Current Biology *18*, 1162–1167, August 5, 2008 ©2008 Elsevier Ltd All rights reserved DOI 10.1016/j.cub.2008.06.072

Report

Experience Shapes the Utility of Natural Statistics for Perceptual Contour Integration

D. Samuel Schwarzkopf[1] and Zoe Kourtzi[1,]*
[1]School of Psychology
University of Birmingham
Edgbaston, Birmingham B15 2TT
United Kingdom

Summary

Segmenting meaningful targets from cluttered scenes is a fundamental function of the visual system. Evolution and development have been suggested to optimize the brain's solution to this computationally challenging task by tuning the visual system to features that co-occur frequently in natural scenes (e.g., collinear edges) [1–3]. However, the role of shorter-term experience in shaping the utility of scene statistics remains largely unknown. Here, we ask whether collinearity is a specialized case, or whether the brain can learn to recruit any image regularity for the purpose of target identification. Consistent with long-term optimization for typical scene statistics, observers were better at detecting collinear contours than configurations of elements oriented at orthogonal or acute angles to the contour path. However, training resulted in improved detection of orthogonal contours that lasted for several months, suggesting retuning rather than transient changes of visual sensitivity. Improvement was also observed for acute contours but only after longer training. These results demonstrate that the brain flexibly exploits image regularities and learns to use discontinuities typically associated with surface boundaries (orthogonal, acute alignments) for contour linking and target identification. Thus, short-term experience in adulthood shapes the interpretation of scenes by assigning new statistical utility to image regularities.

Results and Discussion

We investigated the role of short-term experience in shaping the ability of the visual system to capitalize on image regularities for the identification of targets in cluttered scenes. Previous studies have shown that learning enhances the ability of observers to detect targets in noise [4–15]. However, the image statistics of the stimuli employed in previous work are consistent with regularities that typically define contours in natural scenes (e.g., collinearity, cocircularity) and for which the visual system is potentially optimized through evolution and development [1–3]. In contrast, to investigate the role of short-term learning in the optimization of visual recognition processes, we chose stimuli that violate these prevalent principles of contour linking.

In particular, we tested whether learning enhances the ability of naive observers to detect contours (Figure 1, Figure S1 available online) that were embedded in noise (i.e., background of randomly oriented Gabor elements) and defined by three different regularities. That is, the Gabor elements defining the contours were aligned either (1) along the contour path (collinear contours), (2) orthogonally to the path (orthogonal contours), or (3) at an acute angle to the contour path (acute contours). Although these contour types contain the same amount of image regularities (aligned local elements) as shown by the analysis of local co-occurrence statistics (Figure 1, Supplemental Data), they are thought to typically serve different purposes in the interpretation of natural scenes. Whereas collinear alignments signify highly probable continuities that have been suggested to mediate contour integration, parallel elements oriented at an angle to contour paths (orthogonal, acute) are more likely to indicate discontinuities (i.e., texture boundaries) that serve as a cue for surface segmentation rather than contour integration [1, 2, 16–18]. Our findings show that the visual system learns to use discontinuities (orthogonal, acute alignments) for contour linking, providing evidence that short-term experience boosts the observers' ability to detect camouflaged targets by shaping the behavioral relevance (i.e., utility) of image statistics.

Specifically, observers (n = 14) judged which of the two stimuli presented successively in a trial contained contours (collinear, orthogonal, acute) rather than only random elements (two-interval forced choice task). We manipulated the alignment of the local Gabor elements with respect to the mean orientation by introducing orientation variability at the local elements (orientation jitter). Consistent with previous studies [19–23] providing evidence for the strength of collinearity as a cue for contour integration in natural scenes, our measurements showed that before training observers were more sensitive to collinear than to orthogonal or acute alignments. Only after training was the observers' sensitivity to the regularities present in orthogonal stimuli enhanced and their performance in detecting contours similar for orthogonal and collinear stimuli (Figure 2A, Figure S2 for individual subject psychometric curves). In particular, before training, observers' accuracy for collinear contours was high for low-orientation jitter and decreased progressively with increasing orientation jitter, consistent with the orientation co-occurrence statistics (Figure 1B). In contrast, performance on orthogonal and acute contours was not significantly different from chance across all orientation jitters. Importantly, training the observers (n = 14) on the detection of orthogonal contours with feedback resulted in increased accuracy (Figure 2A) and decreased response times (Figure S3). Similar learning effects for orthogonal contours were observed when the three contour types were tested with either a blocked (Figure 2A, n = 14) or interleaved (Figure S4A, n = 5) design controlling for task-related strategies and suggesting training-dependent changes in the visual sensitivity for orthogonal contours.

