

Compulsory averaging of crowded orientation signals in human vision

Laura Parkes¹, Jennifer Lund², Alessandra Angelucci², Joshua A. Solomon³ & Michael Morgan³

¹Institute of Neurology, University College London, Queen Square, London

²Institute of Ophthalmology, University College London, Bath St., London EC1V

³Applied Vision Research Centre, The City University, Northampton Square, London EC1V 0HB

Corresponding Author:

Michael Morgan

Tel: 44-(0)20 7477 0183

Fax: 44-(0) 20 7477 0182

Email: m.morgan@city.ac.uk

ABSTRACT

Classification of a *target* object in peripheral vision can be impaired when *distractor* objects appear close to it, even when the observer knows which object is the target. To determine the cause of this phenomenon (“crowding”), we asked human observers to report the orientation (clockwise or anti-clockwise) of one or more tilted grating patches (the targets) when presented amongst horizontal distractors. Threshold tilts increased linearly with the number of distractors and decreased with the number of targets. This suggests that the estimated orientation of the target is pooled with those of the distractors. An early noise, which corrupts local estimates of orientation and a late noise, which corrupts their average, must be invoked to explain the results. Obligatory averaging was further supported by the finding that distractors with a slight tilt in the direction of the target do not impair performance as much as horizontal distractors, which in turn do not impair performance as much as distractors with a slight tilt in the direction opposite that of the target. We conclude that local estimates of orientation are not degraded by crowding, but observers have no conscious access to these estimates and must rely on an average signal.

INTRODUCTION

The literature on crowding has shown that detection and recognition of form in peripheral vision are degraded by the presence of nearby distractors¹⁻³. The term “crowding” has sometimes been used interchangeably with the term “lateral masking”³, with the implication that it involves degradation of the signal arising from the target. This interpretation of crowding was challenged by He *et al.*⁴ who demonstrated orientation-specific adaptation to a target whose orientation observers were unable to report. Sagi & Julesz⁵ also found limited conscious access to the local orientation signal in a visual search task. He *et al.* suggest that local processing is unimpaired by crowding, but that the local signal cannot reach consciousness. One mechanism for this might be an obligatory pooling of the signal arising from the target with those arising from the distractors, but no direct evidence for pooling within crowded arrays has yet been presented.

We attempted to obtain clear evidence for pooling by measuring the abilities of observers to report the orientation of tilted targets when they appeared amongst horizontal distractors in peripheral vision. We used arrays of micro-Gabor patches⁶ (Fig. 1) that were presented for 100 msec and centered at a retinal eccentricity of 2.5 deg. To investigate the possibility that integration occurs within a single, large linear filter, we also manipulated the phase relations of the gratings within the patches. In the “phase coherent” condition the carrier gratings of the patches had the same spatial phase with respect to one another: in other words, every micro-Gabor was a window onto the same underlying grating. In the “phase incoherent” condition the carrier phase was randomised within each patch. The latter condition was intended to discourage pooling within a large, linear filter.

RESULTS

Experiment 1

We first measured orientation thresholds when a sub-set of the patches (the targets) were tilted from the horizontal while the rest (the distractors) were horizontal (top panels of Fig. 2). Thresholds decreased with the number of target patches with a slope

of -1.0 in log-log co-ordinates. This is exactly as predicted by a simple early-noise model of spatial averaging^{7,8}: the total number of noise sources is constant at 9, but each target contributes its own signal; therefore the average signal/noise ratio is proportional to the number of targets.

Experiment 2

We next measured orientation thresholds when no distractors were present (lower panels of Fig. 2). Thresholds again decreased with the number of target patches, however, the slope was less than the -0.5 predicted by the simple early-noise model. We fit the data from Experiments 1 and 2 with a slightly more complicated model of spatial averaging. As in the simple model, the independent, noisy orientation signals arising from all of the patches were averaged. In our model, this average (noisy) orientation signal is further perturbed by another (late) noise process (for details see **METHODS**)^{9,10}. The model has two parameters: the variance of the early noise and the variance of the late noise. These parameters were allowed to vary between observers but not experiments. This Averaging Model fit the data from both observers well.

The data were also fit by the Max Model of Signal Detection Theory, which assumes that observers base their decisions solely upon the patch having the greatest apparent tilt (see Methods). This model fit the data from Experiment 2 reasonably well, but it could not simultaneously produce the slope of -1 obtained from Experiment 1 (see Fig. 2).

