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A Memory System in the Adult Visual Cortex

INTRODUCTION

This review addresses several aspects of human learning and memory as related to basic visual processing. It is an attempt to suggest a tentative, specific, context for some of the basic questions raised by the phenomenon of perceptual learning, i.e., the finding that genuine and long-lasting changes are induced by experience (practice) in adult visual processing. Our main conjecture is that certain types of memories—perceptual skills of the type evolving through texture discrimination learning is our paradigm—are mediated by discrete, experience-dependent changes in the specific sensory system involved in the performance of the task. We suggest there is a reasonable case to be made for the hypothesis that all levels of visual processing, including the primary visual cortex, could under specific retinal input and task-defined conditions, undergo long-term, experience-dependent changes (functional plasticity). Furthermore, there is evidence indicating the possibility that the locus of these changes is determined by the double constraint of retinal input (selectivity; differential activation by the specific stimulus) and task demands (relevancy). Thus the conjecture is that the acquisition (learning) and retention (memory) of visual skills would occur at the earliest level within the visual processing stream where the minimally sufficient neuronal computing capability (expressed either as

single-unit response properties, or as the product of a local neuronal assembly) is available for representing stimulus parameters that are the relevant input for the performance of a specific task (The Minimal Level Hypothesis). Adult perceptual learning is contingent on the functional architecture of the sensory system but, at the same time, modifies it.

Until recently, it was commonly believed that the functional properties of neurons within early sensory processing areas, as well as the circuitry of the sensory cortex, are fixed in adulthood. However, in parallel to psychophysical evidence in humans,^{1,2,7,20,39,42,47} there is an accumulating body of electrophysiological evidence suggesting that even at the earliest stages of sensory processing, neuronal properties are subject to experience-dependent plasticity in the adult brain.^{34,43,44,49,54} Although much of the work concerning adult cortical plasticity has been done in sensory modalities other than vision, the main focus of this review is the conjectured correspondence between perceptual (visual skill) learning and functional (developmental, as well as adult) cortical plasticity. This conjecture has provided several strong constraints and new testable predictions on the nature of the neural substrates underlying some types of human learning.

The observation that prompted our experiments was the finding that adult observers practicing in a simple visual discrimination task (in which optimal stimuli for "automatic," preattentive texture segregation were presented^{4,14,16,37,46}) showed remarkable day-to-day improvements. Psychophysical data and computational models have previously suggested that the performance of this task is determined by low-level, stimulus-dependent visual processing stages.^{15,16,29,45} Therefore the finding that adult observers show large gains in the performance of such a basic task of form vision was unexpected. One would have expected that during the course of normal development, indeed as a result of everyday experience, this task would be perfected to the limit. However, this result suggested a possible probe, by way of psychophysical measurements, into the nature and extent of the modifications induced by practice in the adult visual system. Potentially, we were posed to look at not only what changes with repeated sensory experience (practice), but rather at where and when these changes occur within the adult brain.

To investigate these questions we restated a general problem: what are the neural mechanisms mediating the acquisition and retention of improved performance as a function of practice—in terms that could provide psychophysical constraints for the functional characterization of neuronal assemblies undergoing practice-related changes. A cornerstone of perceptual learning research in recent years, has been the notion that a dependence of the learning process on specific stimulus parameters should provide these constraints.^{1,2,7,20,39,42,47} For example, if the learning effect can be shown to be retinotopically local, i.e., it would not transfer (or generalize) from a trained to an untrained part of the visual-field, it must presumably involve changes in an early, low-level processing stage where the retinotopic organization of the visual input is still retained. Similarly, a high degree of monocularly (i.e., learning that would not transfer from a trained to an untrained eye) would suggest that learning affected a level within the visual system where cells preferentially

respond to input from one retina (monocular cells). This is because information about the eye of origin of the signal is not retained in mid- and high-level visual processing area.⁵⁵ These considerations suggested the following general design for our psychophysical experiments: we recorded the course of learning, using a specific stimulus configuration, until performance has asymptoted. Then, the specificity (dependence) of the learning process for basic attributes of the sensory experience was probed by measuring the effects, on performance, of discrete manipulations of the stimuli's physical parameters. Finally, this procedure was extended to provide a closer look at the time course of learning and the effects of task demands (extra-retinal constraints on learning).