We quantified improvement on the contour detection task during training by two measures: accuracy (percent correct) at zero local orientation jitter, and the orientation jitter at 68% correct performance (threshold) fitting a logistic function (Supplemental Data). Accuracy and threshold measurements increased across training sessions (Figure S5) and were significantly higher after than before training. In contrast, performance for untrained contour types (collinear, acute) did not change significantly with training. In particular,

---

*Correspondence: z.kourtzi@bham.ac.uk

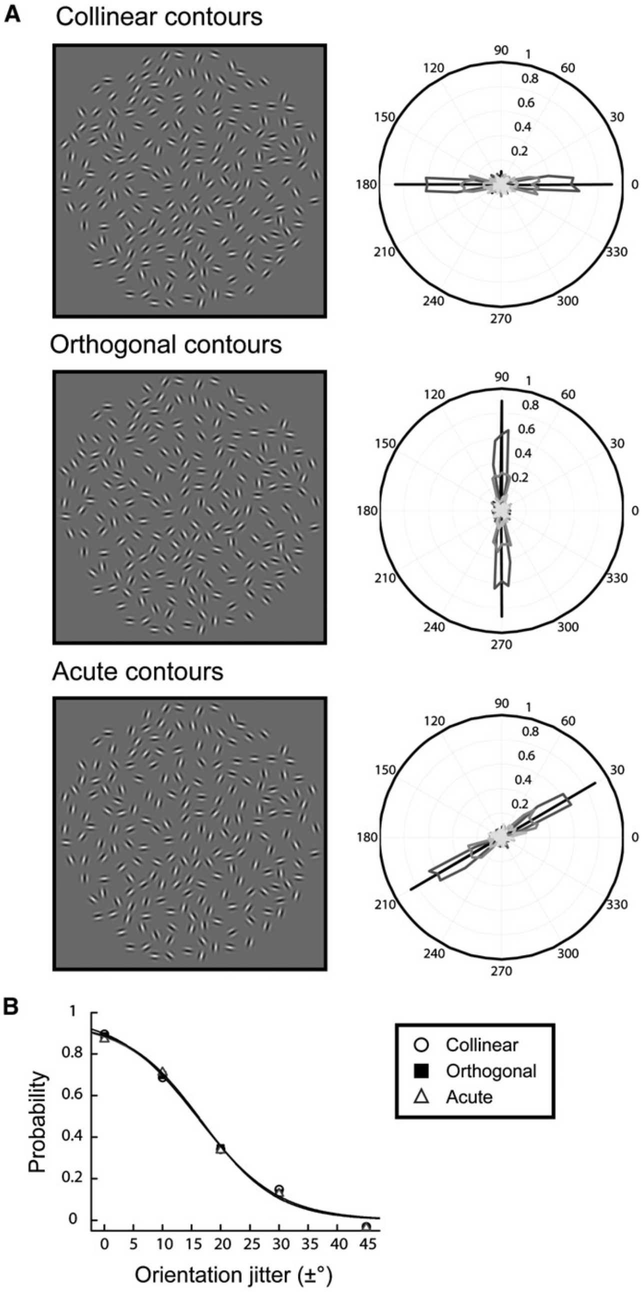


Figure 1. Stimulus Conditions

(A) Examples of stimuli: collinear contours (elements aligned along the contour path), orthogonal contours (elements oriented at 90° to the contour path), and acute contours (elements oriented at 30° to the contour path). For demonstration purposes, Figure S1 shows the same stimuli with the contrast of the background elements reduced. Contours oriented at 45° are shown as example. Local orientation co-occurrence statistics for Gabor elements and their nearest neighbors were calculated by vectorial addition (Supplemental Data). These statistics for each stimulus condition are depicted by polar plots to the right of the stimulus examples. The plots show the probability of the same orientation appearing in the vicinity of each Gabor element (reference) in each of the three stimulus conditions compared to the random stimuli. Polar angles depict the location of neighboring Gabor elements relative to the orientation of the reference element. The radial axis indicates the relative probability that elements of the same orientation are found in this location at different orientation jitters (grayscale coded: colors from dark to light gray indicate 0°–45° orientation jitter).

