Perceptual Learning of Spatial Localization: Specificity for Orientation, Position, and Context

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Crist, Roy E., Mitesh K. Kapadia, Gerald Westheimer, and Charles D. Gilbert. Perceptual learning of spatial localization: specificity for orientation, position, and context. J. Neurophysiol. 78: 2889–2894, 1997. Discrimination of simple visual attributes can improve significantly with practice. We have trained human observers to perform peripherally presented tasks involving the localization of short line segments and examined the specificity of the learning for the visual location, orientation, and geometric arrangement of the trained stimulus. Several weeks of training resulted in dramatic threshold reductions. The learning was specific for the orientation and location of the trained stimulus, indicating the involvement of the earliest cortical stages in the visual pathway where the orientation and location of stimuli are mapped with highest resolution. Furthermore, improvement was also specific for both the configuration of the trained stimulus and the attribute of the stimulus that was under scrutiny during training. This degree of specificity suggests that the learning cannot be achieved by cortical recruitment alone, as proposed in current models, but is likely to involve a refinement of lateral interactions within the cortex and possibly a gating of lower level changes by attentional mechanisms.

INTRODUCTION

The ability to discriminate small changes in sensory attributes improves considerably with practice. This form of implicit learning, known as perceptual learning, has been studied for well over a century (for review see Gibson 1953). In the visual system, psychophysical evidence exists for the learning of nearly every stimulus attribute, including position, depth, orientation, motion, texture, and spatial phase (for review see Gilbert 1994). Strikingly, even hyperacuity tasks, which require observers to discern spatial differences smaller than the distance between individual photoreceptors, show considerable improvement with training (Fahle and Edelman 1993; Kapadia et al. 1994; Levi and Polat 1996; McKee and Westheimer 1978; Poggio et al. 1992). Many of these studies show that the learning is specific for the trained location and for stimulus orientation, although the resolution of this specificity has not been studied in detail. Because the various cortical areas differ in terms of the resolution of topographic maps and orientation specificity, the stimulus specificity of the learning allows one to make inferences concerning the level of visual processing where the learning is based. Armed with training paradigms that produce large amounts of improvement and that show specificity indicative of the involvement of early stages in cortical processing, one can investigate the physiological basis of the learning.

Although perceptual learning has been observed in every sensory modality, its neuronal basis has been studied in few model systems (e.g., Recanzone et al. 1992, 1993; Weinberger et al. 1990). Various kinds of cortical changes have been associated with improvement in perceptual performance and such changes have been identified in primary sensory cortices, suggesting that the mechanisms of learning may be general to the neocortex as a whole and not just a specialized property of the temporal lobe where it has been classically studied. Independent studies of plasticity of receptive field properties and functional architecture of primary visual cortex heighten the possibility that plasticity associated with perceptual learning might be found there. Although certain receptive field properties are mutable only during a critical period of limited duration early in postnatal development (Hubel and Wiesel 1977), a number of other properties, most notably visual topography and receptive field size, can be influenced by visual experience throughout life. The initial evidence for this came from making retinal lesions, which lead to a remapping of cortical topography in area V1 (Chino et al. 1992; Gilbert et al. 1990; Gilbert and Wiesel 1992; Heinen and Skavenski 1991; Kaas et al. 1990). A detailed investigation of the site of the changes indicate that they occur initially in primary visual cortex, that the substrate is likely to be the long range horizontal connections intrinsic to V1, and that the mechanism involves axonal sprouting and synaptogenesis (Darian-Smith and Gilbert 1994, 1995; Das and Gilbert 1995a). Some of the changes develop over a period of months, whereas others occur much more rapidly, over a time scale of minutes. Receptive field changes have been induced not only by making lesions, but by exposing the animal to short periods of patterned stimulation (Das and Gilbert 1995b; Pettet and Gilbert 1992). That visual experience can lead to the changes in the response properties of cells in the primary visual cortex raises the possibility that repeated exposure to the same stimulus can produce the stable changes necessary for learning.