Experiment 3

It could be argued that the linear decrease of thresholds with target number found in Experiment 1 was due to contrast summation within an extremely narrow-band channel tuned to the target orientation only. This implausible suggestion is contradicted by the weak summation found in Experiment 2, but to rule it out completely we measured contrast thresholds for various numbers of targets using a 2AFC paradigm (see **Methods**). (No distractors were used.) In Figure 2, these thresholds form shallow curves having slopes of -0.23 (MM) and -0.29 (LP). Contrast summation with our stimuli is thus entirely consistent with oft-reported¹¹

“fourth-root summation” (i.e. a slope of -0.25), and cannot be the basis for the much steeper slopes obtained in Experiment 1.

Experiment 4

In Experiment 1 the positions of the targets were randomised within a 9-patch array. To investigate the ability of observers to localise such targets, we repeated the experiment with 3 target patches, placed either in a West-Centre-East or a North-Centre-South alignment. On each trial the observer had to report not only the orientation of the targets but also their spatial alignment (NS vs EW). As in previous experiments, five levels of target tilt were randomly interleaved to find the tilt threshold from the psychometric function (see **Methods**). Unlike orientation classifications we found that reports of spatial alignment did not improve with the level of target tilt. When averaged over all levels of target tilt, accuracy was (non-significantly) less than 50% correct.

Table 1

Observer	MM	LP
Tilt threshold	7.8 deg	5.34 deg
% correct for location	45%	48%

Experiment 5

Since the central position always contained a target, the high orientation thresholds found in Experiment 4 suggest that observers are unable to ignore the distractors. We confirmed this by “intrinsically” cueing observers to the position of the target. In this experiment, the observers knew the target would always occupy the central position, yet their performances were even worse than they had been in Experiment 1, when the position of the target was randomised. Thus, unlike large, widely-spaced patches^{7,8} our stimuli meet the operational requirement for crowding: distractors impair performance even when the position of the target is cued. The effects of distractors cannot, therefore, be ascribed solely to spatial uncertainty as formalised by Signal Detection Theory.¹²

Experiment 6

To check whether cueing might be more effective in the fovea, we shifted the stimulus array so that it was centred upon the same position as the fixation point. In this experiment, the fixation point disappeared just before the stimulus array appeared, otherwise all methods were identical to those of Experiments 1 and 5. When the position of the targets were randomised, thresholds were proportional to the number of targets, just as they had been when the array was centred at 2.5 deg eccentricity (Fig. 3). However, when a single target was always present in the central position, thresholds were independent of distractor number. Thus, unlike our peripheral display, our foveal display does not meet the operational requirement for crowding. Note that it would be premature to conclude that this difference reflected qualitatively different visual pathways. It could be explained by a differences in cortical magnification or contrast sensitivity.

Experiment 7

Finally, to test an obvious prediction of the Averaging Model, we gave tilts to the distractors. When the distractors were present, there were four of them and they surrounded the target, occupying the NE, SE, SW and NW compass directions (see Fig. 4). Eight staircases were paired into four conditions: 1) no distractors, 2) horizontal distractors, 3) distractors having a tilt $-1/2$ that of the target and 4) distractors having a tilt $+1/2$ that of the target. (A similar trial-to-trial covariance of target and distractor tilts was used in an earlier experiment with non-crowded arrays⁷.) One of each pair of staircases used CW tilts; the other used ACW tilts. All staircases converged upon the tilts for which responses were correct with frequency 0.81. Psychometric functions are shown in Fig. 4 and their slopes are tabulated in Table 2. Note that psychometric slopes are inversely proportional to threshold: the shallower the psychometric function, the more poorly the observer classifies the target tilt. Psychometric slopes obtained without distractors were similar to those obtained with distractors having a tilt $+1/2$ that of the target. On the other hand, non-tilted distractors caused a considerable reduction in psychometric slope and oppositely-tilted distractors absolutely devastated performance. Note that even though this last condition boasts the greatest orientation contrast between target and distractors, the psychometric functions are so flat that no positive slope could be estimated from MM's data. All of

these results are consistent with a decision rule which averages noisily-encoded tilts from each target and distractors.