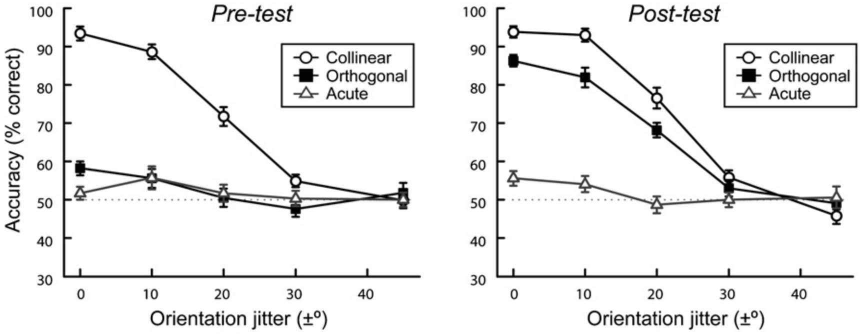
(B) Amount of information present in stimuli containing collinear (circles), orthogonal (squares), and acute (triangles) contours. The probabilities of local orientation co-occurrence were fitted with a Gaussian and the amplitude of this fit is plotted across orientation jitters and fitted with a logistic psychometric function (lines).

a repeated-measures ANOVA showed a significant interaction (accuracy, $F_{1.7,22.2} = 61.2$, $p < 0.001$; threshold, $F_{1.4,18.7} = 106.1$, $p < 0.001$) between stimulus (collinear, orthogonal, acute contours) and session (pre-, post-test). Figure 3 shows learning effects for individual observers by plotting accuracy at zero orientation jitter before training against accuracy after training. Accuracies for orthogonal contours are shifted to the left of the equidistant line (diagonal), consistent with improved performance after training, whereas accuracies for collinear and acute contours are clustered along the diagonal, consistent with the lack of significant learning transfer for these contour types. The lack of improvement for acute or collinear contours after training on orthogonal contours suggests that the improvement for orthogonal contours could not be simply due to practice with the task or exposure to the stimuli during the two test (pre-, post-test) sessions. Further support for this comes from a control experiment (Figure S6A, n = 3) that showed no differences in the detection of orthogonal contours when observers were tested on the two test sessions but did not receive any training in between the test sessions.

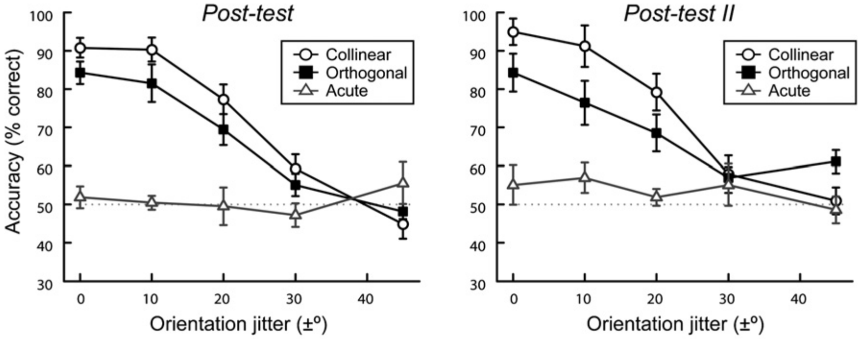
Interestingly, this learning effect for orthogonal contours lasted for a prolonged period. For observers tested 3–5 months (Figure 2B, n = 6) and again 6–8 months (Figure S4B, n = 4) after training, improvement in the detection of orthogonal contours was maintained despite the fact that observers had no additional exposure to these stimuli. These results suggest that the lasting learning effects for orthogonal contours are related to the optimization of perceptual integration processes through experience rather than reflecting simply transient changes in visual sensitivity. Further, similar learning effects were observed when observers (n = 5) did not receive feedback on their responses during training (Figure 2C, unsupervised training). Training resulted in improved performance for orthogonal contours but not collinear or acute contours across sessions (Figure S5), as indicated by a significant interaction of stimulus and session for the 68% threshold ($F_{1.4,5.7} = 13.6$, $p < 0.01$). These results suggest that behavioral improvement may occur without external feedback as when observers search for camouflaged objects in natural scenes, consistent with previous studies [12, 24] showing that the visual system learns in an opportunistic manner by capitalizing on spatiotemporal correlations. The role of task and feedback in learning remains a controversial issue [25] and future work is needed to investigate whether learning occurs when observers are repeatedly exposed to orthogonal contours while performing a task that does not require contour detection.