Here we used psychophysical techniques to explore the neuronal basis of perceptual learning. We attempted to devise a stimulus that would be amenable to the study of the underlying cortical changes: one that showed a large and sustained improvement over an extended period of time, one that showed specificity suggestive of the involvement of early stages of visual cortical processing, and one that could be approached in terms of known cortical properties of receptive field interactions, cortical connectivity, and cortical functional architecture. In this study, we examined the ability of human observers to improve on a peripherally presented bisection task with practice and to generalize any improvement to performance of other discrimination tasks. Perfor-
performance of the bisection task improved dramatically with training and was highly specific for the stimulus used during training.

METHODS

Observers were presented with simple patterns of short line segments generated under the control of a PC-compatible computer (Gateway P5-60) on an HP1345a vector scope. Bright stimuli (70 cd/m²) were presented against a dim background (<1 cd/m²) and viewed at a distance of 1.5 m. Two observers performed the positional specificity experiment (Fig. 3) with the same bisection stimulus presented on a CRT display (NEC MultiSync 6FG). Observers had normal or corrected vision, viewed the stimuli binocularly, using a head and chin rest, and maintained fixation on a small point. Stimuli were presented 5° away from the fovea.

To determine an observer’s threshold for a specific task, the method of constant stimuli was used. Each trial consisted of a brief presentation of the stimulus (200 ms) followed by a period of 1 s during which the observer was required to make one of two possible responses. No feedback about the accuracy of the response was given. With each presentation, the target parameter of the stimulus, either the relative position of a line or its orientation, was randomly assigned one of seven values evenly distributed about its mean value. Responses were made on a keyboard and collected by computer. Thresholds were determined by fitting the data with a psychometric curve by the method of probits. Individual stimuli will be described below with the results of each experiment.

To determine whether or not improvement on a particular discrimination task would generalize to performance of a different discrimination task, an observer’s threshold for both tasks was measured before and after training on one task. Initial and final thresholds were determined by collecting two blocks of 150 trials on two consecutive days. Each training session consisted of three to six blocks of trials and three to five sessions were conducted weekly. The performance of the subjects was tracked throughout training and training continued until there was a substantial improvement. At the conclusion of training, thresholds for both tasks were remeasured and the amount of improvement shown for the trained discrimination was compared with any change in the level of performance on the untrained task.

RESULTS

Bisection performance improves with training

Figure 1A, inset, shows a diagram of the three-line bisection discrimination task. Each trial consisted of a brief presentation of three parallel lines with the center line in one of seven positions between the two reference lines. Observers were instructed to indicate whether the center line appeared closer to the left or the right reference. The learning curve of one observer, constructed by plotting the threshold measured for each day the bisection discrimination was performed, is shown in Fig. 1A. Observer K. B. reached an asymptotic level of performance after ~6 wk of training, at which point the threshold had decreased by a factor of 2.6. In addition, the threshold of this observer was measured ~2 months after training had been discontinued and it was found that the improvement had been fully retained.

All eleven observers trained with the bisection task during this study manifested improvement with training (Fig. 1B). Across the population there was variability in the initial thresholds measured, the amount of improvement obtained, and the time course over which the improvement occurred.

Similar interobserver variance has been reported for perceptual learning involving foveally presented hyperacuity tasks (Fahle and Henke-Fahle 1996). On average, training resulted in a threshold reduction of 51%; however, improvement ranged from as little as 22% to as much as 71%.

Improvement is specific for the trained orientation

To determine whether learning of the bisection discrimination task is specific for the orientation of the stimulus used during training, the threshold of three observers was determined with a bisection stimulus of orthogonal orientation (as indicated below the abscissa of Fig. 2) before training. Shown here are the average before- and after-training thresholds for three observers trained on bisection discrimination task. A ratio of <1 indicating improvement. All observers showed significant improvement after training. For clarity, a typical standard error is shown for one data point only.
little improvement with the orientation discrimination task. Yet, when one of these observers was subsequently trained on orientation discrimination, a substantial improvement was observed, demonstrating that the lack of improvement described above was not the result of an inherent difficulty in learning this task. Thus learning of the bisection task is specific to the bisection task itself and does not generalize to the performance of another visual discrimination.