Table 2

Observer	No distractors	Distractor tilt 0	Distractor tilt +0.5	Distractor tilt -0.5
MM	5.9	1.9	9.7	?
JAS	8.6	3.8	8.2	0.8

DISCUSSION

The key finding in the present experiment is the ability of observers to report the average orientation of a set of tilted stimuli, even when they are completely unable to abstract information about particular patches from the array. Previous studies have demonstrated that flanking distractors impair orientational acuity⁴ and have proposed a mixture of masking and pooling as an explanation³ but have not simultaneously shown access to the averaged signal. Crowding has traditionally been considered an undesirable factor limiting performance, which may be exacerbated in certain clinical conditions like Amblyopia¹³. However, our results show that crowding is accompanied by a residual ability of the observer to report a statistical property of the ensemble: in this case, its average orientation. The average orientation is a textural property of the array, and thus it appears that crowding and texture perception are opposite sides of the same coin. We might say that “crowding” is simply the name we give to texture perception when we do not wish it to occur.

Access to the pooled but not the local signal appears to be specific to crowded arrays. With widely-spaced arrays cueing the target position abolishes the effects of

distractors^{3,7,8} as did knowledge of position in our foveal arrays (Experiment 6). Using non-crowded arrays Baldassi & Burr⁸ found only a slight superiority of orientational over positional classification, and this only with relatively small numbers (~4) of distractors. We have shown elsewhere¹⁴ that this small effect can be predicted from the Max Model of Signal Detection Theory.

In Experiment 1 we found averaging of individual orientation signals even when the patches were phase-incoherent. If classifications were based on large, linear receptive fields covering all nine patches, phase incoherence would be expected to raise thresholds, since it introduces randomness into the orientation spectrum. The fact that it did not do so argues that the individual orientation signals are combined without respect to their phase, either by lateral interactions in primary visual cortex^{15,16}, or by some higher-order collector unit¹⁷⁻²¹. The dimensions of the stimulus array we used at 2.5 deg eccentricity were such that they could easily have been included within the classical receptive field of V2 neurones. The diameter of the whole array was ~ 1.0 deg (10λ), and the anatomically-determined receptive field at 2.5 deg eccentricity is about 1.2 deg²². Fields in V2 are approximately 3 times larger again²³. It would be interesting to determine in physiological experiments whether single cells in V1 and V2 are able to integrate across phase-incoherent stimuli in the way that observers do in our experiments. The same stimuli presented foveally would be too large to be comprised within a single classical receptive field, but might fit within a V2 receptive field.

In Experiment 2 we did find an effect of phase coherence when no distractors were present, particularly in the collinear condition. This effect does not necessarily imply any specialised mechanisms for collinearity detection. At the positions between each micro-Gabor, the detectors maximally stimulated by the coherent stimuli are those whose preferred orientation is identical to that of the target. The phase-incoherent patches stimulate largely off-axis detectors in these positions, giving rise to misleading orientation signals²⁴. The fact that the effect of phase disappeared when further non-collinear patches were added recalls previous results for contrast detection²⁵.

When the presence of distractors does not impair an observer's ability to locate a target that target is said to 'pop out'. Our results indicate that, when the target does not pop out, the visual system is compelled to average local estimates of orientation. It would be interesting to learn whether or not compulsory averaging occurs even when the target does pop out, due to a large orientation difference. One study suggests that it might. Sagi & Julesz⁵ found that observers could report the positions, but not the orientation of three tilted targets displayed in a large field of distractors. Location without identification^{5,14,26,27} and compulsory averaging both argue against direct conscious access to the activity in V1²⁸, where the brain forms its initial estimates of local orientation²⁹.