MAGNITUDE AND SPECIFICITY OF THE LEARNING PROCESS

The psychophysical paradigm is quite simple. (Detailed description of stimulus parameters and testing procedure are to be found elsewhere.^{20,22}) Examples of a stimulus and a masking pattern are shown in Figure 1(a). In these studies, observers were required to identify the shape of a small target texture composed of three high-contrast line-elements differing only in their orientation from a background texture made of identical elements. The target shape was defined by the geometrical arrangement of the target elements. For each observer, element orientation and target location (within a restricted part of the visual field) were kept unchanged throughout training. A very brief presentation time (10 ms)—so no eye movement could displace the projection of the stimulus on the retina—was employed to ensure that the target consistently appeared in a specific retinal location, and fixation was enforced by a concurrent letter discrimination task presented at the center of the display. Performance was measured as the mean correct response for increasingly shorter time intervals between the briefly presented stimulus and a patterned mask (stimulus-to-onset-asynchrony, SOA). As the SOA sets the limit on stimulus availability, it is a measure of the time the visual system requires to obtain a workable precept (representation) of the sensory input (sensory processing time) independent of motor response times. (On the biological significance of such a measure of human performance, see Merzenich and Jenkins³³ and Tallal⁵¹ in this volume).

The main effect of practice was a leftward shift of the performance curves which indicate genuine increases in the visual system's sensitivity on consecutive sessions spaced 1–3 days apart (Figure 1(b)). Thus these increments in performance reflect perceptual learning retained from session to the next. The learning effect is quite large: Where perception completely fails on the initial session, observers can perform > 90% correct discrimination on the following day (Figure 1(b)). In terms of SOA, the visual system's sensitivity was more than doubled by the time performance asymptoted.