Finally, we compared the effects of training on orthogonal contours with training on collinear or acute contours. Training on collinear contours (n = 3) showed a slight increase in detection performance but lack of transfer to the other contour types (Figure S6B). This may reflect saturation in detection performance, because observers were already good at detecting collinear contours before training. In contrast, after training on acute contours (n = 7) with elements at 30° or 45° angle to the contour path (Figure 4), performance improved across sessions (regression slope: 2.56, $R^2 = 0.53$, $p < 0.001$). However, learning to detect acute contours required longer training (5400 trials); that is, detection performance after training on acute contours for the same time (1800 trials) as for orthogonal

A Training orthogonal contours with feedback



B Training orthogonal contours: long-term-test after 3-5 months



C Training orthogonal contours without feedback

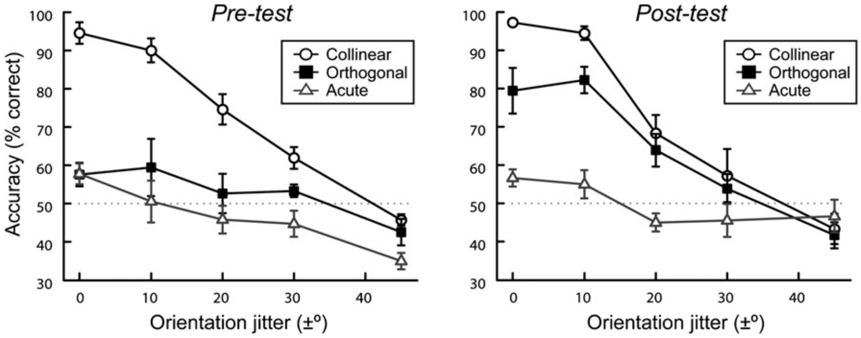


Figure 2. Training on Orthogonal Contours

Psychometric curves (average across observers) for contour-detection performance (percent correct) plotted as a function of local orientation jitter.

(A) Performance for observers (n = 14) before (pretest, left) and after (post-test, right) training on orthogonal contours with feedback. There was a significant improvement in performance for orthogonal contours ($F_{1,13}$ = 300.3, $p < 0.001$), but not for collinear ($F_{1,13} < 1$, p = 0.79) or acute ($F_{1,13}$ = 2.9, p = 0.11) contours.

(B) Performance for observers (n = 6) trained on orthogonal contours with feedback and tested immediately after training (left) and 3–5 months later (right). There was no significant difference in performance between the post-test immediately after training and the second post-test 3–5 months after training (accuracy, $F_{1,5} < 1$, p = 0.48; threshold, $F_{1,5} < 1$, p = 0.71).

(C) Performance for observers (n = 5) before (pretest, left) and after (post-test, right) training on orthogonal contours without feedback. Training resulted in significant improvement in the detection threshold for orthogonal contours ($F_{1,4}$ = 12.9, $p < 0.05$) but not for collinear ($F_{1,4} < 1$, p = 0.61) or acute ($F_{1,4}$ = 0) contours.

Circles, collinear contours; squares, orthogonal contours; triangles, acute contours. Error bars denote ±1 standard error of the mean across observers.

contours (n = 3) was significantly weaker than performance after training on orthogonal contours (t(15) = 7.0, $p < 0.001$).

Could the prolonged training necessary for learning acute compared to orthogonal contours be due to differential sensitivity for these contour types before training? In a total of 38 observers tested across experiments in our study, detection accuracy for orthogonal and acute contours did not differ significantly before training (orthogonal, 56.9% ± 2.9%; acute, 53.3% ± 4.9%, t(74) = 1.5, p = 0.13). However, previous studies have reported higher detection performance for orthogonal than acute contours [23] and better detection performance for orthogonal contours than that observed in our study [19–23]. Unlike previous studies that were conducted on experienced observers, we tested naive participants. Previous experience with the stimuli may have resulted in enhanced performance for orthogonal contours in these studies, consistent with the training-dependent improvement we observed. Further analyses showed that variability in performance before training did not have a significant effect on the outcome of training. We split the data from observers trained on orthogonal contours into two groups based on their pretraining performance: subjects with low pretest levels (accuracy at zero jitter below 60% correct) (n = 12) and subjects with high pretest levels (accuracy at or above 60% correct) (n = 11). No significant differences were observed in detection performance after training between groups (t(21) = 0.86, p = 0.40). This result was confirmed by the lack of a significant correlation (R = 0.26, p = 0.24) between the pre- and post-training data of observers trained on orthogonal contours. Taken together, these results suggest that the behavioral improvement for contour detection reported in our study reflects training-dependent changes in visual sensitivity for image regularities (i.e., orthogonal, acute alignments) rather than differential task difficulty for the detection of these contour types.