Methods

(a) Stimuli and psychophysics

In Experiment 1 - 6, stimuli were generated by a Cambridge Research Systems VSG graphics card with 12-bit luminance resolution and displayed on a gamma-corrected Mitsubishi DiamondPro display (resolution 512 x 512 pixels in a display area 23.5 x 23.5 cm; viewing distance 200 cm); frame rate 100 Hz; Mean Luminance 20 cd/m²). The individual patches (see Fig. 1) were horizontal 12 cycle/deg Gabor patches (sine wave gratings windowed by a Gaussian with a standard deviation of twice the wavelength of the grating [2λ]). The centre-centre separation of each of these patches from the central patch in the array was 5λ . The contrast of the individual patches was 100%, which was 2.25 times the detection threshold for a single patch determined by a 2AFC (spatial) procedure for observer MM, and 2.32 times detection threshold for observer LP. On each trial, the observer fixated a central point on the monitor and pressed a response button to see the next stimulus, which was accompanied by an auditory warning signal. The array flashed for 100 msec randomly to the left or right of the fixation point at a horizontal eccentricity of 2.5 deg, measured from the fixation point to the central element of the array. In separate blocks of trials, either 1, 2, 3, 4, 7 or 9 of the patches were slightly tilted CW or ACW from the horizontal. The remaining patches (the 'distractors') were all horizontal. The observer had to press one of two buttons (forced choice) to report whether the array appeared tilted CW or ACW. Inside each block, 40 trials at each of 5 levels of tilt from the horizontal were randomly interleaved, in order to construct a psychometric function, relating the probability of a correct response to the amount of tilt. 'Phase coherent' and 'Phase incoherent' conditions were also randomly interleaved in a block, with 20 trials for each condition at each of the 5 tilts. Thus each block comprised 200 trials. Each block was repeated at least 3 times. The psychometric functions were combined over blocks and fitted with a Weibull function to extract the 75% correct point and the slope. A bootstrap procedure³⁰ was used to determine the standard deviations of the estimates. The observers were two of the authors (LP and MM). Contrast sensitivity was determined by a standard 2 alternative spatial forced choice procedure, in which the target array was flashed for 100 msec either 2.5 deg to the left

or right of the fixation point. Five contrast levels were randomly interleaved and Psychometric functions fitted to Weibull functions. The stimuli were phase-incoherent.

In Experiment 7 stimuli were generated on a Macintosh computer display. A video signal with 12-bit precision was attained using an ISR Video Attenuator³¹. The PSYCHOPHYSICA³² software used in this experiment is available on the Internet at <http://vision.arc.nasa.gov/mathematica/psychophysica.html>. Maximum and minimum display luminances were 32 and <0.1 cd. m⁻² respectively. The background luminance was held constant at 16 cd. m⁻² and the frame rate was 66.7 Hz. Display resolution was 22.6 pixels/cm and the viewing distance was 243 cm. Each Gabor pattern had odd symmetry. For each Gabor pattern, on each trial, one of the two phases satisfying this constraint was randomly selected. The centre-centre distance between target and each distractor was 0.47° (i.e. $4\sqrt{2}\lambda$). Forty trials on each of eight interleaved staircases were run in a single block of trials. The eight staircases were paired into four conditions: 1) no distractors, 2) horizontal distractors, 3) distractors having a tilt $-1/2$ that of the target and 4) distractors having a tilt $+1/2$ that of the target. One of each pair of staircases used CW tilts; the other used ACW tilts. All staircases converged upon the tilt for which responses were correct with frequency 0.81. The observer were the authors MM and JAS. All other methods were identical with those of the previous experiments.

(b) Modelling

The Averaging Model assumes that the orientation of each of the targets and distractors is initially encoded independently, with additive Gaussian noise (the early noise component). The noisy early signals are then averaged, late Gaussian noise is added, and the observer responds CW if the average is > 0 , otherwise ACW.

Proportion correct P , can be described as a function of the target's tilt μ :

$$P(\mu; n_t, n_d, \sigma_e, \sigma_t) = 1 - \Phi \left[\frac{-\mu n_t}{(n_t + n_d) \sqrt{\sigma_t^2 + \frac{\sigma_e^2}{(n_t + n_d)}}} \right], \quad (1)$$

where $\Phi(x)$ is the standard normal CDF, n_t and n_d are the numbers of targets and distractors, respectively, and σ_e and σ_t are the standard deviations of the zero-mean

Gaussian early and late noises, respectively. Thus, (75%-correct) threshold can be calculated as

$$P^{-1}(\mu) = 1 - \Phi(-0.67) \cdot$$

The curves in Fig. 2 were generated with the following parameter values (in degrees): LP incoherent: $\sigma_e = 4.8$, $\sigma_l = 2.1$; MJM incoherent: $\sigma_e = 2.6$, $\sigma_l = 1.7$; LP coherent: $\sigma_e = 3.8$, $\sigma_l = 2.2$; MJM coherent: $\sigma_e = 1.5$, $\sigma_l = 1.5$.