Improvement of visual localization is dependent on context

The previous experiment demonstrated that improvement obtained with bisection training is specific for the attribute of the stimulus that is the object of discrimination; the improvement does not reflect a general improvement in perceptual ability. In the next experiment, we investigated whether the improvement of the discrimination of a single attribute of a stimulus is specific for the configuration of the stimulus as a whole. The performances of observers

Improvement is specific for the trained visual location

To determine whether the improvement obtained by training on the bisection discrimination is specific for the trained visual location, we measured observers’ thresholds at several different locations (Fig. 3A) before and after training. For the eight observers who participated in this experiment, thresholds were reduced an average of 45% in the trained location (Fig. 3B). When the task was presented at other visual locations of the same eccentricity, the ability of the observers to generalize the improvement obtained with training was reduced with distance (Fig. 3C). At 8°, only one-half (27% reduction in threshold) of the improvement shown at the trained location was observed. Subjects differed in their ability to generalize performance to other visual locations; even when the task was presented only one degree from the trained location, some subjects showed as little as an 8% reduction in threshold.

Improvement with the bisection task does not transfer to other discrimination tasks

Investigations in somatosensory and auditory cortex have suggested that perceptual learning occurs through an expansion in the cortical territory allocated for the representation of trained stimuli (Recanzone et al. 1992, 1993; Weinberger et al. 1990). If so, one would expect that learning would generalize to any discrimination task that could activate the expanded neuronal ensemble. To determine whether learning transfers to other discrimination tasks presented in the trained location, we measured the thresholds of two observers for both the bisection task and an orientation discrimination task before and after bisection training. The orientation task was composed of a single line of the same mean location and orientation as the central line of the bisection task. Each trial of the orientation task consisted of a brief presentation with the line at one of seven orientations centered around vertical. Observers were instructed to report whether the line appeared tilted clockwise or counterclockwise. Fig. 4A shows the average before- and after-training thresholds of two observers. Despite a more than threefold improvement on the trained bisection task, the observers showed very little improvement with the orientation discrimination task. Yet, when one of these observers was subsequently trained on orientation discrimination, a substantial improvement was observed, demonstrating that the lack of improvement described above was not the result of an inherent difficulty in learning this task. Thus learning of the bisection task is specific to the bisection task itself and does not generalize to the performance of another visual discrimination.

FIG. 2. Learning is specific for trained orientation. Average thresholds of 3 subjects in this experiment measured before (light gray) and after (dark gray) training with bisection discrimination task at one orientation (left) and with an untrained orthogonally oriented task (right). Learning showed little transfer from trained to untrained orientation.

FIG. 3. Learning shows specificity for trained position. A: fixation point (FP), location for bisection training, and 4 other sites where bisection thresholds were measured before and after training. B: average thresholds measured before (light gray) and after (dark gray) training at one location. Data represent 6 subjects who were tested at all 4 sites and 2 additional subjects who were tested only at 1 and 2°. Although there was some improvement as far as 8° from trained location, data show that at least a component of learning was specific for trained position. C: average change in performance after training at each location. Change has been defined to be 1 – ratio of initial threshold to final threshold of each subject at each location. Training-related improvements decline as stimulus is moved away from trained location.
in the trained bisection and in an untrained vernier discrimination task were compared. In our vernier discrimination, the observer was asked to localize a line with the same orientation and visual field location as the central line of the bisection task. Each trial of the vernier discrimination consisted of a brief presentation of the two lines with the lower line in one of seven positions, either collinear with or offset from the upper reference line. In Fig. 4B, the average thresholds of six observers are shown for both the trained bisection task and the untrained vernier discrimination. Training with the bisection task led on average to a more than twofold reduction in threshold. Yet vernier thresholds were almost unchanged. One observer was subsequently trained on the vernier discrimination and showed a 65% reduction in threshold. Thus an observer’s improved ability to localize a line of a specific orientation and in a particular position in the visual field is dependent on the context in which the line appears or the reference to which its position is compared.