In summary, our findings provide novel evidence that learning shapes the utility of image regularities for the detection of contours in cluttered scenes. Although collinearity is a prevalent principle for perceptual integration in natural scenes, we show that the brain learns to exploit other image regularities (i.e., orthogonal and acute alignments) that typically signify discontinuities for contour linking. What is the neural basis of this experience-dependent optimization of perceptual integration processes? Recent neurophysiological studies propose that learning may support efficient target detection [26] by enhancing the salience of targets through increased correlation of neuronal signals related to the target features and decorrelation of signals related to target and background features [25, 27]. Recurrent processing involving intrinsic connections and feedback from higher visual areas [11, 25, 28–30] has been

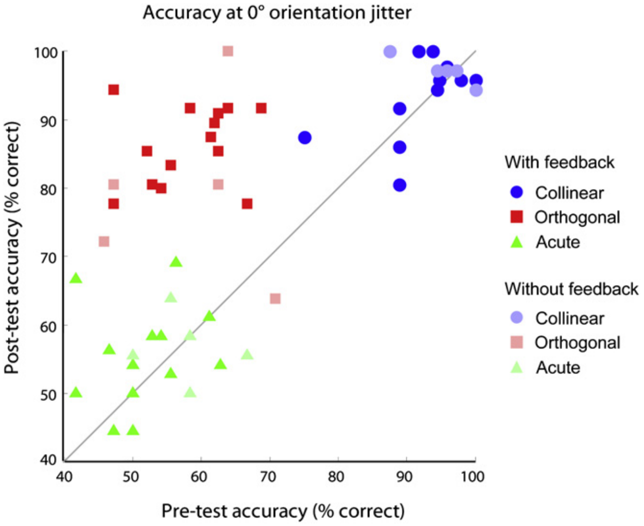


Figure 3. Training on Orthogonal Contours: Individual Observer Data

Accuracy (percent correct) at zero orientation jitter after training is plotted against accuracy before training for individual observers trained on orthogonal contours. Blue circles, collinear contours; red squares, orthogonal (trained) contours; green triangles, acute contours. Dark colors indicate accuracy for training with feedback, and lighter colors indicate accuracy for training without feedback.

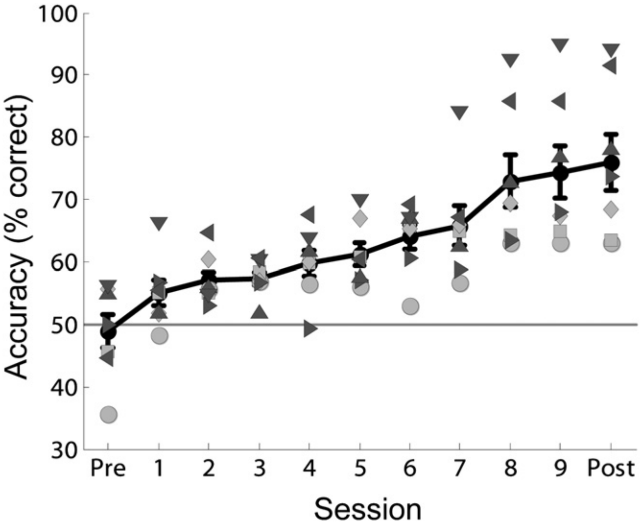


Figure 4. Training on Acute Contours

Detection performance for observers trained with feedback for 5400 trials on acute contours (n = 3 for acute contours with elements at 30° angle, light gray symbols; n = 4 for acute contours with elements at 45°, dark gray symbols). Symbols denote performance at zero orientation jitter. Mean accuracy (percent correct) across all observers (black solid line) is shown for each session (pre, pretest; post, post-test; numbered training sessions). Error bars denote ±1 standard error of the mean across observers.

suggested to modulate perceptual integration and figure-ground segmentation as early as in V1 [31, 32]. Experience-dependent plasticity in these circuits may result in retuning of neural sensitivity to contours defined by discontinuities.

