Interocular transfer in perceptual learning of a pop-out discrimination task

ANIEK A. SCHOUPS* AND GUY A. ORBAN

Laboratorium voor Neuro- en Psychofysiologie, Katholieke Universiteit Leuven, Campus Gasthuisberg, B-3000 Leuven, Belgium

ABSTRACT The specificity of the improvement in perceptual learning is often used to localize the neuronal changes underlying this type of adult plasticity. We investigated a visual texture discrimination task previously reported to be accomplished preattentively and for which learning-related changes were inferred to occur at a very early level of the visual processing stream. The stimulus was a matrix of lines from which a target popped out, due to an orientation difference between the three target lines and the background lines. The task was to report the global orientation of the target and was performed monocularly. The subjects' performance improved dramatically with training over the course of 2–3 weeks, after which we tested the specificity of the improvement for the eye trained. In all subjects tested, there was complete interocular transfer of the learning effect. The neuronal correlates of this learning are therefore most likely localized in a visual area where input from the two eyes has come together.

The specificity of improvement in performance with perceptual training is widely regarded as the key to the neurological localization of the learning effect. For simple tasks, the learning effect is specific for some particular stimulus attributes, such as orientation (1–3) and spatial frequency (4). Moreover, the improvement in performance observed in these simple tasks remains restricted to stimulus position in the subject's visual field (3–8). By contrast, for more complex tasks, the learned improvement transferred to different stimulus attributes as well as to other positions in the visual field (9).

Specificity of the learning effect to particular stimulus attributes and to stimulus position implies that the improvement in performance is due to changes in populations of neurons at early stages of the visual pathway, where neurons are highly specialized for simple stimulus attributes and for stimulus position and size, in contrast to neurons in higher visual areas, which generalize over these stimulus variables.

Another important facet of perceptual learning is eye-specificity. Monocularity of the learning effect indicates that the neuronal correlates of the learning must be present in an area where input from the two eyes is still segregated, and thus in layer 4 of the primary visual cortex or in the lateral geniculate nucleus. Specificity to the eye trained is a very rare phenomenon in perceptual learning and only likely for very simple tasks. In most tasks, such as pop-out detection (8, 10), orientation discrimination (3), discrimination of grating spatial phase (4), discrimination of the direction of motion or color discrimination (11–13), and discrimination of random dot displacement (14), interocular transfer of learning is observed. In fact, monocularity of the learning effect has been reported in only two perceptual learning studies. One of them is a study of vernier hyperacuity training (6). However, in hyperacuity tests, minor differences in refraction between the two eyes could cause significant performance differences. Moreover, a

recent study (15) did show interocular transfer in a vernier acuity task similar to that used in ref. 6. The other reported case of monocular learning is Karni and Sagi's study (5) of a texture discrimination task. In their paradigm, three tilted (oblique) lines are aligned so that they form a target rectangle amidst a background of horizontal lines, and the task is to report the global orientation of this target. The target is reported to "pop out," and the task performed in an "automatic and preattentive" manner (16). Since it was reported that a background of tilted lines increases the difficulty of such a task (17, 18), we wondered whether perceptual learning of the more difficult task would be localized higher in the visual pathway, resulting in binocularity of its learning effect. We therefore used Karni and Sagi's (5) learning paradigm with the horizontal background lines as a control and compared the specificity of learning in their task with that in the task using the stimulus with the tilted background lines. We found marked improvement with training in the performance of either task. However, in both tasks, the learning effect transferred almost completely from trained to untrained eye. Position and orientation specificity were also tested with mixed results. (These data are beyond the scope of this publication and will be published elsewhere.) We conclude that perceptual learning in even a simple texture discrimination task occurs at a stage in the visual pathway where binocular convergence of visual input has occurred—i.e., at a stage higher than layer 4 of the primary visual cortex.