**Fig. 4.** Learning is specific for stimulus configuration. A: bisection to orientation discrimination. Average thresholds of 2 subjects in this experiment before (light gray) and after (dark gray) bisection training (left and center). Improvement in bisection task did not generalize to an orientation discrimination task in same location of visual field. One observer was subsequently trained on orientation task and showed considerable improvement (right). B: bisection to vernier discrimination. Average threshold of 6 observers measured before (light gray) and after (dark gray) bisection training. Learning in bisection task did not generalize to vernier task. One observer was subsequently trained on vernier task and showed considerable improvement. C: vernier to orientation discrimination. One observer was trained on a vernier discrimination task and showed considerable improvements. Learning did not generalize to an orientation discrimination task.

**Fig. 5.** Transfer of learning between similar discrimination tasks. Average thresholds for 3 observers measured before (light gray) and after (dark gray) bisection training. Improvement showed substantial transfer to a similar bisection task in which distance between outer lines was doubled.

**Orientation discrimination is not improved by vernier training**

We have shown that improvement on the bisection task is specific for the attribute of the stimulus analyzed during training and the context in which the stimulus is presented. A further test for the specificity of learning consisted of measuring transfer of learning between an orientation discrimination task and a vernier discrimination task. The stimuli consisted of the vernier task described in the preceding section and an orientation discrimination task involving a line in the same position and of length equal to that of the two bars composing the vernier stimulus. In Fig. 4C, we show the thresholds of one observer for both the vernier and orientation tasks determined before and after training on vernier discrimination. Although the observer showed a 65% reduction in threshold for the trained vernier discrimination, <10% improvement was seen for the orientation discrimination task.

**Transfer between similar discrimination tasks**

Improvement with the bisection discrimination task does not generalize to performance of other discrimination tasks. To explore the extent of this specificity, we examined the ability of observers to perform a bisection task in which the separation of the flanking lines had been doubled (as indicated below the abscissa of Fig. 5) after training with our standard bisection task. Figure 5 shows the average before-and after-training thresholds of three observers. Here a substantial improvement is seen in the performance of the untrained discrimination task after training (a 39% threshold reduction). This finding suggests that if there is sufficient similarity between two tasks, learning will generalize from one to the other.

**Discussion**

We have shown large reductions in peripheral bisection thresholds of human observers after several weeks of training. This accords well with a previous study of peripheral hyperacuity (Beard et al. 1995) but contrasts with foveal hyperacuity thresholds that improve somewhat in the first few hundred trials (Poggio et al. 1992), but little, if at all,
The ability of observers to generalize improvement with a particular discrimination task to performance of other tasks can be used to explore potential loci for the neuronal mechanisms underlying the learning. This approach is based on differences in the functional properties of the areas occupying different echelons of the sensory processing hierarchy. Of particular interest for localizing the mechanisms of perceptual learning in the visual system is the specificity of the improvement for the position and orientation of the trained stimulus. Specificity for visual field location suggests an involvement of earlier stages in the visual cortical pathway where receptive fields are smallest and the retinotopic map is most precise. Similarly, orientation tuning is sharpest early in visual pathway and learning that is specific for the orientation of the trained stimulus is likely to involve mechanisms operating at such early stages.

We have examined the ability of our observers to generalize the improvement shown after training to performance of the bisection task at both the orthogonal orientation and other retinotopic locations. Little improvement was seen for observers whose performance was tested with an orthogonally oriented stimulus. Furthermore, the improved bisection performance shown by our observers did not fully generalize to performance of the same task presented only 1° away. Learning of the bisection task, then, shows a similar specificity for location as that shown for the learning of orientation discrimination (Schoups et al. 1995). This specificity implicates early levels of the cortical visual hierarchy in the learning process.

Nonetheless some improvement in bisection performance was shown 8° from the trained location, demonstrating that a component of the learning is not restricted to the trained position. Part of the transfer may be the result of a general improvement on the part of the observer to respond to hyperacuity stimuli and familiarity with the testing situation (procedural learning). Compatible with this view is the small but consistent reduction of threshold for each of the untrained discrimination tasks after training with another task. However it has yet to be shown whether or not procedural learning alone may account for the small training effect at the furthest distances or whether this improvement reflects mechanisms operating at stages of the visual pathway less retinotopically organized—mechanisms specific for stimulus configuration but invariant to translation and rotation. These findings suggest that although at least a component of the learning takes place in early levels of visual processing, learning may be a distributed process involving multiple cortical areas.