Interestingly, our findings show that longer training is necessary for acute than for orthogonal alignments. Previous studies showing center-surround interactions beyond the classical receptive field of V1 neurons [33–37] provide insights in understanding these differences in the integration of parallel local elements to global contours. Numerous studies suggest that these center-surround interactions are complex and may vary from facilitatory to inhibitory depending on contrast and context (for reviews [30, 38–40]. A possible scenario offered by this previous work is that facilitatory interactions along the neurons' preferred orientation may support collinear correlations, whereas inhibitory interactions along an axis orthogonal to the cell's preferred orientation may relate to decorrelation of signals in texture boundaries and surface segmentation [2]. Thus, it is possible that orthogonal alignments are more effective cues for segmentation than acute ones because of potentially stronger center-surround modulations for elements at right than at acute angles to the neurons' preferred orientation. In line with this interpretation, a previous study showing poor performance for experienced observers in the detection of acute contours [23] suggests that the associations linking edges into contours are weaker for acute than for collinear or orthogonal alignments. We demonstrate that the visual system is able to exploit acute alignments for contour linking through learning, potentially by enhancing these weak associations. However, in naive observers, longer training is necessary for boosting these weak associations and detecting acute contours in cluttered scenes than the amount of training sufficient for detecting orthogonal contours. Although previous studies on edge co-occurrence statistics suggest similar probability of occurrence for different types of parallel alignments (orthogonal, acute) in natural scenes [2, 16], further work is needed to investigate whether the behavioral and neural bias for orthogonal contours relate to higher-order statistics in textures [23]. It is possible that prolonged training is necessary for stronger improvement when learning to exploit these statistics for contour linking, similar to the extensive exposure necessary for the recalibration of visual processing in cases of atypical input (e.g., distortions or visual field reversal [41, 42]).

Conclusions

Evolution and long-term experience during development [1–3, 9, 40] have been suggested to shape the neural architecture of the visual cortex in a manner that resembles the geometry of natural scenes and supports the integration of collinear edges. Here, we provide evidence that experience at shorter time scales in adulthood plays an important role in the functional optimization of the visual system for the perceptual interpretation of natural scenes. We show that learning enhances the ability of the observers to detect targets in cluttered scenes whose local statistics do not typically signify contours in the natural environment. These findings suggest that experience shapes the interpretation of natural scenes by retuning the utility of image regularities to support the perceptual integration of contours. That is, the visual system learns to capitalize on statistical regularities in the visual input. Similar experience-dependent mechanisms may contribute in the first place, during the early postnatal period, to the enhanced perceptual salience of collinear contours that appear frequently in natural scenes and are therefore reinforced in natural environments.

Experimental Procedures

Participants

A total of 38 observers (mean age, 23.8 ± 0.6 years; range, 18–34 years) participated in the study. Each observer participated in only one of the experiments and none of the observers had previous experience with contour integration experiments. All observers had normal or corrected to normal vision and gave written informed consent, and the study was approved by the local ethics committee.

Stimuli

Stimuli were Gabor fields comprising 200 elements presented within a circular aperture (8° of visual angle in diameter) (Figure 1, Figure S1) and rendered on an equiluminant gray background (mean luminance = 17.5 cd/m^2). The effective width of the Gabor patches was 0.35° of visual angle. Target stimuli contained five parallel contours that were defined by Gabor elements placed along straight paths and were embedded in a background of randomly positioned and oriented Gabor elements.

We generated stimuli for three different conditions (Figure 1) defined by the mean orientation of the local elements with respect to the orientation of the contour: Gabor elements could be aligned either along the contour path (collinear contours), perpendicular (orthogonal contours), or at an angle of 30° or 45° (acute contours). All contours in a stimulus had the same global orientation that varied between 15° and 165° (12.25°–169.75°, when training on acute contours with 45° element alignment), in increments of 30° (22.5°) excluding cardinal orientations across stimuli. We also generated random stimuli that were created by shuffling the local orientations of all the elements in the field. That is, for every stimulus in each condition (collinear, orthogonal, acute), we generated a shuffled stimulus. Further details on stimulus generation are reported in the Supplemental Data.

