

The Neural Basis of Perceptual Learning Review

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Perceptual learning is a lifelong process. We begin by encoding information about the basic structure of the natural world and continue to assimilate information about specific patterns with which we become familiar. The specificity of the learning suggests that all areas of the cerebral cortex are plastic and can represent various aspects of learned information. The neural substrate of perceptual learning relates to the nature of the neural code itself, including changes in cortical maps, in the temporal characteristics of neuronal responses, and in modulation of contextual influences. Top-down control of these representations suggests that learning involves an interaction between multiple cortical areas.

Introduction

Learning comes in many forms, some of which are explicit memories of objects, places, or events (declarative learning) and some of which are implicit and do not require conscious awareness (nondeclarative learning). In vision, one tends to think of learning in terms of storing the representation of complex objects, such as a person's face. The information for this kind of memory is largely represented in the temporal lobe. This idea originated from the finding that lesions of certain portions of the temporal lobe lead to the loss of the ability to recognize faces, a syndrome known as prosopagnosia. Since we retain the ability to learn new faces throughout normal lives, one would expect that the temporal lobe should retain the ability to exhibit plasticity, the ability to undergo functional change, throughout adulthood. While some forms of memory are based in the temporal lobe, other forms of memory, particularly implicit memory, are represented in a large number of brain regions outside the temporal lobe. One form of implicit memory, perceptual learning, involves improving one's ability, with practice, to discriminate differences in the attributes of simple stimuli. Perceptual learning involves areas of neocortex upstream in the visual pathway from the temporal lobe, extending even into primary sensory cortex.

While these various forms of learning differ in which brain regions they are represented (and the distinct inputs these areas receive), the mechanisms underlying the different forms of memory may be quite similar at the level of signal transduction cascades and circuitry. Because of this possibility, increasing interest has been directed toward understanding perceptual learning as a basis for understanding the mechanisms of learning in general, since it involves cortical areas at the early

stages of visual processing, where most is known about neocortical circuitry, receptive field properties, and functional architecture. These cortical areas are therefore more tractable for exploring the underlying mechanisms.

The experience-dependent alteration of functional properties and circuits is termed "plasticity." William James originally applied the term to brain function when he wrote "Plasticity... means the possession of a structure weak enough to yield an influence but strong enough not to yield all at once" (James, 1890). Its current usage was defined by Jerzy Konorski, who emphasized the difference between the immediate "reaction" of nerve cells to incoming changes, which he called excitability, and the "permanent transformation" of a system of neurons, which he called plasticity (Konorski, 1948). Plasticity would include the changes associated with extinction, conditioning, or habit formation. Konorski suggested that plasticity was uniquely a property of the cerebral cortex and foresaw that it could be mediated by the transformation of a preexisting set of potential connections into actual connections, by either a functional or morphological change.

The idea that even primary sensory cortex could remain plastic in adulthood is quite new. In the past, plasticity of early sensory areas was thought to be limited to a period in early postnatal life known as the critical period. The cortical basis of critical period plasticity was discovered by Hubel and Wiesel, who found that the balance of input from the two eyes, or ocular dominance, could be altered by restricting visual experience to one eye. The capacity for the primary visual cortex to undergo this change is limited to the first few months or years of life, depending on the species. One might have assumed that these findings implied that in adulthood primary sensory cortex should be fixed in its properties and connections. It has become clear, however, that the critical period applies to a limited set of properties and connections, each property subject to its own critical period. Other properties remain mutable throughout life. The way in which cortical areas differ is not in their capacity to undergo experience-dependent or learning-dependent change, but in the particular form of learning they represent. In this review, we discuss the evidence for adult cortical plasticity, the properties of perceptual learning and the implications of these properties for the cortical representation of learned information, and the ways in which neural circuits have been found to mediate perceptual learning.

The Psychophysics of Perceptual Learning

To begin, we will consider the characteristics of perceptual learning, and the implications of these characteristics for the neuronal representation of learned information. Recent studies examining perceptual learning in a variety of visual submodalities show common themes, one of which being that the improvement obtained by practicing a perceptual discrimination task is often restricted to stimuli similar to the trained stimulus. This

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specificity suggests that part of the neural substrate of the learning effect must reside in the early stages of the sensory processing pathway. It is here that stimulus features are represented with the finest resolution.

While few would disagree that the perception of complex phenomena is dependent upon experience, it is less well recognized that the ability to perceive even simple stimulus attributes, which might be described as perceptual primitives (Westheimer, 1996), remains pliant well into adulthood. Psychologists and psychophysicists have known since before the turn of the century that training can improve the ability to make discriminations in a wide variety of sensory modalities; tasks involving visual acuity, somatosensory spatial resolution, discrimination of hue, estimation of weight, and discrimination of acoustical pitch all show improvement with practice (for review, see Gibson, 1953). Training can improve the discrimination of small differences in the offset of two lines (vernier acuity) even though initial thresholds are already in the hyperacuity range (McKee and Westheimer, 1978). A number of studies have elaborated on the idea that the spatial resolution of the visual system, at least in the realm of hyperacuity, can improve with practice (Poggio et al., 1992; Fahle and Edelman, 1993; Kapadia et al., 1994; Beard et al., 1995; Saarinen and Levi, 1995; Fahle and Morgan, 1996). Other visual perceptual tasks that improve with training include the ability to discriminate orientation (Vogels and Orban, 1985; Shiu and Pashler, 1992; Schoups et al., 1995), the direction of motion (Ball and Sekuler, 1982, 1987), the differences in the waveforms of two sinusoidal stimuli (Fiorentini and Berardi, 1980, 1981; Berardi and Fiorentini, 1987), and the ability to segregate elements of the visual scene using textural cues (Karni and Sagi, 1991, 1993). Training has been found to increase the ability of observers to detect small differences in the depth of two targets (Fendick and Westheimer, 1983; Westheimer and Truong, 1988) as well as the ability to perceive depth in random-dot stereograms (Ramachandran and Braddick, 1973).

The specificity of learning for the trained task as opposed to the degree of transfer to other tasks has profound implications for the underlying neural mechanisms. This issue was a focal point of theories of learning and education in the 19th century and is being revisited in the present day. The classic idea of formal education held that study in one discipline, such as Latin, would enhance one's ability in other disciplines, and that the brain, like a muscle, would increase in capacity with mental exercise. In the late 1800's, the psychologist Edward Thorndike challenged this idea, proposing instead that expertise in any given discipline was specific to the associations required for that discipline, and transfer between disciplines was only possible to the degree to which they shared common elements (Thorndike, 1898). These ideas formed the groundwork for the field of behaviorism, including the work of Pavlov and Skinner, who emphasized the importance of the linkage between stimulus and reward for associative learning and that shaping responses required maintaining a close similarity between tasks.

Recent investigations have reinforced the idea that perceptual learning is often highly specific for the particular stimulus configuration used during training (re-

viewed in Gilbert, 1994). The expectation that the effects of perceptual learning will aid in the localization of the process of discrimination and the mechanism of learning within the visual system rests on this specificity. Specificity in learning for position in visual space and for the orientation of a stimulus suggests the involvement of early stages in cortical visual processing, where the receptive fields are the smallest, the visual topography most precisely mapped, and orientation specificity is the sharpest (Figures 1A–1D; Crist et al., 1997). A mechanism underlying learning which is highly specific for the location of the trained stimulus must avail itself of the positional information present in early visual areas. A number of psychophysical studies have found specificity for the location in visual space where the training task was presented. In motion discrimination tasks, the gain in performance with learning at one location is lost when the task is moved more than a couple of degrees from the trained location (Ball and Sekuler, 1987). The improvement of texture discrimination through training is specific for the quadrant of space where the stimulus is presented during training, and no transfer of the learning is seen when the test stimulus is moved as little as 3° from the trained location (Karni and Sagi, 1991). Learning of waveform discrimination is limited to the trained visual hemifield (Berardi and Fiorentini, 1987). Lastly, improvement with a stereoacuity discrimination task presented in the periphery fails to transfer when the task is presented 3° away (Westheimer and Truong, 1988). Even if the visuotopic specificity of perceptual learning suggests involvement of early cortical stages in visual processing, it is not absolute. The learning observed in a three-line bisection task, for example, transfers to positions up to about 8° away, a distance greater than the size of receptive fields in V1, opening the possibility of the involvement of longer range spatial interactions across V1 or interactions between multiple cortical areas (Crist et al., 1997).