A prevalent concern regarding the cortical basis of perceptual learning, on the basis of experiments in the somatosensory and auditory systems, is that there is an expansion of the cortical territory representing the trained stimulus (Recanzone et al. 1992, 1993). According to this view, improvements in performance are attributed to the participation of a larger neuronal ensemble in the discrimination task. If improvement in visual discrimination performance relied on simple cortical recruitment, one would expect learning to generalize to any discrimination involving a stimulus that would activate cells in the same area of cortex. We found to the contrary that learning did not transfer to a number of discrimination tasks that were composed of lines with similar orientation and spatial position as the bisection stimulus, though presumably both stimuli would activate overlapping populations of neurons in area V1. The lack of transfer between vernier and bisection tasks is particularly telling because both tasks involve the localization of the same line, implying that learning is context dependent. Similar results were obtained by Fahle and Morgan (1996) who found that learning did not transfer between vernier and bisection stimuli composed of dots. The lack of improvement in these tasks constrains current models of perceptual learning, requiring a more complicated neuronal substrate than simple cortical recruitment. It is worth noting that the responses of neurons in primary visual cortex show substantial modulation by stimuli outside their classical receptive fields (e.g., Gilbert and Wiesel 1990; Kapadia et al. 1995; Knierim and Van Essen 1992; Lamme 1995; Nelson and Frost 1985), which may be mediated by long range horizontal connections (Gilbert et al. 1996). Furthermore such lateral interactions have also been shown to be tuned for specific geometric relationships in the stimulus pattern (Kapadia et al. 1995) and can be modified by training (Polat and Sagi 1994). One means of generating learning specific for the precise configuration and context of a stimulus would be to modulate specific subsets of lateral interactions. Moreover, such low level changes could be modified by attentional mechanisms and be manifest only when the observer is performing the trained discrimination task.

In addition to addressing questions about the locus of the cortical mechanisms by which learning occurs, experiments showing learning associated with a particular percept can also help in the parsing of the mechanisms underlying that percept. For example, it has been suggested that vernier acuity involves the detection of the implicit orientation generated by the two lines comprising the stimulus (Andrews 1967a,b). If vernier and orientation discriminations did indeed involve the same cortical mechanism, then one would expect a transfer of learning from one to the other. In fact there is no such transfer (Fig. 4C), adding weight to the argument that these tasks must be subserved by different cortical mechanisms (Westheimer 1996). Even when the same attribute is involved, tasks involving different stimulus configurations may still involve distinct cortical mechanisms. Our bisection and vernier experiments were designed so that they require the judgment of location of a given line, but with respect to two different reference patterns. In the vernier task, the reference was a parallel line fixed in position just above the test line, whereas in the bisection task there were two parallel lines, placed laterally, one on each side. The fact that there was no transfer of learning from bisection to vernier tasks shows that the cortical mechanisms for position comparison of a test line are specific for the comparison patterns, even when both are made of lines that are parallel to the test line.

We have described a visual discrimination task, three-line bisection, which shows specificity reflective of the early stages of cortical processing. This specificity is in agreement
with a number of previous studies that have shown that perceptual learning is often highly specific for the trained stimulus. We have used the transfer of learning paradigm to demonstrate that, in addition to being specific for the location and orientation of the trained stimulus, learning of the binocular section task is specific for the attribute of the stimulus that was analyzed during training and for the configuration of the stimulus within which the discrimination was made. This degree of specificity for the trained task suggests that perceptual learning of this type of visual discrimination cannot be accounted for by a simple recruitment of additional cortical territory. It is now known that the responses of single units in V1 are dependent on both the recent history of stimulation and the context within which stimulation occurs. Learning which involves fine-grain resolution of the attributes of a visual stimulus may rely on these dynamic properties of the earliest cortical stage of the visual pathway.

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