Procedure

Observers completed two psychophysical test sessions, one prior to training (pretest) and one after training (post-test). During training, observers completed 3–5 sessions (i.e., 1800–3000 trials) for training on orthogonal and collinear contours, and 9 sessions (i.e., 5400 trials) for training on acute contours. In both test and training sessions, observers performed a two-interval forced choice (2IFC) contour detection task. In test sessions, performance for all three contour types was tested and observers completed 540 trials per session (i.e., 36 trials per level of orientation jitter and stimulus condition). In training sessions, observers were trained on one of the three contour types for 600 trials per session (120 trials per orientation jitter level). Different groups of observers were trained on different contour types. More details are included in Supplemental Data.

Supplemental Data

Supplemental Data include Supplemental Experimental Procedures and six figures and are available at http://www.current-biology.com/cgi/content/full/18/15/1162/DC1/.

Acknowledgments

We would like to thank Vera Chen and Sarah Rappaport for help with pilot experiments. We would also like to thank Keith May and Robert Hess for helpful discussions, and Denis Levi, Pieter Roelfsema, and Frank Sengpiel for their valuable comments and suggestions on the manuscript. The work was supported by a BBSRC grant (BB/D52199X/1) and the Cognitive Foresight Initiative (BB/E027436/1) to Z.K.