In addition to specificity for position, perceptual learning is specific for the orientation of the stimulus elements (Ramachandran and Braddick, 1973; McKee and Westheimer, 1978; Fiorentini and Berardi, 1980, 1981; Ball and Sekuler, 1987; Karni and Sagi, 1991; Poggio et al., 1992; Fahle and Edelman, 1993; Schoups et al., 1995; Westheimer et al., 2001). Cells in the early part of the visual pathway, particularly in V1, are highly selective for the orientation of visual contours (Hubel and Wiesel, 1959), and orientation is an important parameter in the columnar architecture of V1 (Hubel and Wiesel, 1977). Later stages of the visual pathway, however, possess cells with broader orientation tuning and are characterized by functional architecture that may be organized around more complex stimulus attributes. Therefore, forms of learning that show specificity for the orientation of the trained stimulus are likely to be mediated by mechanisms in the early stages of the visual pathway where a more accurate representation of the orientation of stimulus elements is present.

After the convergence of inputs from the two eyes, which creates the binocular cells present in V1 and in subsequent areas, information about the eye of origin is most likely lost. Therefore, perceptual learning restricted to the eye used during monocular training would also suggest that the learning effect is mediated by

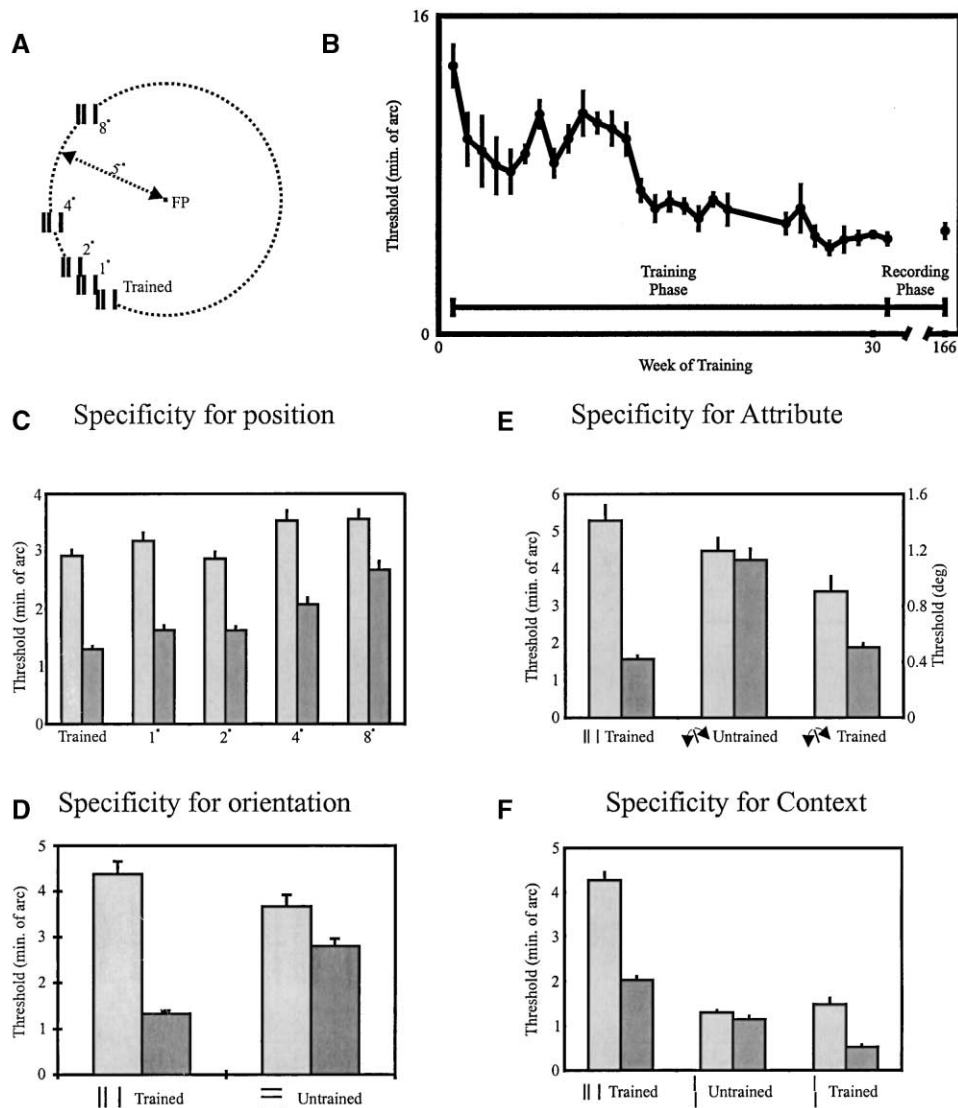


Figure 1. Specificity of Perceptual Learning for Location and for Stimulus Context

Perceptual learning can affect many sensory attributes, such as the perception of position in space. (A) In this paradigm, three-line bisection, the task involves categorizing a stimulus consisting of a set of three parallel lines as one in which the center line is located nearer the left-most or the right-most lines of the three. A certain offset from the central position is required in order to see the configuration consistently as one of the two alternate possibilities, and this is the threshold in the task. (B) The threshold improves by a factor of three with repeated performance of the task, not requiring error feedback. The subjects are trained in a particular location of the visual field (A), and the training is relatively specific for the trained location (C). (D) The training is specific for the orientation of the trained lines, not transferring to the bisection array rotated by 90°. (E) The training is specific for the trained attribute, position, and does not transfer to other attributes, such as orientation. (F) The training is specific for the configuration of lines, that is, it shows specificity for context, not transferring to a vernier discrimination task. If trained on vernier discrimination, the subject then can show substantial improvement on that task. (Image adapted from Crist et al., 1997.)

mechanisms located at or before the level of input to V1. Indeed, a lack of interocular transfer has been reported in a few studies of perceptual learning (Karni and Sagi, 1991; Poggio et al., 1992). However, these reports are difficult to reconcile with the orientation specificity for the learning, because orientation tuning first appears in cortical cells that are also binocular. Other studies of perceptual learning do show interocular transfer (Fiorentini and Berardi, 1980, 1981; Ball and Sekuler, 1987; Schoups et al., 1995; Beard et al., 1995).

Improvement of performance on visual discrimination

tasks depends on the specific configuration of the elements of which the trained stimulus is composed and, therefore, is specific not just for simple attributes but for complex shapes. For example, improvement on a vernier acuity task fails to transfer between a stimulus composed of lines and one composed of dots (Poggio et al., 1992). There is no transfer of learning between a bisection task, where one determines the position of a dot or line relative to two similar lines placed in a side-by-side configuration, and a vernier task, where one determines the position of the same feature relative to

a different context, a colinear line, or to contextual lines of different orientation (Figure 1F; Fahle and Morgan, 1996; Crist et al., 1997; Westheimer et al., 2001). Facilitatory interactions between Gabor elements (a grating patch) used in a contrast detection task depend on the distance between target and mask elements and their arrangement along an axis defined by the local orientation of the Gabor patterns (Polat and Sagi, 1994). Similarly, transfer of improvement in the detection of differences in depth of stimulus elements depends on the spacing of the elements and upon their surrounding context (Fendick and Westheimer, 1983; Fahle and Westheimer, 1988; Westheimer and Truong, 1988). Contrary to the dependence of perceptual learning on the orientation or the location of stimulus elements discussed above, the specificity of learning to more complex features requires a mechanism that is context dependent. This leads to the alternate possibilities that the learning involves higher order cortical areas that can encode more complex stimulus features, that such features can be encoded at earlier stages in sensory processing, or some combination of the two.