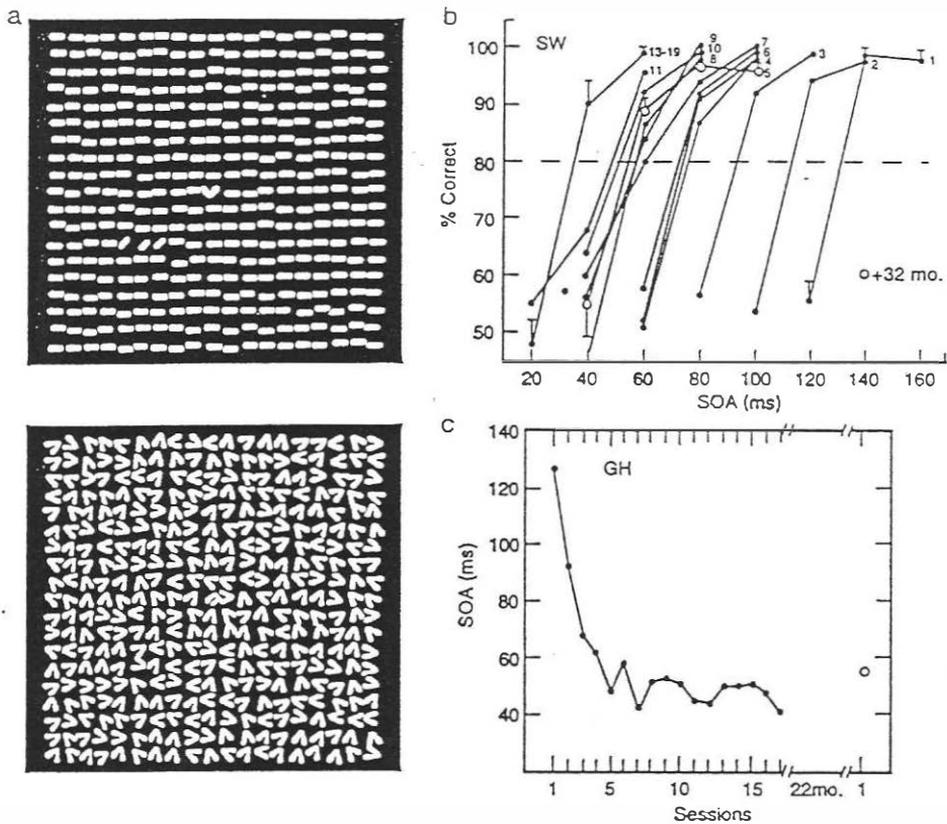


FIGURE 1 Computer-generated displays (a). (top) A test stimulus with a small target texture (three diagonal bars) embedded within a background of horizontal elements. Display size was 14° by 14° of visual angle viewed from a distance of 110 cm, with an array of 19-by-19 slightly jittered line segments (subtending $0.42^\circ \times 0.03^\circ$ each, with a luminance of 35 cd/m^2 and spaced 0.70° apart). A small rotated letter (either T or L) at the center of display served as the fixation target. The target texture's position was varied randomly from trial to trial but always within a specific display quadrant and within 2.5° – 5° of visual angle from center of display. (bottom) Mask pattern made of randomly oriented V-shaped micropatterns and at the center, a compound micropattern of superimposed T and L. (b) Psychometric curves for performance on consecutive daily sessions (spaced 1–2 days apart) for observer SW (\square), and on a probe session 32 months later (o) (she had no psychophysical experience with visual textures in the interval). Results indicate persistent day-to-day improvements and almost no forgetting on a timescale of years. Each data point represents the mean percent correct responses (\pm sd) from three to five consecutive blocks (150–250 trials) for a specific SOA. The initial performance curve is on the right; as learning occurs, the curves are displaced to the left (shorter processing times needed for task performance) indicating improved sensitivity. The left-most curve represents asymptotic performance. (---), 80% correct (threshold) performance. (c) Learning curve for observer GH. SOA required for threshold discrimination on consecutive daily sessions (\square), and for a probe session 22 months later (o). Each point refers to a single session, interpolated from the respective psychometric curve. The large learning effect has not decayed in the interval (where no psychophysical testing or training was done). [Reprinted, with permission, from Karni and Sagi.²²]

This large improvement was found to be highly specific for some simple physical attributes of the retinal input.²⁰ (a) It is very local in a retinotopic sense. Indeed, displacing the target by just 3° of visual angle from a previously trained visual-field locality, necessitated retraining. (b) It is specific for the background elements' orientation. Thus, new independent learning is required when the background elements' orientation were flipped to the orthogonal or rotated by 45°. Surprisingly, learning was not specific for the target elements' orientation. However, learning was restricted to the target textures location; i.e., repeated exposure to background elements per se was not enough to induce texture discrimination learning. This apparent paradox can be resolved by assuming that learning occurs only where texture gradients, relative to a specific background, are available as essential input.²¹ Finally, (c) learning is monocular. The effects of practice show little transfer from a trained to an untrained eye.

WHERE PRACTICE MAKES PERFECT

The above results indicate that a substantial part of the texture discrimination learning effect is subserved by retinal-input-dependent changes at a level within the visual system where monocularly, and the retinotopic organization of the visual input, are still retained and different orientations are processed independently. Furthermore, an orientation-gradient dependent mechanism may be implicated.

The most parsimonious, yet biologically plausible, interpretation of these results is that texture discrimination learning involves experience-dependent local plasticity within primary visual cortex (Area 17). This tentative localization is in agreement with the fine-grained retinotopy of the learning effect. However, it is the significant monocularly of the learning effect that implicates changes occurring at or before area 17 as a locus of learning. Only at these early stages of visual processing one finds neurons that preferentially respond to input from one retina and are thus committed to processing information from a specific eye. Orientation-selective neurons which would still have disparate monocular inputs, and thus satisfy all the above constraints, are found, in primates, only in V1,^{12,55} which corresponds to area 17 in the human brain.

Though by no means conclusive, a strictly reductionistic interpretation of these results is possible. The learning effect may be accounted for by Hebbian activity-dependent synaptic changes (functional plasticity).^{20,21} Consider the interaction between (a) first-level ("presynaptic") orientation-selective, monocular cells and (b) second-level ("postsynaptic") gradient-sensitive, binocular cells. These second-level cells would respond to simultaneous activity generated in disparate first-level cells responding to stimuli presented within a specific (but quite large) retinotopic neighborhood. Both these types of cells have been described in primate V1.⁵³ At,

and only at, retinal locations presented with texture borders, a concurrent, correlated activation of both first-level and second-level cells will occur, leading to enhanced synaptic connections with repeated stimulus presentation. Other mechanisms that could, presumably, subserve texture discrimination learning in early visual processing stages, such as the improvement of background orientation long-range horizontal connections are discussed by Karni²¹ and Karnia and Sagi.²⁰ Yet again, Hebbian rules of correlated-activity-dependent synaptic modification could support experience-dependent changes at this level (see Polat and Sagi^{40,41} and Katz, Victor, and Purpura²⁷ in this volume). Of course, single-synapse plasticity as the neuronal implementation of a human memory phenomenon is simplistic. However the basic idea of experience-dependent modification of local, discrete, neuronal response properties as the locus of human learning, is defensible. More than 40 years ago, Mishkin and Forgays, investigating the retinotopy of word recognition, have suggested a very similar idea as the Hebbian interpretation for the development of visual-field-specific reading skills.³⁵ More recently, several examples of stimulus specific perceptual learning, in nonhuman primates, have suggested functional plasticity in primary somatosensory^{32,43} and auditory^{44,54} cortex. The resemblance of the monkey data to the human learning data, is striking.

WHAT IMPROVES?

Two testable predictions of this functional localization of the learning process to improved local representation of gradient-defined contours can be made. One, a low-level orientation-gradient computing mechanism is involved in the learning process (undergoes an experience-dependent shift in processing efficiency). If so, a reasonable expectation would be that practicing texture discrimination will concurrently improve texture-gradient-defined target detection, and possibly vice versa. A second prediction would be that learning should transfer across the target's global shape. For example, once the appropriate sensory input parameters are used any global shape, defined by a texture gradient boundary, should be better represented after learning has occurred.