The averaging model can be applied to the case where four distractors are tilted (Experiment 7). It predicts that when the distractors have a $+ \frac{1}{2}$ tilt (see Methods) then performance will be similar to performance without distractors, provided that $\sigma_e \sim 2\sigma_l$. Note that this condition is reasonably well satisfied for MM in the incoherent condition, which is the relevant case for Experiment 7.

The Max model can be derived from Signal Detection Theory³³:

$$P(\mu; n_t, n_d, \sigma_e, \sigma_l) = \frac{1}{2} + \left[\frac{1}{2} - \Phi\left(\frac{\mu}{\sigma_e}\right) \right] \int_{-\infty}^{\infty} D_u \left[\Phi^{n_t}\left(\frac{u-\mu}{\sigma_e}\right) \right] \Phi\left(\frac{u}{\sigma_l}\right) \Phi^{n_d}\left(\frac{u}{\sigma_e}\right) du \cdot (2)$$

The (simultaneous) fits of the Max model to the data of Expts 1 and 2 cannot be improved with $\sigma_l > 0$. The curves in Fig. 2 were generated with the following parameter values (in degrees):): LP incoherent: $\sigma_e = 4.2$; MJM incoherent: $\sigma_e = 3.9$; LP coherent: $\sigma_e = 2.9$; MJM coherent: $\sigma_e = 2.4$.

Figure Legends

Fig. 1. An array of Gabor patches, similar to those used in the Experiments. In the example shown, three of the patches are tilted clockwise. The remainder (the 'distractors') are all horizontal. Sensitivity to tilt was measured as a function of the number of tilted stimuli, varying from 1 to 9 (no distractors). To get an accurate impression of how the stimuli appeared in the experiment, the reader should view this figure from a distance of ~100 cm.

Fig. 2. Orientation thresholds for classification from Experiments 1 & 2. In Experiment 1 (top panels; observer LP left, observer MM right), thresholds (vertical axis) for reporting the direction of tilt (from horizontal) were measured as a function of the number of tilted patches in an array of 9 patches, the rest of which were horizontal. Open and Solid symbols show thresholds in the phase coherent condition and phase incoherent conditions respectively (see text for explanation). The curves show fits of the Averaging and Max Models of Signal Detection Theory (see text for details).

In Experiment 2 (lower panels), orientation thresholds were again measured as a function of the number of tilted patches. In these experiments, no distractors were used and the targets occupied the fixed positions shown as icons on the horizontal axis. Thus, when there were 3 targets they were collinear. This seems to have given an advantage to the phase-coherent stimuli, possibly because they stimulate detectors positioned in between the patches. However, no collinear advantage was found with 9-patch arrays.

Fig. 3. Results of foveal presentation (Experiment 6). The square symbols (and bottom horizontal axis) show orientation thresholds for various numbers of randomly positioned targets within an array of 9 patches. The triangular symbols (and top

horizontal axis) show orientation thresholds for a single target at fixation, amongst various numbers of distractors. The continuous line is the best-fitting curve to the square data points with a slope of -1 . The dotted curve is the best-fitting curve to the triangular data points with a slope of zero.

Whether in central vision or 2.5 deg eccentricity (Fig. 2), distractors have a similar effect when the targets are randomly positioned. However, when fixating upon a target whose position is not randomised, distractors have no effect whatsoever.

Fig. 4. Effect of distractor tilt (Experiment 7). Each group of four panels shows psychometric data from the same observer (*a – d*: JAS, *e – h*: MM) in four different conditions. The conditions are illustrated in each inset: in *a* and *e* there were no distractors, in *b* and *f* all of the distractors were horizontal, in *c* and *g* the tilt of each distractor was -0.5 that of the target and in *d* and *h* the tilt of each distractor was $+0.5$ that of the target. Each point shows the frequency of ACW responses for a given target tilt. Error bars contain the 95%-confidence intervals. Each panel also shows the maximum-likelihood fit of a cumulative Gaussian to the psychometric data. (Their minima and maxima were constrained to be 0.01 and 0.99, respectively.) Each Gaussian has a mean near zero. The Gaussians in *a* and *d* have similar spreads, roughly one-half that of the Gaussian in *b*. These results are consistent with a decision rule which averages noisily-encoded tilts from each element (target and distractors). Note that the staircases all started with zero tilt and collected only two responses at that value before moving to larger tilts; this is why the zero tilt points have such large error bars