METHODS

Stimulus. The stimulus was an array of line segments (see Fig. 1*A*). The target consisted of three horizontally or vertically aligned lines, which segregated from the background lines by their orientation difference. Two types of stimuli were used in this study. One was that described by Karni and Sagi (5), in which the target lines are oblique and the background lines are horizontal. We trained four subjects on the discrimination task using this stimulus. In the other stimulus, the target lines were also oblique, but the background lines were oblique as well, oriented orthogonally to the target lines (see Fig. 1*A*). Three subjects were trained in the discrimination task using this stimulus. In both types of stimuli, the line in the center of the matrix was replaced by a letter ("T" or "L"). In all cases, the mask consisted of superimposed target and background lines, and a compound pattern of superimposed T and L at the center.

Task: Performance Tests and Training. Subjects had normal or corrected to normal eyesight. Refraction of both eyes was tested before training and did not to differ by more than 0.25 diopter. To control for fixation, the subjects performed two tasks concurrently. For each trial subjects were asked first to identify the letter at fixation point and then to report the global orientation (H or V) of the target. After each trial, accuracy feedback was presented through a computer tone only for the

Abbreviation: SOA, stimulus-to-mask-onset asynchrony.
*To whom reprint requests should be addressed.

fixation control task. Performance for the letter identification task (the fixation control task) improved very quickly and reached asymptote well before performance for the target orientation identification task.

Monocular training. The subjects ($n = 6$) viewed the stimuli monocularly, in a dark room, using a chin support. On the first day, subjects were tested for monocular performance in the discrimination task by using either eye. Eye dominance was tested by using a simple sighting method. The subject was asked to view a distant object with both eyes through a small aperture in a card. The subject was asked to close each eye in turn to see if the object disappeared. The eye used to sight the object was judged to be dominant. Subsequent daily training sessions were monocular and consisted of 8–16 blocks of 50 trials each. The trial sequence was as described by Karni and Sagi (5). Subjects were instructed to fixate a small cross and then to activate the stimulus presentation sequence, which was as follows: blank screen (250–350 msec), the stimulus (17 msec), blank interstimulus interval (variable), the mask (100 msec), and blank screen until response (no time limit). Performance was measured as the percent correct responses for different intervals between stimulus onset and mask onset (SOA, stimulus-to-

mask-onset asynchrony). At the beginning of each daily session, the SOA was set to the shortest SOA in which a 90% correct performance was obtained in the previous session and was then decreased in steps of 17 msec until chance performance was reached. Per SOA time setting, 100–250 trials were run. A psychometric curve representing the correct response level as a function of SOA was constructed daily. Threshold SOA was defined by the 80% correct response level, as derived from the psychometric curves for each daily session (see Fig. 1B).

Testing transfer of the learning effect. After reaching stable threshold SOA, the subjects were tested monocularly for performance with the untrained eye. Testing was identical to the training protocols insofar as that the subjects were first tested with a high SOA, which was then decreased according to performance.

Double flash resolution. Two subjects were tested for their performance in a double flash resolution task before and after training. The subjects had to indicate whether they saw one or two pulses of centrally-presented squares of $2° \times 2°$, displayed for 17 msec. To determine threshold resolution time, we used
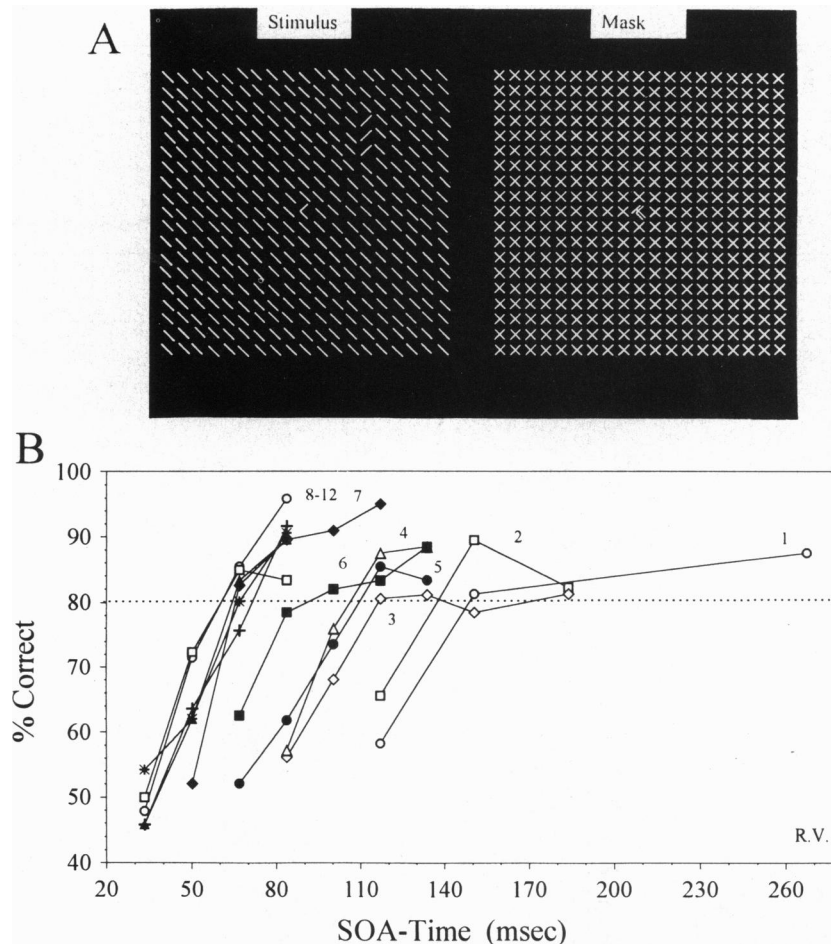