The dependence of learning on position and orientation, which argues for the involvement of early cortical stages in visual processing, may seem to conflict with its specificity for complex stimulus features, which has traditionally been associated with later stages. In later cortical areas, such as inferotemporal cortex (IT), an area that is thought to be involved in object recognition (Tanaka et al., 1991), the cells are known to be selective for complex stimuli. Discrimination training leads to changes in the response properties of cells in IT (Sakai and Miyashita, 1994) and in the middle temporal cortex (Zohary et al., 1994). It is possible, therefore, that perceptual learning, which is highly specific for the exact form of the trained stimulus, relies on mechanisms which operate in later cortical areas. On the other hand, the later stages of the visual pathway have cells with large receptive fields and broad orientation tuning. These features make the specificity of perceptual learning for the location and orientation of the trained stimulus difficult to explain in terms of processing in higher cortical areas. Therefore, one has to consider the possibility that early stages are capable of encoding much more complex stimuli than originally believed and that the learning of a specific task occurs in a distributed fashion throughout the sensory pathway and reflects the properties of a cortical area depending on the role that it plays in the trained discrimination.

Top-Down Influences in Perceptual Learning

Perceptual learning shows strong interaction with attention, indicating that it is under top-down control. Attention is necessary for consolidation of memory (Shiu and Pashler, 1992; Ahissar and Hochstein, 1993; Ito et al., 1998; Braun, 1998; Treisman et al., 1992; Fahle and Morgan, 1996; Crist et al., 1997). One of the consequences of learning is to release the dependence of performance from attentional control, leading to an automatization of the task (Schneider and Shiffrin, 1977; Shiffrin and Schneider, 1977). The alteration in attentional involvement with learning is seen in the changing patterns of brain activation associated with learning, where cortical

regions involved in the perception of visual motion such as area MT become more active, and the superior colliculus and anterior cingulate, which are involved in mediating attentional control, become less active (Posner et al., 1988; Rees et al., 1997; Vaina et al., 1998). Attentional effects themselves, moreover, are subject to learning (Ito et al., 1998). The induction of changes with perceptual learning therefore cannot occur with passive stimulation, but require the active involvement of the observer. As we will discuss below, the manifestation of some of the physiological changes associated with learning may itself be under top-down control, with recall of the learned information involving an interaction between multiple cortical areas and a combination of local intrinsic circuits and feedback connections from higher order cortical areas.

Lesion-Induced Cortical Plasticity

Given the psychophysical characteristics of perceptual learning outlined above, one can ask what neural changes are consistent with these characteristics. The initial evidence for cortical plasticity in the adult came from experiments involving peripheral nerve lesions or digit amputations. The cortical territory originally representing the denervated or amputated digit shifts its representation to the adjoining digits (Rasmusson, 1982, 1988; Merzenich et al., 1983a, 1983b, 1984; Rasmusson and Nance, 1986; Calford and Tweedale, 1988, 1991). Similar effects have been seen in the motor system (Sanes et al., 1988, 1990, 1992; Donoghue et al., 1990), the auditory system (Robertson and Irvine, 1989; Rajan et al., 1993), as well as the visual system (Gilbert et al., 1990; Kaas et al., 1990; Chino et al., 1991, 1992; Heinen and Skavenski, 1991; Gilbert and Wiesel, 1992). The time course of these changes covers a wide range, from changes occurring immediately after the disruption of sensory input, to more extensive changes developing over weeks and months (Calford and Tweedale, 1988; Gilbert and Wiesel, 1992; Darian-Smith and Gilbert, 1995). In primary visual cortex, large shifts in receptive field position and remapping of cortical topography are seen following retinal lesions. Other manipulations, including cortical lesions and activating neurons with patterns of visual stimulation, such as an artificial scotoma or paired visual stimuli, can produce rapid changes in size, orientation, position, and shape of the receptive field (Pettet and Gilbert, 1992; Fregnac et al., 1992; Volchan and Gilbert, 1994; Das and Gilbert, 1995; Eysel and Schweigart, 1999).

Considerable attention has been given to the site at which the reorganization takes place. Though changes in cortical topography associated with peripheral lesions may involve rearrangements at the cortical level, plasticity at antecedent levels would propagate to the cortex, without requiring cortical plasticity. For example, cutting peripheral nerves changes topography within the dorsal horn of the spinal cord, which is associated with sprouting of the afferents to the cord (Devor and Wall, 1978, 1981; McMahan and Kett-White, 1991; Cameron et al., 1992; Florence et al., 1993; Lamotte and Kapadia, 1993). Changes have also been observed in the thalamus following peripheral nerve section (Wells and Tripp, 1987; Rhoades et al., 1987; Garraghty and

Kaas, 1991). Thalamocortical connections have been proposed to mediate changes intrinsic to the cortex (Merzenich et al., 1983a; Calford and Tweedale, 1988; Rajan et al., 1993; Snow and Wilson, 1991). However, with some experimental manipulations the cortical changes appear not to be mediated subcortically or via thalamocortical afferents (Rasmusson and Nance, 1986; Rasmusson, 1988). Rather they are mediated by feedback connections from cortex to thalamus, such as that seen during reversible inactivation of S1 cortex or blockade of peripheral trigeminal nerve fibers (Krupa et al., 1999). Cells in the primary auditory cortex of the big brown bat can shift their best frequency with either electrical stimulation or conditioning with short tone bursts, and the fact that both manipulations produce similar changes in the inferior colliculus suggests a role for corticofugal feedback (Chowdhury and Suga, 2000; Gao and Suga, 2000). Although a small amount of functional recovery has been seen in the lateral geniculate nucleus (LGN) following retinal lesions (Eysel et al., 1980, 1981), the changes occurring in the primary visual cortex are much more extensive. This indicates that connections intrinsic to the cortex are most likely responsible for the alteration in the cortical map, rather than changes at antecedent stages (Gilbert and Wiesel, 1992; Darian-Smith and Gilbert, 1995).

The ability of a given brain structure to participate in alteration of topography depends on a preexisting framework of connections and on whether that framework is capable of mediating shifts in receptive fields. The extent of the reorganization observed in the visual cortex suggests involvement of long-range horizontal connections, which link cells with widely separated receptive fields. These horizontal connections (Gilbert and Wiesel, 1979, 1983, 1989; Rockland and Lund, 1982, 1983; Martin and Whitteridge, 1984) travel for 6–8 mm parallel to the cortical surface, which approximates the extent of reorganization seen following retinal lesions. These connections normally play a role in the modulation of neuronal responses by the context within which features are presented, endowing cells with selectivity for complex stimulus configurations not predicted from their response to a simple stimulus placed in different positions around the visual field (Kapadia et al., 1995, 2000). By altering the strength of the connections, they can change from a modulatory influence to a stronger, driving influence, thereby allowing the target cells to shift their receptive fields to new positions. Given the scale of changes observed in the cortex following peripheral lesions (Gilbert et al., 1990; Kaas et al., 1990; Heinen and Skavenski, 1991; Pons et al., 1991; Chino et al., 1992; Gilbert and Wiesel, 1992; Schmid et al., 1996), it is reasonable to look to long-range connections within cortex as potential mediators of the reorganization. In fact, sprouting of intrinsic long-range horizontal connections is associated with the functional reorganization following retinal and peripheral sensory lesions (Darian-Smith and Gilbert, 1995; Florence et al., 1998).

Plasticity in topographic maps is also seen where multiple sensory modalities have to be integrated and where sensory motor transformations are involved. This is seen in the alignment of visual and auditory maps in the inferior colliculus of the barn owl. The colliculus contains an auditory map of space based on the tuning

of neurons for interaural differences in the timings of sounds. Depending on the position of an auditory stimulus in space, the sound will reach one ear before or after the other. The auditory maps can change, in juvenile owls, without manipulating auditory input, by shifting the visual spatial maps with prisms. As a result of the change in the visual map, the auditory neurons acquire sensitivity to interaural delays outside their normal range, therefore producing a shift in the map of sound stimulus position (Knudsen and Knudsen, 1990). The auditory spatial map is generated by the projection from the central to the external nucleus of the inferior colliculus, and the shifted map in the external nucleus is generated by a sprouting of these connections (Feldman and Knudsen, 1997). The adult owl can reestablish previously “learned” functional connections but cannot establish new ones, with early experience defining the repertory of experience-dependent changes that adult neurons can assume (Knudsen, 1998).