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References

1. Bouma, H. Interaction effects in parafoveal letter recognition. *Nature* **226**, 177-178 (1970).
2. Levi, D., Klein, S. & Aitsabaomo, A. P. Vernier acuity, crowding and cortical magnification factor. *Vision Research* **25**, 963-967 (1985).
3. Wilkinson, F., Wilson, H. R. & Ellemberg, D. Lateral interactions in peripherally viewed texture arrays. *J Opt Soc Am A* **14**, 2057-68 (1997).
4. He, S., Cavanagh, P. & Intriligator, J. Attentional resolution and the locus of visual awareness. *Nature* **383**, 334-337 (1996).
5. Sagi, D. & Julesz, B. "Where" and "what" in vision. *Science* **228**, 1217-9 (1985).
6. Morgan, M. J., Mason, A. J. & Baldassi, S. Are there separate first-order and second-order mechanisms for orientation discrimination? *Vision Res* **40**, 1751-63 (2000).
7. Morgan, M., Castet, E. & Ward, R. Visual search for a tilted target: tests of the spatial uncertainty model. *QJEP* **51**, 347-371 (1998).
8. Baldassi, S. & Burr, D. C. Feature-based integration of orientation signals in visual search. *Vision Research* **40**, 1293-1300 (2000).
9. Heeley, D. W. & Buchanan-Smith, H. M. Mechanisms specialized for the perception of image geometry. *Vision Res* **36**, 3607-27. (1996).
10. Morgan, M. J., Hole, G. J. & Ward, R. M. Evidence for positional coding in hyperacuity. *J.opt.Soc.Am. A* **7**, 297-304 (1990).
11. Bonnef, Y. & Sagi, D. Contrast integration across space. *Vision Res.* **39**, 2597-2602 (1999).
12. Palmer, J., Verghese, P. & Pavel, M. The psychophysics of visual search [In Process Citation]. *Vision Res* **40**, 1227-68 (2000).
13. Levi, D. M. & Klein, S. A. Hyperacuity and amblyopia. *Nature* **298**, 268-270 (1982).
14. Solomon, J. & Morgan, M. Odd-men-out are poorly localised in brief exposures. *Journal of Vision* **Submitted** (2000).
15. Polat, U. & Sagi, D. The architecture of perceptual spatial interactions. *Vision Research* **34**, 73-78 (1994).
16. Usher, M., Bonnef, Y., Sagi, D. & Herrmann, M. Mechanisms for spatial integration in visual detection: a model based on lateral interactions. *Spat Vis* **12**, 187-209 (1999).
17. Morgan, M. J. & Hotopf, N. Perceived diagonals in grids and lattices. *Vision Research* **29**, 1005-1015 (1989).
18. Malik, J. & Perona, P. Preattentive texture discrimination with early visual mechanisms. *Journal of the Optical Society of America* **A7**, 923-932 (1990).

19. Lin, L.-M. & Wilson, H. R. Fourier and non-Fourier pattern discrimination compared. *Vision Res.* **36**, 1907-1918 (1996).
20. Dakin, S. C. Orientation variance as a quantifier of structure in texture. *Spatial Vision* **12**, 1-30 (1999).
21. Morgan, M. & Baldassi, S. How the human visual system encodes the orientation of a texture and why it makes mistakes. *Current Biology* **7**, 999-1002 (1997).
22. Dow, B. M., Vautin, R. G. & Bauer, R. The mapping of visual space onto foveal striate cortex in the macaque monkey. *J. Neurosci.* **5**, 890-902 (1985).
23. Levitt, J. B., Kiper, D. C. & Movshon, J. A. Receptive fields and functional architecture of macaque V2. *J Neurophysiol* **71**, 2517-42 (1994).
24. Solomon, J. A., Watson, A. B. & Morgan, M. J. Transducer model produces facilitation from opposite-sign flanks. *Vision Res* **39**, 987-92 (1999).
25. Solomon, J. & Morgan, M. Facilitation by collinear flanks is abolished by non-collinear flanks. *Vision Research* **40**, 279-286 (2000).
26. Kolb, F. C. & Braun, J. Blindsight in normal observers. *Nature* **377**, 336-338 (1995).
27. Morgan, M. J., Mason, A. J. S. & Solomon, J. S. "Blindsight" in normal observers. *Nature* **385**, 401-2 (1997).
28. Crick, F. C. & Koch, C. *Nature* **375**, 121-123 (1995).
29. Hubel, D. H. & Wiesel, T. N. Receptive fields of single neurons in the cat's striate cortex. *Journal of Physiology* **148**, 574-591 (1959).
30. Efron, B. Bootstrap methods: another look at the jackknife. *The Annals of Statistics* **7**, 1-26 (1979).
31. Pelli, D. G. & Zhang, L. Accurate control of contrast on microcomputer displays. *Vision Res* **31**, 1337-50 (1991).
32. Watson, A. B. & Solomon, J. A. Psychophysica: Mathematica notebooks for psychophysical experiments (cinematica--psychometrica--quest). *Spat Vis* **10**, 447-66 (1997).
33. Green, D. M. & Swets, J. A. *Signal Detection Theory and Psychophysics* (Wiley, New York, 1966).