FIG. 1.   (A) The stimulus (*Left*) with tilted background lines. The stimulus was a $14° \times 14°$ matrix consisting of 19×19 green lines (width, 0.015°; length, 0.5°) on a black background. Three lines, with right oblique orientation, were aligned such that they formed a vertical (as in the stimulus shown here) or horizontal rectangle. The task was to report the global orientation of this target rectangle. The surrounding lines, with left oblique orientation, formed the background. During training, target position varied randomly from trial to trial but remained within the same quadrant, within 2.5°–5° from the fixation point and at least 1° from the horizontal and vertical meridian. The mask (*Right*) was an identically sized matrix, consisting of crossed oblique lines. The individual line elements of the stimulus and mask jittered randomly over a distance of 0.09°. During testing and training, 1 of 20 different (i.e., only differing from one another by the jitter) stimuli and 1 of 20 different masks were shown on each trial. The stimuli were displayed on a Philips Brilliance color monitor (resolution, 1024×768; frame refresh rate, 60 Hz). In the other type of stimulus used (not shown here) the target lines were also oblique but the orientation of the background lines was horizontal; its mask consisted of crossed oblique and horizontal lines. (B) Psychometric curves for subject RV trained with the stimulus shown in A. The curves represent consecutive training sessions (numbered as indicated above the curves). Each data point is the mean percent correct responses from 2–5 blocks of 50 trials each, for a specific SOA. The stippled line is the 80% correct response level used to determine the subject's threshold SOA for each training session.

two randomly intermingled staircases that converged on the 50% correct detection criterion.

RESULTS

Using either stimulus, all subjects improved in the texture discrimination task. Fig. 1B shows the psychometric curves for all consecutive training days for subject RV monocularly practicing texture discrimination with the stimulus shown in Fig. 1A. The time interval between stimulus onset and the appearance of the mask (SOA) sets the temporal limit of stimulus availability. The SOA required for 80% correct performance became shorter with training. The results shown in Fig. 1B are representative for all subjects, in that the psychometric curve shifted toward lower SOA values over consecutive training sessions—i.e., performances improved as a function of practice. The monocular learning curves of all subjects are shown in Fig. 2, where the 80% threshold SOA is given as a function of the number of training sessions. Subjects whose performance is shown in Fig 2A were trained with the stimulus with horizontal background lines, whereas those in Fig. 2B were trained with oblique background lines. For all

subjects, thresholds on the first day of training were significantly different from thresholds on the last day of training (ANOVA, $P < 0.001$). Pretraining threshold SOAs were similar for all subjects in Fig. 2A and B (except for subject PJ). The three subjects who trained with the oblique background lines (Fig. 2B) seemed to learn more slowly than the subjects in Fig. 2A, requiring more intermediate SOAs to reach the final threshold SOA. After practice, threshold SOAs in Fig. 2B fell to a third of the pretraining value, to a median SOA of 61.2 msec. Threshold SOAs of the subjects in Fig. 2A (median SOA for the four subjects, 81.3 msec) were slightly higher than in Fig. 2B and were also higher than the values reported by Karni and Sagi (5). The latter difference could be due to a difference in masking efficiency, since we used a superposition of target and background lines as masks, different from that described by Karni and Sagi (5). Otherwise, stimulus and training paradigm in Fig. 2A were identical to those used by Karni and Sagi. We observed no reduction in threshold SOA within training sessions; rather, the training effect was apparent only from one daily session to the next.