Neural Representation of Perceptual Learning

Though the capacity for plasticity in adult primary sensory cortices was originally demonstrated as resulting from peripheral lesions, it is reasonable to assume that it didn't evolve for this purpose, but that it is used in the normal functioning of the cerebral cortex throughout life. The cortex is constantly assimilating changes in the sensory environment and is encoding information about novel stimuli throughout life. The way in which learned information is represented in the nervous system is inseparable from the nature of the neural code itself: how is a percept represented by the activity of a neuronal ensemble? There are many views on this. One view is based on the complementary ideas of rate code, line label, vector summation, and probability summation. According to this view, each cell is tuned for many different attributes, and it represents a labeled line for each attribute, such as position in space or orientation. In the domain of position, for example, different cells are labeled lines for different positions, and the strength of a cell's firing provides an indication of the proximity of a stimulus to its position. Put another way, a cell's activity can be represented by a vector whose direction indicates the value of the attribute (the line label) and whose length indicates the strength of firing. At any given time, an ensemble of neurons tuned to different stimulus values are active, and the stimulus properties can be ascertained by summing the vectors contributed by all the cells. Since cells are variable in their response to a given stimulus, increasing the number of cells available to evaluate the stimulus will increase the signal-to-noise ratio and the precision in the judgment. This is known as probability summation and explains how cortical recruitment, an increase in the size of the cortical area representing the trained sensory surface, may account for perceptual learning. Alternatively, sharpening the tuning of cells for an attribute can improve one's discrimination performance, because changing the value of an attribute such as position or orientation produces more modulation in the cells' responses. This kind of effect would allow learning to be represented by *decreasing* the size of the ensemble of neurons involved in the task.

Yet another possibility is that learning can be repre-

sented by changing the temporal relationships in the firing of neurons with each other and with the stimulus. The synchronization in the firing within a particular ensemble of neurons could signal the presence of a particular stimulus configuration. Other independent considerations include changes in the cortical locus representing the trained stimulus, and top-down influences, where properties change according to the task being performed.

Different changes associated with learning presume different fundamental rules for representing learned information. It has been argued that the brain is designed to identify and encode correlations present in the sensory environment. This is consistent with the Hebbian rule, which argues that connections are strengthened when the pre- and postsynaptic cells are activated together. The contrary argument holds that the brain is trying to decorrelate activity between neurons, that is, to make each neuron as different as possible in its functional specificity relative to the other members of the population. In this view, the neurons within an ensemble attempt to space themselves as far apart as they can in their representation of the stimulus domain. This requires removal of information that is common to two stimuli and enhancing the response to features that are unique to a stimulus, which is seen as a sharpening of a neuron's tuning. The mechanism required for this is thought to be decorrelation, or an anti-Hebbian rule (Barlow and Foldiak, 1989). Both mechanisms are likely to operate within the nervous system, decorrelation being prominent where the maximum amount of information has to be carried over a limited number of channels, such as in the optic nerve. Accentuating correlations may be more prominent where the nervous system has to find solutions to ill-posed problems and where prior knowledge of the structure of the sensory environment helps in parsing visual scenes into foreground and background or in distinguishing speech sounds from noise.

Increase in Size of Representation

Some of the changes associated with learning involve alterations in cortical topography, the maps of the sensory surface (e.g., the somatotopic map of the body or the retinotopic map of visual space). When training owl monkeys in a tactile frequency-discrimination task, restricted to one segment of one finger, several changes in the spatial properties of digit representation in somatosensory area 3b are found. These include a 1.5- to 3-fold increase in the area of representation of the stimulated digit, larger receptive fields in this area, and an increase in the amount of receptive field overlap between cells at adjoining cortical sites (Recanzone et al., 1992a, 1992b). The improvement is better when the training is active, with animals required to perform a discrimination task, than with passive stimulation while the animal is attending to a different, auditory stimulus (Figure 2A). In these experiments, the size of the somatotopic maps shows a weak though significant correlation with learning, and receptive field size is unaffected. When the receptive field sizes are measured across different skin locations and in different experimental animals, they show no correlation with the change in behavioral performance. Also, no correlation at all is found between the area of cortical representation and the levels of performance for a particular digit. The correlation

between the size of the cortical area representing the trained skin surface and the level of performance was considered inadequate for cortical recruitment to account for the behavioral changes (Recanzone et al., 1992b). Rather, they show that the improvement could be better explained by a learning-induced change in the temporal coherence of neural responses (see below).

In the auditory system, animals were trained to discriminate small differences in the frequency of sequentially presented tones and showed a 4-fold improvement in frequency discrimination threshold. The improvement was specific for the tested frequency. As a result of the improvement, the auditory cortex showed an increase in the size of the representation of the trained frequency (Recanzone et al., 1993). Conditioning leads to a shift in the frequency of the optimum stimulus for cells toward the conditioned stimulus frequency, equivalent to an increase in the size of the representation of that frequency (Weinberger et al., 1990). In the motor system, one sees similar changes, where animals trained on a task requiring skilled use of the digits show an increase in the motor cortex (M1) representation of the digits, and those trained on a task involving forearm movements increase the cortical representation of the forearm (Nudo et al., 1996). Also, muscles that contract together in the trained behavior become represented in nearby cortical locations, indicating that stimuli or behaviors occurring together in time (that is, those showing a correlation), are represented contiguously. Another example of the expansion of maps associated with trained behaviors is seen following cortical lesions. When small lesions are made in the primary somatosensory cortex representing fingertips involved in a behavioral task, and animals are retrained to perform the task, new representations of the trained fingertips emerge (Xerri et al., 1998).

One might expect, given the fixed size of a cortical area, that increasing the size of the representation of one part of the sensory surface would necessarily lead to a decrease in the size of the representation of the nontrained areas and, therefore, a decrease in performance. This is not seen, suggesting that there can be a net increase in the amount of information that one can store in a given area of cortex. If a fixed volume of cortical tissue can increase the amount of information it carries, one does not have to rely exclusively on cortical recruitment to represent the assimilation of information involved in perceptual learning.

Decrease in Size of Representation and Sharpening of Tuning

Sharpening of tuning can lead to improved discrimination of the trained attribute, particularly for those cells where the steepest parts of the tuning curves coincide with the value of the trained attribute. By sharpening tuning, neurons decrease the overlap in their responses to a range of different stimuli (Figure 2B). A change in tuning does not imply a change in cortical magnification, though because of the decrease in overlap one might expect fewer cells to be activated by a given stimulus. Animals trained on an auditory frequency discrimination task have both a sharpening of tuning and a shift in tuning toward the trained frequency (e.g., both sharpening and cortical recruitment; Weinberger et al., 1990; Recanzone et al., 1993). The ability to discriminate global motion from a small number of coherent dots increases

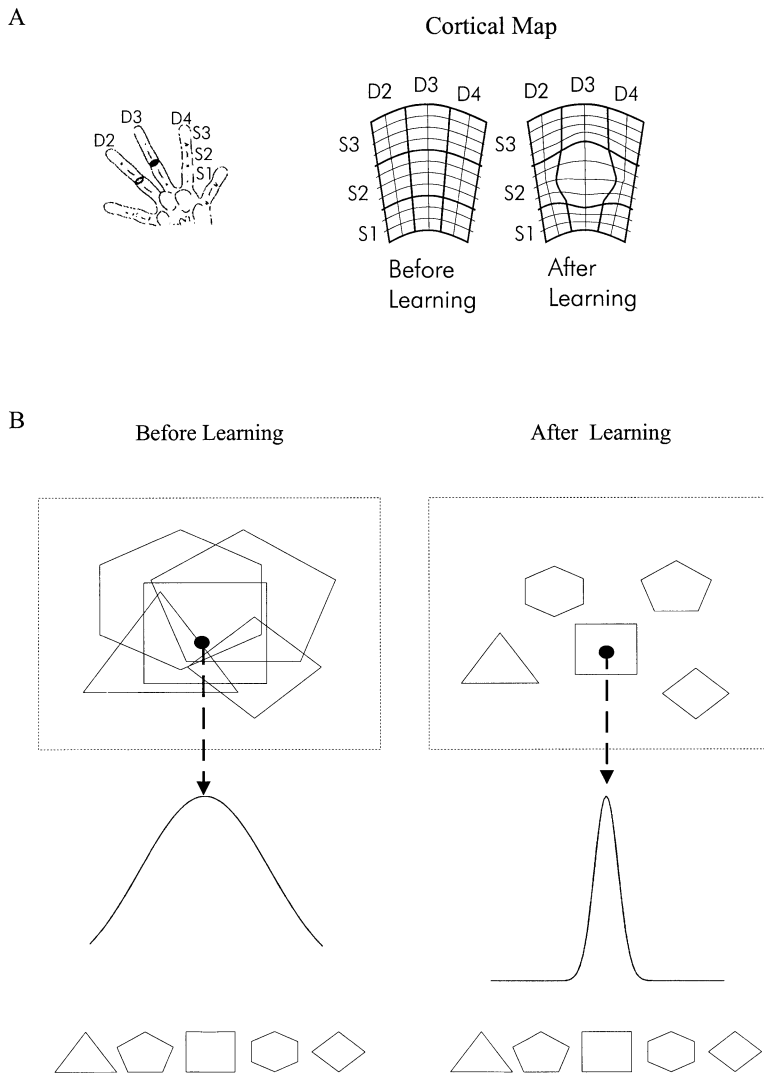


Figure 2. Changes in Spatial Representations with Learning

(A) Increase in the cortical area representing the trained sensory surface. The cortical representation of the small area of skin trained in a tactile discrimination task (dark patch, digit 3 segment 2) is expanded relative to the representation of the corresponding location on an adjacent, untrained control digit (light patch, digit 2 segment 2; Recanzone et al., 1992b).