Received: February 26, 2008
Revised: June 26, 2008
Accepted: June 27, 2008

References

1. Geisler, W.S. (2008). Visual perception and the statistical properties of natural scenes. Annu. Rev. Psychol. *59*, 167–192.
2. Sigman, M., Cecchi, G.A., Gilbert, C.D., and Magnasco, M.O. (2001). On a common circle: Natural scenes and Gestalt rules. Proc. Natl. Acad. Sci. USA *98*, 1935–1940.
3. Simoncelli, E.P., and Olshausen, B.A. (2001). Natural image statistics and neural representation. Annu. Rev. Neurosci. *24*, 1193–1216.
4. Dosher, B.A., and Lu, Z.L. (1998). Perceptual learning reflects external noise filtering and internal noise reduction through channel reweighting. Proc. Natl. Acad. Sci. USA *95*, 13988–13993.
5. Furmanski, C.S., and Engel, S.A. (2000). Perceptual learning in object recognition: Object specificity and size invariance. Vision Res. *40*, 473–484.
6. Eckstein, M.P., Abbey, C.K., Pham, B.T., and Shimozaki, S.S. (2004). Perceptual learning through optimization of attentional weighting: Human versus optimal Bayesian learner. J. Vis. *4*, 1006–1019.
7. Li, R.W., Levi, D.M., and Klein, S.A. (2004). Perceptual learning improves efficiency by re-tuning the decision ‘template’ for position discrimination. Nat. Neurosci. *7*, 178–183.
8. Gold, J., Bennett, P.J., and Sekuler, A.B. (1999). Signal but not noise changes with perceptual learning. Nature *402*, 176–178.
9. Kovacs, I., Kozma, P., Feher, A., and Benedek, G. (1999). Late maturation of visual spatial integration in humans. Proc. Natl. Acad. Sci. USA *96*, 12204–12209.
10. Sigman, M., and Gilbert, C.D. (2000). Learning to find a shape. Nat. Neurosci. *3*, 264–269.
11. Gilbert, C.D., Sigman, M., and Crist, R.E. (2001). The neural basis of perceptual learning. Neuron *31*, 681–697.
12. Brady, M.J., and Kersten, D. (2003). Bootstrapped learning of novel objects. J. Vis. *3*, 413–422.
13. Fahle, M. (2004). Perceptual learning: a case for early selection. J. Vis. *4*, 879–890.
14. Fine, I., and Jacobs, R.A. (2002). Comparing perceptual learning tasks: A review. J. Vis. *2*, 190–203.
15. Sagi, D., and Tanne, D. (1994). Perceptual learning: Learning to see. Curr. Opin. Neurobiol. *4*, 195–199.
16. Geisler, W.S., Perry, J.S., Super, B.J., and Gallogly, D.P. (2001). Edge co-occurrence in natural images predicts contour grouping performance. Vision Res. *41*, 711–724.
17. Kruger, N., and Worgotter, F. (2002). Multi-modal estimation of collinearity and parallelism in natural image sequences. Network *13*, 553–576.
18. Elder, J.H., and Goldberg, R.M. (2002). Ecological statistics of Gestalt laws for the perceptual organization of contours. J. Vis. *2*, 324–353.
19. Field, D.J., Hayes, A., and Hess, R.F. (1993). Contour integration by the human visual system: evidence for a local “association field”. Vision Res. *33*, 173–193.
20. Hess, R., and Field, D. (1999). Integration of contours: New insights. Trends Cogn. Sci. *3*, 480–486.
21. Bex, P.J., Simmers, A.J., and Dakin, S.C. (2001). Snakes and ladders: The role of temporal modulation in visual contour integration. Vision Res. *41*, 3775–3782.
22. Hess, R.F., Ledgeway, T., and Dakin, S. (2000). Impoverished second-order input to global linking in human vision. Vision Res. *40*, 3309–3318.
23. Ledgeway, T., Hess, R.F., and Geisler, W.S. (2005). Grouping local orientation and direction signals to extract spatial contours: Empirical tests of “association field” models of contour integration. Vision Res. *45*, 2511–2522.
24. Fiser, J., and Aslin, R.N. (2002). Statistical learning of new visual feature combinations by infants. Proc. Natl. Acad. Sci. USA *99*, 15822–15826.
25. Li, W., Piech, V., and Gilbert, C.D. (2008). Learning to link visual contours. Neuron *57*, 442–451.
26. Barlow, H. (1990). Conditions for versatile learning, Helmholtz’s unconscious inference, and the task of perception. Vision Res. *30*, 1561–1571.
27. Jagadeesh, B., Chelazzi, L., Mishkin, M., and Desimone, R. (2001). Learning increases stimulus salience in anterior inferior temporal cortex of the macaque. J. Neurophysiol. *86*, 290–303.
28. Gilbert, C.D., and Wiesel, T.N. (1989). Columnar specificity of intrinsic horizontal and corticocortical connections in cat visual cortex. J. Neurosci. *9*, 2432–2442.
29. Hochstein, S., and Ahissar, M. (2002). View from the top: Hierarchies and reverse hierarchies in the visual system. Neuron *36*, 791–804.
30. Fitzpatrick, D. (2000). Seeing beyond the receptive field in primary visual cortex. Curr. Opin. Neurobiol. *10*, 438–443.
31. Zipser, K., Lamme, V.A., and Schiller, P.H. (1996). Contextual modulation in primary visual cortex. J. Neurosci. *16*, 7376–7389.
32. Roelfsema, P.R. (2006). Cortical algorithms for perceptual grouping. Annu. Rev. Neurosci. *29*, 203–227.
33. Knierim, J.J., and van Essen, D.C. (1992). Neuronal responses to static texture patterns in area V1 of the alert macaque monkey. J. Neurophysiol. *67*, 961–980.
34. Kapadia, M.K., Westheimer, G., and Gilbert, C.D. (2000). Spatial distribution of contextual interactions in primary visual cortex and in visual perception. J. Neurophysiol. *84*, 2048–2062.
35. Li, Z. (1998). A neural model of contour integration in the primary visual cortex. Neural Comput. *10*, 903–940.

36. Ursino, M., and La Cara, G.E. (2004). A model of contextual interactions and contour detection in primary visual cortex. Neural Netw. *17*, 719–735.
37. Yen, S.C., and Finkel, L.H. (1998). Extraction of perceptually salient contours by striate cortical networks. Vision Res. *38*, 719–741.
38. Angelucci, A., and Bressloff, P.C. (2006). Contribution of feedforward, lateral and feedback connections to the classical receptive field center and extra-classical receptive field surround of primate V1 neurons. Prog. Brain Res. *154*, 93–120.
39. Chisum, H.J., and Fitzpatrick, D. (2004). The contribution of vertical and horizontal connections to the receptive field center and surround in V1. Neural Netw. *17*, 681–693.
40. Gilbert, C.D. (1992). Horizontal integration and cortical dynamics. Neuron *9*, 1–13.
41. Sugita, Y. (1996). Global plasticity in adult visual cortex following reversal of visual input. Nature *380*, 523–526.
42. Adams, W.J., Banks, M.S., and van Ee, R. (2001). Adaptation to three-dimensional distortions in human vision. Nat. Neurosci. *4*, 1063–1064.