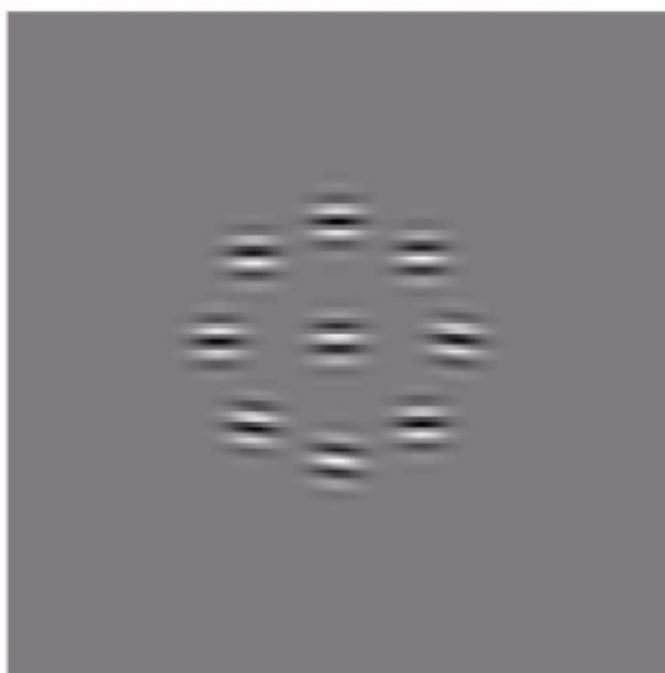
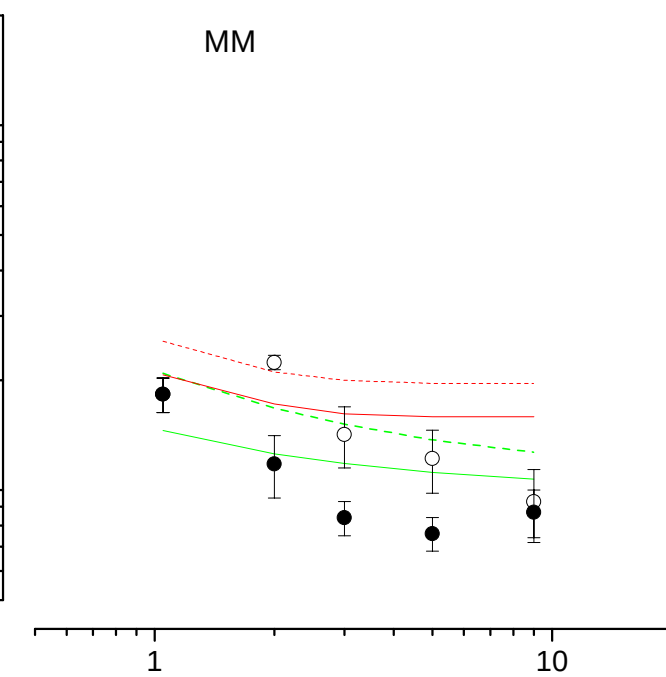
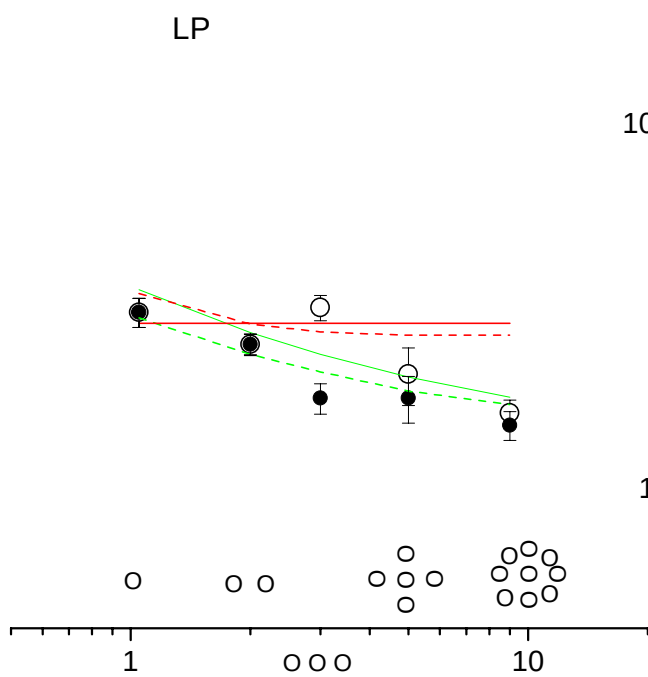