(B) Decrease in the cortical area representing a trained feature and the corresponding sharpening of tuning of cells selective for that feature. Before training, cells are more broadly selective, and representations of different stimuli are highly overlapping. After training, cells become more selective, and the cortical representations of each feature shrink and become nonoverlapping.

with practice and this improvement correlates with a higher sensitivity of neurons in area MT (Zohary et al., 1994). Animals trained on an orientation discrimination task show steepening of the slopes of orientation tuning curves for neurons in primary visual cortex (Schoups et al., 2001). In effect, small changes in line orientation produce larger changes in neuronal responses, accounting for the improved performance in orientation discrimination.

The evidence that training can lead to a shrinkage of representations of trained attributes comes from several sources. In the antennal lobe of the honeybee, different families of odors normally have overlapping representations, but when the bee is trained on one odorant, the representation of that odorant becomes smaller, more compact, and nonoverlapping with other odorants (Faber et al., 2000). The representation of song syllables in the neostriatum of the canary, mapped with the expression pattern of the early immediate response gene ZENK, depends on familiarity. Familiar syllables have localized and tonotopic representation, unfamiliar syllables have a much broader representation (Ribeiro et al., 1998). In the realm of explicit learning, neurons in

the inferotemporal cortex increase stimulus selectivity when animals are trained to recognize an object, and there is a consequent decrease in the number of neurons responding to a given object (Logothetis et al., 1995; Kobatake et al., 1998; Miyashita and Hayashi, 2000). Similar changes are also seen in the prefrontal cortex (Rainer and Miller, 2000).

One can interpret these changes in terms of the idea that with learning neurons acquire greater selectivity and distance themselves from each other as much as possible in their coverage of the stimulus domain. This increase in selectivity and distance is thought to be due to a decorrelation of their activity, which is also referred to as an orthogonalization of representations.

Change in the Locus of Representation

As a consequence of learning, the representation of complex objects may be shifted from higher to lower areas. This shift could account for a perceptual change toward an automatic and parallel processing of familiar shapes. A distinction between parallel and serial processing in visual search tasks is proposed to reflect a difference between early and late stages of sensory processing (Treisman and Gelade, 1980). This classifica-

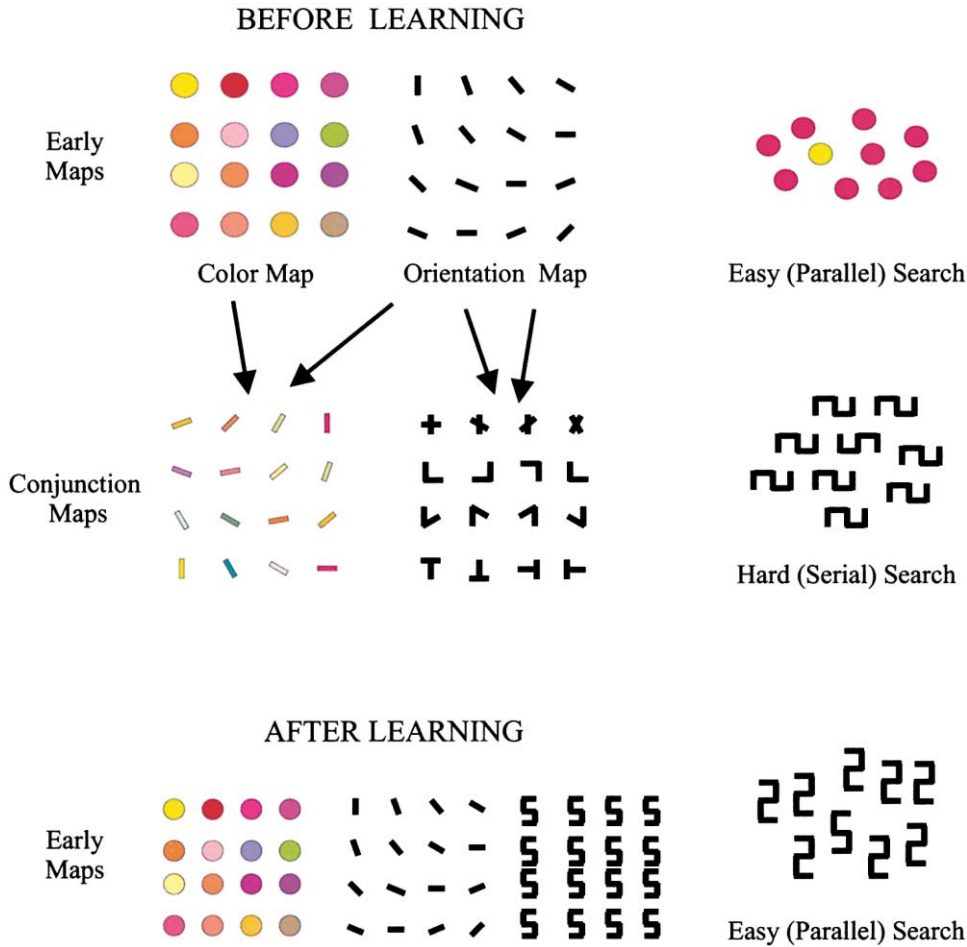


Figure 3. Change in the Locus of Representation from Later to Earlier Stages in Processing as Represented by Changes in Performance in Visual Search Tasks

Certain search tasks are easy and rapid, with the elements in the search array being processed in parallel: the efficiency of search is independent of the number of distractors, as if all elements are processed at the same time. These are thought to be mediated by cortical areas containing retinotopically organized “feature maps,” with cells selective for the features present in the search array. Other search tasks, for example, ones involving shapes, require combining features (conjunction maps) and are processed in an element-by-element serial fashion (middle row, right). Familiar shapes, such as alphanumeric characters, take on a pop-out quality, such as a “5” shape in a field of “2” shapes (bottom right). This can be understood as a development of new feature maps for trained shapes, which results from perceptual learning and allows the trained conjunctions to be represented as features (bottom left).

tion may represent two ends of a continuum, rather than two separate mechanisms of processing (Duncan and Humphrey, 1989; Braun and Sagi, 1990; Joseph et al., 1997; Nakayama and Joseph, 1997; Sigman and Gilbert, 2000). A given stimulus and search task may involve serial processing before training and shift to parallel processing with practice. The stimulus elements that can be detected by parallel search, which “pop-out” from the scene, correspond to elementary features that are coded by neurons at early stages. The early stages consist of a set of retinotopically organized maps coding for an elementary attribute such as color or orientation. More complex objects comprised of a conjunction of these features require attentional feedback for feature binding and, therefore, entail serial search, with performance decreasing with the number of distractors. A shape is considered to be a conjunction of elementary features or strokes, and identifying shapes would require serial search. But shapes to which subjects be-

come very familiar can assume a special significance and become identifiable by parallel search. This is seen for alphanumeric characters: it is easy to pick out a “5” shape in a field of “2” shapes, but not when the figures are rotated by 90°, which causes them to lose their familiarity (Figure 3; Wang et al., 1994). In a task involving identifying a triangle (a conjunction of three segments), learning progresses sequentially over the visual field. This suggests that in early stages of visual processing, where maps are topographic, cells acquire specificity for more complex but highly familiar shapes, shifting the representation of these shapes from later to earlier stages in the visual pathway (Sigman and Gilbert, 2000). This shift has the benefit of facilitating recognition that has to be done rapidly and in parallel, but has the cost of repeating the representation of the trained shape at many points in the cortical map.