It is possible that part of the learning is brought about by a nonspecific improvement in temporal resolution. We therefore
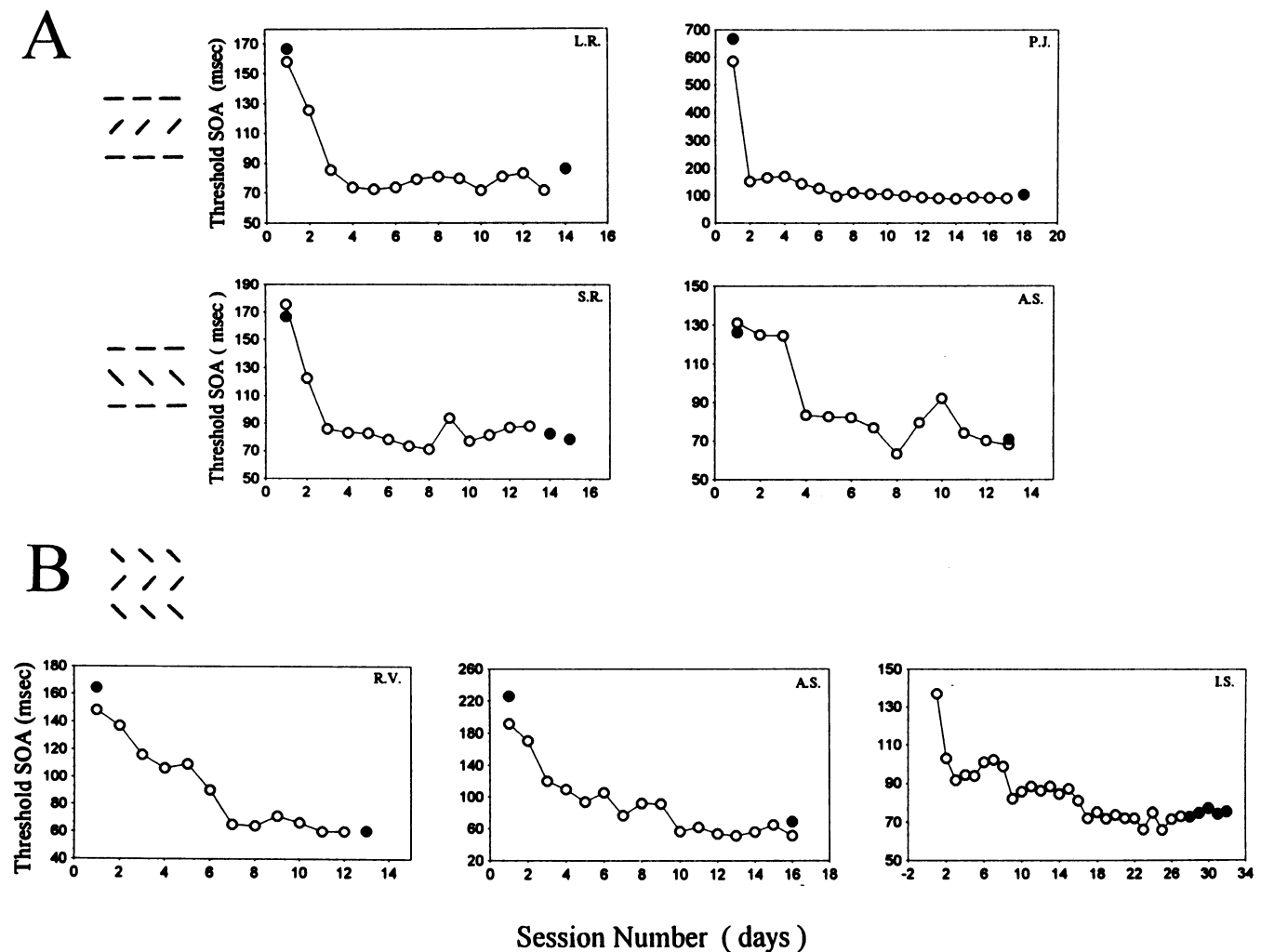

