199. 472
- Zanker, J., & Quenzer, T. (1999). How to tell circles from ellipses:
 Perceiving the regularity of simple shapes. *Naturwissenschaften*, 86,
 492–495. 473

UNCORRECTED