Evidence for this proposed shift in representation comes from experiments where processing is disrupted

by transcranial magnetic stimulation (TMS). One of the cortical regions that is known to be involved in mediating conjunctural search, finding objects possessing a combination of two different attributes, is the parietal cortex (Corbetta et al., 1995; Arguin et al., 1990; Friedman-Hill et al., 1995). Stimulation of the right parietal cortex, which disrupts processing within this region (Pascual-Leone et al., 2000), impairs the performance on serial, but not parallel, visual search tasks (Ashbridge et al., 1997). Moreover, this effect is selective to the novelty of the task, since stimulation of the right parietal cortex impairs performance on naïve but not on trained subjects on a conjunction task (Walsh et al., 1998). It is still not known whether these effects are attentional or reflect changes in the representation of an object across the visual pathway as it becomes familiar. This idea of shift of representation has also been observed, at a different scale, in the rat barrel cortex. Rats were trained on a gap-cross task in which they have to sense, using their whiskers, the separation between two platforms. It was found that rats were not able to learn the task if a lesion in the supragranular layers is made prior to training, thus disrupting feedback from other cortical regions (Cauller, 1995). However, if the lesion is performed after training, rats continue to perform the task. (Diamond et al., 1999). This implies that feedback is necessary for the consolidation of learning, but that after learning occurs the representation is independent of feedback.

Given the large number of possible complex stimulus configurations, one might wonder whether there is a limit to the number of shapes that a given cortical area can encode. This question relates also to the issue of coverage, how many neurons are required to represent all the attributes to which neurons are tuned? In the primary visual cortex, simple stimulus attributes, such as orientation, appear to be sparsely represented across visual space, with a possible under representation of certain orientations in particular locations. Furthermore, one encounters portions of orientation hypercolumns (a region of cortex containing cells spanning the full range of orientation preference, roughly 0.75 mm in diameter) in which cells have the same orientation and fully overlapping receptive fields (Das and Gilbert, 1997). These regions, which can be several hundred microns in diameter, have cells that are identical in their selectivity for simple stimulus features, but differ widely in their selectivity to complex forms. The cortical representation of this higher order selectivity has a functional architecture of its own (Das and Gilbert, 1999). A piece of cortex of this size contains tens of thousands of cells, allowing the encoding of a rich variety of shapes and raising the possibility for the kind of shifting of representation from later to earlier stages in the visual pathway suggested by psychophysical studies.

Changes in the Temporal Relationships of Neuronal Responses

Another way in which learned information may be represented is in the timing of spikes in neuronal responses. It has been proposed that the precise timing of spikes within a spike train, and the relative timing of spikes between cells, carries more information about a stimulus than the overall spike rate. Several lines of evidence support the idea that changes in spike timing can encode learned information, and this change often corre-

lates better with learning than changes in topographic maps.

The synchronization of cell firing to the stimulus between trained and untrained cortical regions has been proposed to show a better correlation with the change in behavioral threshold than expansion of cortical maps. Mountcastle originally proposed the idea that the temporal organization of the response accounts for behavioral thresholds in frequency discrimination (Mountcastle et al., 1969, 1990). In the animals showing improvement in the frequency discrimination task, a subpopulation of the neurons responding to the trained digit showed a high degree of temporal coherence with the stimulus (Recanzone et al., 1992b, 1993). This would have consequences for the next stage in processing, where synchronously active inputs would have a great influence on the post-synaptic cells. When pairing sensory stimulation by stimuli of defined temporal structure (number of presentations per second) with nucleus basalis activation, which is designed to mimic what happens with training, there is a change of the response dynamics of neurons of primary auditory cortex (Kilgard and Merzenich, 1998). The nucleus basalis, a source of diffuse cholinergic input to cortex, signals the presence of a reward during learning. Under these conditions, neurons fire in phase with the stimulus at higher frequencies. Abnormalities in the temporal structure of neuronal responses have been implicated in dyslexia, and programs designed to entrain cell responses to the normal time course of sounds occurring in the phonemes of natural speech can lead to marked improvement in speech recognition (Merzenich et al., 1996; Tallal et al., 1996).

While changes in the temporal characteristics of responses might logically be involved in discriminating attributes with a temporal character (frequency, pulse rate), can temporal coding subserve learning of nontemporal attributes? Evidence supporting the role of synchrony in olfactory learning comes from studies of the invertebrate olfactory system. The antennal lobe of the locust, a region analogous to the vertebrate olfactory bulb, responds to odors dynamically and in synchronized fashion (Laurent and Davidowitz, 1994; Wehr and Laurent, 1996). The response is oscillatory, with a frequency close to 20 Hz as seen by a peak in the spectrum of the local field potential. The identity of an odor is represented by an ensemble of cells, each of which responds in different cycles of the oscillation in an odor-specific manner. As the locust experiences an odor repeatedly, cells become phase locked to the local field potential, and the power of the oscillations of the local field potential increases (Stopfer and Laurent, 1999; Figure 4). As responses become more synchronized, they decrease in intensity. This effect is odor specific, and, after ~12 min, the system resets to normal. Injection of picrotoxin, a GABAergic blocker, disrupts the synchronization and interferes with fine odor discrimination (MacLeod and Laurent, 1996; Stopfer et al., 1997; MacLeod et al., 1998).

Changes in Contextual Tuning and Task Dependency

Because perceptual learning shows specificity for context and for the spatial configuration of the stimulus, it seems unlikely that cortical recruitment could account for the perceptual changes. If there were an expansion in the area of cortex representing the trained part of

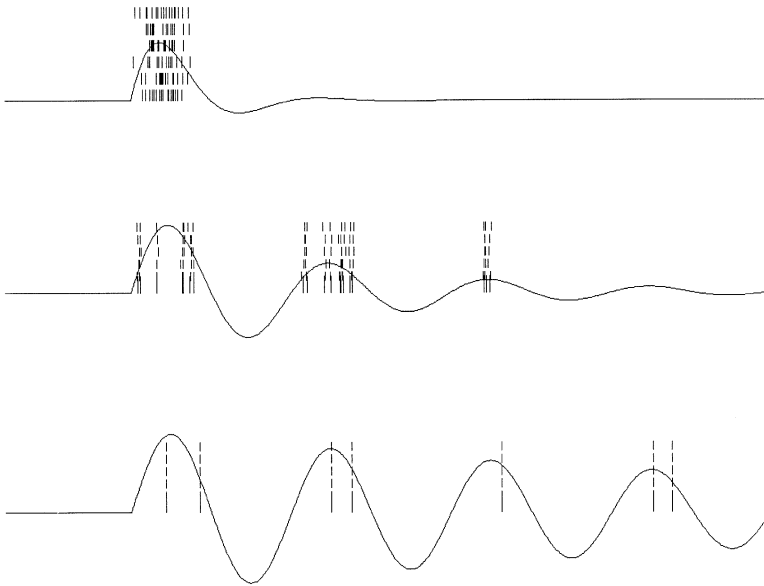


Figure 4. With Repeated Odor Presentations, Response Intensity Decreases while Coherence and Spike Time Precision Increase

Activity is schematically represented in the antennal lobe of the locust (a region analogous to the vertebrate olfactory bulb). Simultaneous local field potential (LFP) is represented by sinusoidal waves, and spiking activity from a projection neuron (PN) is represented by the superimposed raster graphs. The coherence between the firing of PN and the LFP increases during the first trials before reaching an asymptote. This effect is accompanied by a decrease in the average firing rate of each individual neuron (Stopfer and Laurent, 1999).

visual space, one might expect that any task involving the same part of the visual field and therefore the same part of cortex would show improvement. In fact, when animals are trained on a three-line bisection task (described above in the section on the psychophysics of perceptual learning, and shown in Figure 1), there is no change in the magnification factor (the number of millimeters of cortex representing a degree of visual space) in the area of cortex representing the trained stimulus (Crist et al., 2001). Moreover, there is no change in the tuning of cells to simple stimuli, as reflected in measurements of receptive field size and orientation tuning bandwidth. There is, however, a marked effect on the contextual tuning of cells in the trained cortical location, one that is specific to an attribute that is related to the trained task, the modulation in response to a line within the receptive field by a second parallel line placed at varying separations from the central line (Figure 5). The observed effects are specific for this property, since they are not seen for a different contextual influence, that of a colinear line at varying offsets (vernier tuning).