Session Number (days)

FIG. 2.   Learning curves representing the SOA required for 80% correct discrimination on consecutive sessions. ○, Trained eye; ●, untrained eye. (A) Subjects trained for the stimulus with horizontal background lines. Two subjects (LR and PJ) were trained with right oblique target orientation, and two subjects (AS and SR) were trained with left oblique target orientation. (B) Subjects trained for the stimulus shown in Fig. 1A. Background line orientation was left oblique; target line orientation was right oblique. Subject IS was also tested for performance of the task through either eye, and both eyes gave similar results. However, not enough data points were obtained to construct a psychometric curve and extract a threshold SOA of the eye to remain untrained. Subject AS was first trained with oblique background lines (B), and subsequently with horizontal background lines (A). Standard errors, not shown on the graphs for the sake of clarity, amounted to <10% of the threshold SOAs on the first session, and between 1 and 4% on the last training session, for trained and untrained eye.

Neurobiology: Schoups and Orban

Proc. Natl. Acad. Sci. USA 93 (1996)   7361

Table 1. Threshold SOA ± SD (msec) for the resolution of two light pulses before and after monocular training of the pop-out discrimination task

	Before training	After training
Subject LR		
Left eye (untrained)	41.5 ± 0.5	41.6 ± 0.4
Right eye (trained)	42.2 ± 0.2	42.4 ± 0.9
Subject PJ		
Left eye (untrained)	57.9 ± 0.4	58.3 ± 0.0
Right eye (trained)	57.8 ± 0.3	57.9 ± 0.3

Data are derived from two double staircases of 80-trials each. ANOVA showed no effect of eye or training on the threshold SOA for either subject.

showed two pulses of light separated by a dark interval to the same part of the retina to two subjects before and after training for texture discrimination and measured the threshold to perceive the pulses as separate instead of as a single flash. Threshold SOAs for each eye of the two subjects before and after training are shown in Table 1. No effect of training could be observed. Before training for the texture discrimination task the thresholds were already well below the SOA necessary for texture discrimination, and they were unaffected by training.

The effect of monocular training for texture discrimination completely transferred to the other, untrained eye. This is evident from Fig. 2. ANOVA indicated for all subjects a highly significant effect of training both for the trained and the untrained eye ($P < 0.001$). No differences between the two eyes could be demonstrated, neither before nor after training. Eye dominance did not affect the occurrence of interocular transfer: training started with the nondominant eye in subjects AS, RV, and SR, and with the dominant eye in subjects IS, LR, and PJ. Thresholds for the untrained eye (median 84.55 msec for subjects shown in Fig 2A, median 68.7 msec for subjects shown in Fig. 2B) were not different from those measured for the eye that was exposed to the stimulus for 12–26 sessions. Moreover, after continuing to practice the untrained eye, there was no further improvement (see subject IS shown in Fig 2B). Thus, with all subjects, the training effect in both tasks transferred interocularly.

DISCUSSION

As previously demonstrated by Karni and Sagi (5), training for an "automatic preattentive" discrimination task using a texture consisting of oblique target lines and horizontal or vertical background lines leads to improvement in performance. Karni and Sagi found that the learning is local, monocular, and specific for the local orientation of the background lines. We used the same stimulus and training paradigm as that described by Karni and Sagi and extended their study to stimuli consisting of other orientations of target and background lines. In agreement with their observations, we noted that performance improved with training. In addition, we demonstrated that the learning effect could not be ascribed to a nonspecific improvement in temporal resolution.