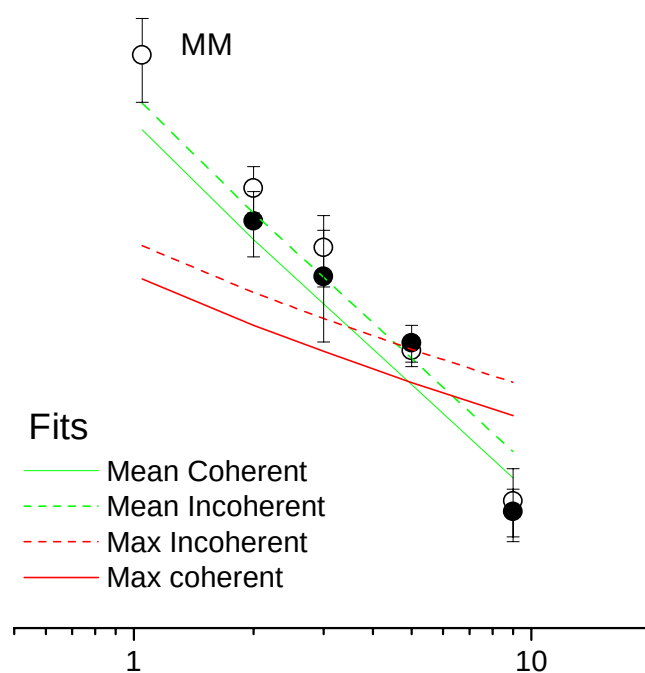
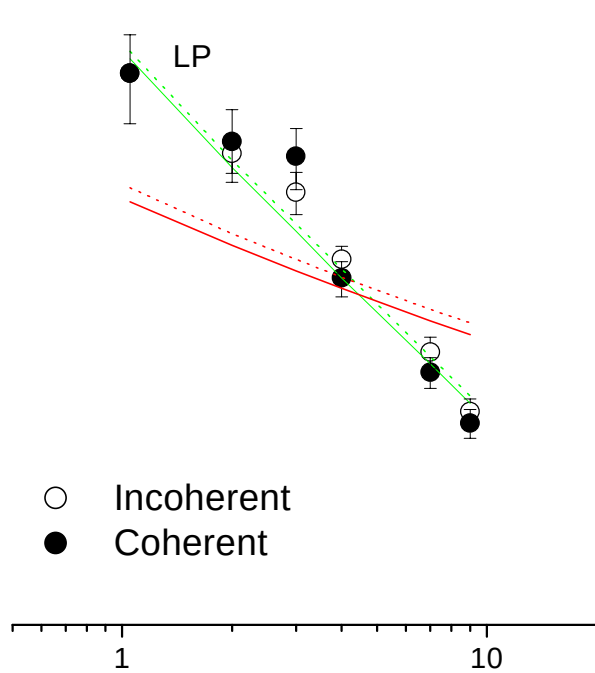


Fig. 1

Orientation Threshold



Number of tilted patches

Fig. 3