These effects of training on contextual influences show powerful top-down control. The change in contextual influence with learning is task dependent, since it is only seen when the animal is performing the trained task, and not when it is doing an unrelated task (Crist et al., 2001). This is a very striking finding, since it shows that the cortex can dynamically modify the processing of visual information according to immediate behavioral requirements. The task dependency of contextual interactions permits the same neurons to mediate entirely different perceptual functions that may require opposing neuronal mechanisms and suggests that neurons may change their line label with behavioral state.

The mechanism of this specific, context-dependent learning may involve a modulation of subsets of horizontal inputs to a cell, at a more refined level than that observed following retinal lesions. In this view, modulation of inputs from cells with receptive fields arrayed along an axis perpendicular to the target line could account for specificity in the localization to references

placed along that axis as opposed to those placed along the colinear axis. This modulation of subsets of inputs would permit both specificity in learning to a particular stimulus configuration and storage of information about a large number of visual discrimination tasks, without having the multiple learned tasks interfering with one another and allowing for retention in the learning for an extended period of time. It also provides an explanation for why learning on a task put in one part of the visual field does not lead to a “robbing” or decrement in performance in other parts of the visual field. The further dependence on task suggests an interaction between a top-down signal, mediated perhaps by feedback connections coming from higher order cortical areas, and local lateral interactions, such as those provided by horizontal connections. This allows the same population of neurons to mediate multiple tasks in situations where different tasks require opposing mechanisms at the receptive field level. For example, side band inhibition may be required for surface segmentation, but side band facilitation may be invoked for the three line bisection task, and cells could shift between one and the other depending on the current perceptual task. This would suggest further that cells may not only change their receptive field properties, but also their line label, the meaning attributed to their responses by successive stages in processing. The idea that top-down signals alter lateral interactions specifically is supported further by studies on modulation of contextual influences by spatial attention (Ito et al., 1998; Ito and Gilbert, 1999).

Learning is state dependent in that it requires reproducing the same physiological environment for both encoding and retrieval. Neurons in rat somatosensory barrel cortex can change their tuning properties with experience if stimulation is paired with the application of acetylcholine, but those changes are seen only when the neuron is in the same physiological environment, that is, in the presence of acetylcholine (Shultz et al., 2000). This implies that, as a consequence of experience, neurons increase the variety of tasks in which they can participate and that these different functions are

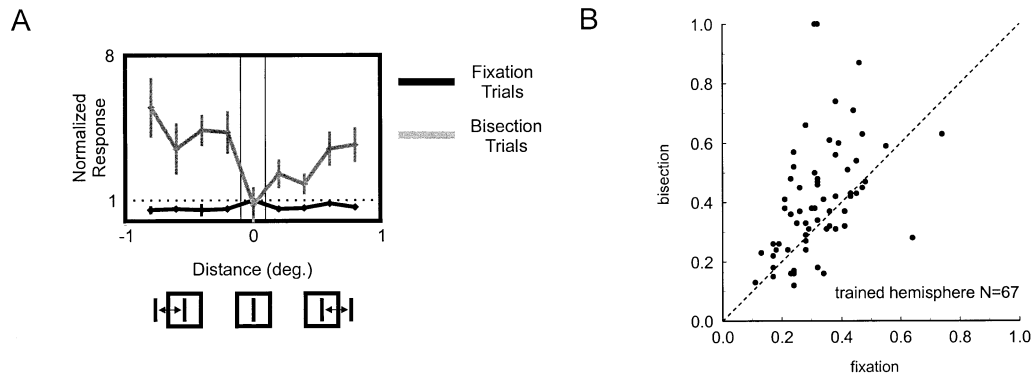


Figure 5. Changes in Contextual Interactions and Task Dependency

Monkeys were trained on the three-line bisection task (see Figure 1), and single cells were recorded in the superficial layers of the primary visual cortex. The response properties of cells were measured when the animals were doing either of two discrimination tasks: detection of a small change in the brightness of the fixation spot, and the three-line bisection task. No difference was seen in the topographic maps following training, nor in the size or orientation tuning of the receptive fields. There was, however, a substantial change in a property related to the task, the contextual modulation of the cell's response to a line segment within the receptive field by a second parallel line, placed outside the receptive field. In the example shown here (A), under the fixation task the second line was generally inhibitory, but the cell's response did not show appreciable modulation with changing line separation. When the animal did the bisection task, the influence of the second line changed from inhibitory to facilitatory, and there was substantial modulation in the degree of facilitation with changing line separation. (B) Based on this, a modulation index was calculated as the difference between the maximum and minimum responses in the two-line separation tuning curve divided by the sum. In the trained hemisphere, many cells showed more modulation when the animal was performing the bisection task than when it performed the fixation task. This difference was not seen in the untrained hemisphere. The effect suggests that the neuronal effects of perceptual learning are seen in primary visual cortex, that learning specifically influences contextual interactions within V1 as opposed to the topographic maps or simple receptive field properties, and that the effects are under strong top-down control, only being present when the animal is performing the task on which it was trained. (Image adapted from Crist et al., 2001.)

gated by the same triggers that induce learning. This idea is further supported by the task dependence of the learning effects described above.

Perceptual Learning—Early versus Adult Experience

Perceptual learning reflects an ongoing process of assimilation of the sensory environment beginning from postnatal life and continuing through adulthood. Whereas it has long been known that some of the functional properties of cortical neurons, such as orientation selectivity, do not require visual experience to develop, the more complex and integrative properties do. Here one must distinguish between activity-dependent organization of the visual cortex that can result from spontaneous activity in utero (Linsker, 1986a, 1986b; Galli and Maffei, 1988; Meister et al., 1991; for contrary evidence, see Crowley and Katz, 1999) and properties resulting from exposure to a structured visual environment. In fact, it is likely that the properties required for intermediate level vision, the processes of contour linkage and grouping, surface segmentation and occlusion, do involve experience of the visual world early in postnatal life. Evidence that the response properties of cells in the visual cortex reflect the structure of natural scenes can be explained either by an evolutionary, phylogenetic mechanism or by a developmental, ontogenetic mechanism. Developmental studies in young children point to at least the involvement of the latter.

Many receptive field properties are related to the structural properties of the visual environment. The higher order properties of visual cortical neurons relate to the way we parse visual scenes based on global patterns, as originally described in the Gestalt rules of perceptual organization. A fundamental rule of the Ge-

stalt school of psychology holds that one normally links contours in a visual scene that follow a principle of "good continuation," maintaining smoothness and constancy of curvature (Wertheimer, 1938). A simple geometric rule encompasses this principle: Straight lines remain straight over large parts of the visual image (colinearity), curved lines keep a constant radius of curvature ("cocircularity"; Sigman et al., 2001; Figure 6C). The most salient contours, by this theory, are those that maintain the same direction.