In contrast to Karni and Sagi's findings (5), however, the learning effect obtained through monocular training did not remain restricted to the trained eye. When viewing the stimuli through the eye that had not been exposed to the stimuli during training, the same improvement was observed as for the trained eye. These findings disagree with those reported by Karni and Sagi, who found no interocular transfer of the learned discrimination task, and therefore concluded that this type of learning would be localized at or before primary visual cortex layer 4. However, there are many psychophysical, physiological, and anatomical data that are hard to reconcile with that conclusion and agree with the data presented here.

(i) Learning pop-out detection has been shown to transfer to the untrained eye, to mirror image stimuli, to enlarged stimuli, and across hemispheres, suggesting that the site of perceptual learning for pop-out detection is at a cortical area beyond V1 (10). These results are supported by the findings of Wolfe and Franzel (19), which suggest that visual search is performed at a stage that utilizes binocular information. A task such as the one we described here is computationally more complex than pop-out detection because it involves not only detection but also discrimination of the global orientation of the target, and is more likely to involve further visual cortical processing than the pop-out detection task.

(ii) It has emerged from psychophysical studies attempting to localize the neuronal correlates of training-related perceptual improvement that the learning effect is most probably implemented in those brain areas that normally decode the stimuli involved in the training paradigm (20). In accord with this idea, Karni and Sagi (5) found monocularity for a basic visual discrimination task that could be accomplished in an automatic, preattentive manner, and they postulated that the learning effect would also be localized at a very low level of the visual system, at or before cortical area 17. However, does this task really occur in an automatic, preattentive way? Verghese and Nakayama (21) showed that even at an orientation difference of 90°, at which the target has been shown to "pop out," the display duration required to discriminate increases with the number of elements, suggesting serial processing. He and Nakayama (22) further postulated that in order to see textures, the system must operate at a level beyond that of early cortical filters.

(iii) In pattern backward masking, mask and target are often presented dichoptically (23). This indicated that the masking occurs centrally, for which we now have physiological evidence (24, 25). The learning effect involved in the task described here is most likely localized centrally as well, in populations of neurons that have access to information from both eyes.

(iv) It is rather unexpected to find monocularity even for simple tasks since the number of monocular neurons is relatively small even in primary visual cortex; more importantly, when training monocularly, binocular cells will be involved as well. As pointed out by Karni and Sagi (5), the learning effect involves orientation-specific mechanisms. However, the likelihood of finding monocularity in orientation-specific learning is even lower because most monocular cells have been shown to be nonselective for stimulus orientation. Indeed, evidence from electrophysiology as well as 2-deoxyglucose (2-DG) and optical imaging studies argues for a correlation between orientation selectivity and binocular input: (a) in layers 4A and 4Cb, cells are probably exclusively monocular and nonoriented (26–28), while in layer 4Ca, more binocular as well as oriented cells (26, 29, 30) and orientation columns (30) are found; (b) in the cytochrome oxidase blobs in layer 3, nonoriented cells tended to be more monocular (30); and (c) as for the uppermost layers studied with optical imaging methods, Blasdel (31) demonstrated that orientation selectivity is highly correlated with binocularity, and that regions strongly dominated by one eye and regions strongly selective for orientation are partially segregated.

(v) A recent study has shown that discrimination of the global orientation of a group of three tilted lines embedded in a background of six by six elements of orthogonal orientation was severely disrupted after a selective lesion of either V2 or V4 in the macaque (32, 33). These data indicate that, at least in macaque monkey, V1 is not sufficient by itself for this type of texture discrimination. The learning effect of this type of texture segregation is then most likely localized beyond layer 4 of area 17, which is consistent with our findings of interocular transfer.

How can we explain the differences between our data and those reported by Karni and Sagi (5)? We initially thought that

a pronounced dominance of either eye could be responsible for the difference between our data and the monocularity of the learning effect observed by Karni and Sagi. Movshon *et al.* (34) have shown that normal subjects showed greater transfer of the tilt-after effect from the dominant eye to the nondominant than *vice versa*. We therefore tested eye dominance of our subjects. However, this does not seem to be a possible factor in determining interocular transfer since interocular transfer of learning was observed whether the transfer was from the dominant to the nondominant eye, or *vice versa*. Therefore, we are at a loss to account for the difference between our data and those reported by Karni and Sagi (5).