The organization of line segments in natural scenes parallels the geometry of interactions of primary visual cortex. (Figures 6A–6B; Kapadia et al., 2000). Long-range interactions tend to connect iso-oriented segments (Gilbert and Wiesel, 1989; Malach et al., 1993; Bosking et al., 1997), and interactions between orthogonal segments, which span a short range in natural scenes, may be mediated by short-range connections spanning singularities in the orientation and topographic maps in the primary visual cortex (Das and Gilbert, 1999). The finding of a correspondence between the contextual interactions observed in visual cortical neurons and the regularities of natural scenes provides an ethological explanation for the development of contextual interactions based on the regularities of the environment. In effect, the most probable correlations between elements of the natural world, such as those represented by the colinear configuration, are enhanced by the visual system. This enhancement of regularities may be mediated by Hebbian mechanisms, where connections are strengthened between neurons that fire together, which would be those with receptive fields aligned with commonly seen contours. Adult perceptual learning of trained shapes can be viewed as a continuation of this

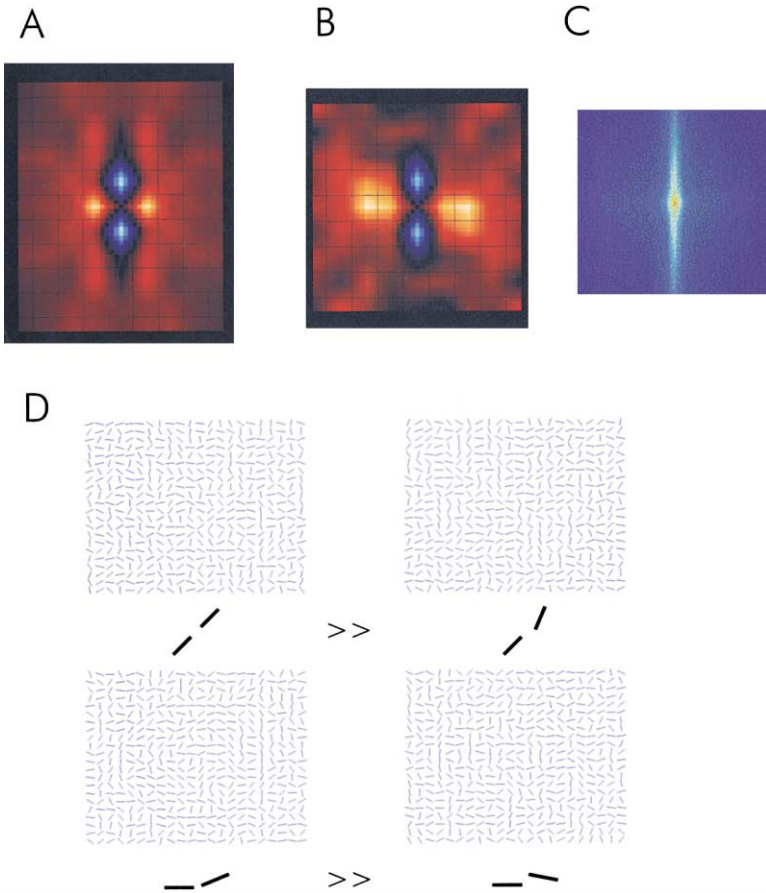


Figure 6. Perceptual Learning Reflecting Early Visual Experience

The pattern of perceptual interactions and receptive field interactions of neurons in primary visual cortex parallels the organization of segments in natural scenes.

(A) Influence of contextual lines on the perceived orientation of a centrally placed vertical line, using the tilt illusion as a probe. When the surrounding lines differ from the central line by 5° orientation, they attract the perceived orientation of the target line when they are placed along the colinear axis (blue regions), but have a repulsive effect when placed on the orthogonal axis (orange regions). (Image adapted from Kapadia et al., 2000.)

(B) Differences between the responses of neurons in primary visual cortex of awake behaving monkeys to a single bar in the receptive field and when presented with two symmetric flanking bars at different locations in the visual field. Different points in the map correspond to different locations of the flanking stimulus. There is strong facilitation along the collinear axis (blue) and inhibition along the orthogonal axis (orange). (Image adapted from Kapadia et al., 2000.)

(C) Probability of finding a pair of iso-oriented segments as a function of their relative distance. For example, when a vertical line segment is present in one part of the visual scene, there is a higher probability of finding other vertical line segments along the colinear axis (seen as the light blue to red areas in the correlation map) than in other positions (the dark blue areas). This indicates that the most typical arrangement of pairs of segments in natural scenes is colinear. (Image adapted from Sigman et al., 2001.)

(D) Saliency of contours in complex visual environments show similar behavior as is observed in the statistics of natural scenes—straight lines are more salient when composed of colinear and iso-oriented line segments, and curved contours are more salient when the line elements lie on a common circle. These global percepts develop over the first few years of life (Kovacs et al., 1999).

process, where the line elements from which these shapes are built commonly occur together, e.g., show a significant correlation (Crist et al., 1997; Crist et al., 2001; Sigman et al., 2001).

The way in which learning would be expected to represent the structure of the natural world depends on whether one believes the cortex is designed to identify common cooccurrences or to identify singular parts of scenes. In an image, there are elements that are distinctive and carry the most information about what is in the scene, and other elements that are redundant. As with image compression techniques used in digital cameras, some receptive field properties serve to remove the redundant information and maintain the ability to reconstruct the entire scene (Atick, 1992; Atick and Redlich, 1992; Barlow, 1960; Barlow and Foldiak, 1989; Dan et al., 1996; Olshausen and Field, 1996a; Van Hateren and Van der Schaaf, 1998). This idea can be understood in terms of an optimization problem—how to find the most efficient code in terms of information transmission—or ethologically, assuming that rare events have particularly important behavioral relevance (Atick, 1992). It has been suggested that the role of receptive fields found in the retina and LGN, which have a circular antagonistic

center-surround structure, is to remove redundancies from natural images, since they enable neurons to respond to edges and not to surfaces of uniform luminance. Since most of the parts of a scene are composed of surfaces, very few retinal neurons will respond when presented with an image, and these are the ones carrying the important information about the image. This idea, which is referred to as a sparse code, has been extended to primary visual cortex, with oriented receptive fields serving to optimize sparseness (Bell and Sejnowski, 1997; Van Hateren and Van der Schaaf, 1998; Olshausen and Field, 1996b). While the center-surround and orientation receptive field properties are present at birth, a continuation of the process of “image compression” can contribute to perceptual learning when the learning is associated with sharpening of tuning and making representations more compact (as described above).

Though, on the face of it, the ideas of enhancement of common cooccurrences and image compression seem to be contradictory and require different rules for synaptic changes, they may both be operative, but under different circumstances. The fact that contextual interactions change with contrast (Kapadia et al., 1999) or

with different signal to noise relationships suggests that the primary visual cortex may dynamically solve different problems according to different perceptual necessities.

However, we must still address whether any correspondence between receptive field properties and the structure of natural scenes emerges through innate mechanisms or whether they develop during early visual experience. Both psychophysical and anatomical evidence suggest that higher order properties of neurons in primary visual cortex, which mediate the process of spatial integration and contour extraction, do develop as a result of early visual experience and, therefore, result from perceptual learning occurring early in life. Psychophysical studies in newborns and infants suggest that grouping and spatial integration develop slowly and improve during the first years of life (Kovacs et al., 1999; Kovacs, 2000; Figure 6D). Children ranging from 5 to 14 years were tested in a contour extraction task based on the rules of good continuation. This task becomes harder as the distance between the element of the contours relative to the mean distance of the background elements increases, and global properties of the contour, such as closure, make the task easier (Field et al., 1993; Kovacs and Julesz, 1993, 1994). Performance in this task improves continuously with age, even past the age of 10 years, as does the scale at which the task can be performed, suggesting that the range of spatial integration increases with age. The mechanism underlying this maturation may be represented by the postnatal development of long-range horizontal connections in primary visual cortex. These connections are simultaneously pruned and enriched, and become more clustered, for months after birth (Callaway and Katz, 1990; Burkhalter et al., 1993). It is not known, however, whether the maturation of these connections continues for as long a period as is observed for the perceptual changes.

Conclusions

Perceptual learning reflects an ongoing process, beginning with our early experience of the regularities of the world and continuing throughout our lives, to assimilate the specific patterns to which we become familiar. At any age, it reflects our experience of correlations present in our sensory environment. This idea follows the suggestion by Helmholtz (1866) that the processing properties of the human visual system are ontogenetic, a result of “unconscious inference,” and represent a Darwinian mechanism for shaping the functional properties of the brain. The fact that all areas of the adult cerebral cortex have the capacity for plasticity, changing functional properties and functional architecture in an experience-dependent fashion, which was originally established following peripheral lesions, is now abundantly evident in experiments on perceptual learning.

The neural mechanism of perceptual learning relates centrally to the nature of the neural code itself. A number of neural correlates of perceptual learning have been identified, ranging from changes in cortical magnification to alteration in the temporal response characteristics of neurons to modulation of contextual influences. Moreover, the kind of information represented by a given cortical area may not be fixed. Instead, learning may induce shifts in the cortical areas in which specific infor-

mation is represented. Functional localization is likely to be a dynamic property of cortical areas. Evidence that some of these changes are under top-down control suggests that perceptual learning arises from a combination of changes in local circuits at early cortical stages in sensory processing and feedback influences coming from higher order cortical areas.

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