1. Vogels, R. & Orban, G. A. (1985) *Vision Res.* **25**, 1679–1687.
2. Shiu, L.-P. & Pashler, H. (1992) *Percept. Psychophys.* **52**, 582–588.
3. Schoups, A., Vogels, R. & Orban, G. (1995) *J. Physiol. (London)* **483**, 797–810.
4. Fiorentini, A. & Berardi, N. (1981) *Vision Res.* **21**, 1149–1158.
5. Karni, A. & Sagi, D. (1991) *Proc. Natl. Acad. Sci. USA* **88**, 4966–4970.
6. Fahle, M. (1994) *Perception* **23**, 411–427.
7. Ramachandran, V. S. (1976) *Nature (London)* **262**, 382–384.
8. Ahissar, M. & Hochstein, S. (1994) in *Early Vision and Beyond*, ed. Papathomas T. V. (MIT Press, Cambridge, MA), pp. 199–206.
9. Vidyasagar, T. R. & Stuart, G. W. (1993) *Proc. R. Soc. London B* **254**, 241–244.
10. Ahissar, M. & Hochstein, S. (1996) *Vision Res.*, in press.
11. Ball, K. & Sekuler, R. (1987) *Vision Res.* **27**, 953–965.
12. Boutet, I., Intriligator, J. & Rivest, J. (1995) *Invest. Ophthalmol. Vis. Sci.* **36**, S375 (abstr.).
13. Griffiths, F. & Chubb, C. (1995) *Invest. Ophthalmol. Vis. Sci.* **36**, S377 (abstr.).
14. Hirsch, J. (1993) *Soc. Neurosci. Abstr.* **19**, 439.
15. Beard, B. L., Levi, D. M. & Reich, L. N. (1995) *Vision Res.* **35**, 1679–1690.
16. Karni, A. & Sagi, D. (1993) *Nature (London)* **365**, 250–252.
17. Rubenstein, B. R. & Sagi, D. (1990) *J. Opt. Soc. Am. A* **7**, 1632–1643.
18. Foster, D. H. & Westland, S. (1995) *Vision Res.* **35**, 733–738.
19. Wolfe, J. M. & Franzel, S. L. (1988) *Percept. Psychophys.* **44**, 81–93.
20. Fuster, J. M. (1995) *Memory in the Cerebral Cortex: An Empirical Approach to Neural Networks in the Human and Nonhuman Primate* (MIT Press, Cambridge, MA), pp. 113–160.
21. Verghese, P. & Nakayama, K. (1994) *Vision Res.* **34**, 2453–2467.
22. He, Z. J. & Nakayama, K. (1994) *Vision Res.* **34**, 151–162.
23. Schiller, P. H. (1965) *J. Exp. Psychol.* **69**, 193–199.
24. Kovács, G., Vogels, R. & Orban, G. A. (1995) *Proc. Natl. Acad. Sci. USA* **92**, 5587–5591.
25. Rolls, E. T. & Tovée, M. J. (1994) *Proc. R. Soc. London B* **257**, 9–15.
26. Blasdel, G. G. & Fitzpatrick, D. (1984) *J. Neurosci.* **4**, 880–895.
27. Tootell, R. B. H., Hamilton, S. L., Silverman, M. S. & Switkes, E. (1988) *J. Neurosci.* **8**, 1500–1530.
28. Rosa, M. G. P., Gatass, R., Fiorani, Jr. & Soares, J. G. M. (1992) *Exp. Brain Res.* **88**, 249–264.
29. Hawken, M. J. & Parker, A. J. (1984) *Exp. Brain Res.* **54**, 367–372.
30. Livingstone, M. S. & Hubel, D. H. (1984) *J. Neurosci.* **4**, 309–356.
31. Blasdel, G. G. (1992) *J. Neurosci.* **12**, 3115–3138.
32. Merigan, W. H., Nealy, T. A. & Maunsell, J. H. R. (1993) *J. Neurosci.* **13**, 3180–3191.
33. Merigan, W. H. (1996) *Visual Neurosci.* **13**, 51–60.
34. Movshon, J. A., Chambers, B. E. I. & Blakemore, C. (1972) *Perception* **1**, 483–490.