LEARNING A VISUAL SKILL

Both these predictions were borne out by our results.^{19,21} Our results show that performance undergoes a remarkable improvement for both texture target discrimination and texture target detection. This outcome is independent of which of these two tasks was used in training. As different (higher) levels of computational complexity are needed to solve a discrimination, as compared to a detection task (using

the very same stimulus), our results suggest the localization of the learning effect into a common processing stage which both these functions utilize. A good candidate would be a local gradient detection mechanism. The output of such a mechanism would be the explicit representation of the location of texture gradients, i.e., the boundaries of texture objects.

There is also complete transfer of the performance gain acquired by training in the discrimination of one pair of target shapes as defined by the three target element configuration (horizontal vs. vertical bars) to a new configuration (left oblique vs. right oblique bars) (Figure 2(a)) and even to more complex shapes such as letters.²⁶ Again, because the target's global shape is physically defined by the texture gradients, an improved mechanism of local gradient representation would improve both shape discriminations equally well. Thus, while texture discrimination learning is dependent on, and very specific for, simple (low level) attributes of

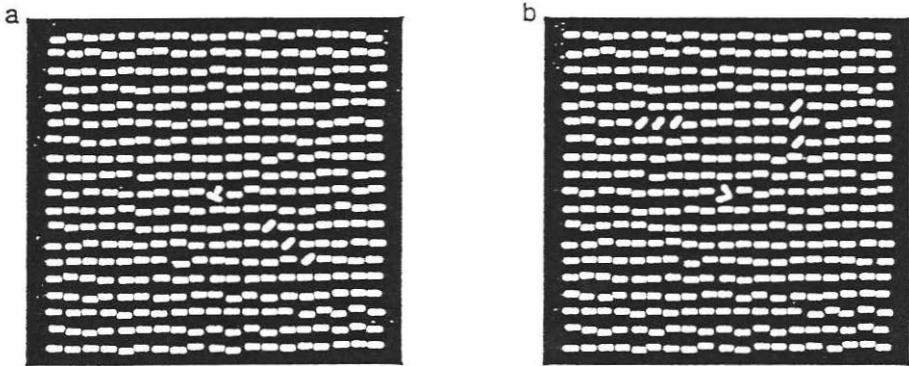


FIGURE 2 Modified stimulus arrays. Display parameters were set as in Figure 1 with two discrete modifications. (a) The target's shape (configuration as defined by the three diagonal elements) was changed to randomly alternate between left and right oblique. Note that the observer's task was to discriminate the target's global shape (left leaning/right leaning), rather than the target texture's elements' orientation (which for some observers were switched too so as not to change the target's width between the two conditions). (b) In this modification of the original stimulus, two physically identical target textures were presented—to the corresponding quadrants of the two hemifields. Each target's shape was alternated randomly, and independently, between horizontal and vertical. Two sets of experiments were run. In the first, observers were instructed to report the shape (orientation) of the target appearing to the left (others to the right) of fixation point with the relevant target (location) unchanged until performance has asymptoted. In the second set of experiments observers were required to compare both targets and report whether the two were the same shape (both horizontal or both vertical) or different (orthogonal to each other). The time course and magnitude of the learning in these two sets of experiments were not significantly different.

the retinal input, it is not specific for higher level attributes of the input such as global shape. Observers can learn "how to" discriminate target shapes irrespective of "what" these target shapes are. This dissociation is a hallmark of procedural ("habit," skill) learning.^{36,50}

One concern in pursuing the possibility that functional changes in the primary visual cortex are the locus of texture discrimination learning, is whether area 17 has a role in orientation-gradient-dependent object/background segmentation. How early in the stream of visual processing does the segmentation of the retinal input by way of gradient defined contours occur? Two recent studies of human subjects, one an evoked potentials study,²⁸ the other a functional magnetic resonance imaging study,²³ have documented a specific (in the latter study, retinotopically local) orientation-gradient-dependent (evoked) response in the human primary visual cortex. This is in agreement with the primate data,⁵³ and indirectly supports our interpretation of the psychophysical data.

THE "GATING" OF LEARNING

A second question concerns the minimal necessary conditions that must be satisfied for adult perceptual learning to occur. Is repetitive, consistent, retinal exposure to an appropriate visual stimulus all that's required to induce experience-dependent changes in the adult brain? It would be surprising, if large and long-term changes in basic visual circuitry were "allowed" without some manner of nonvisual control. Moreover, pursuing the analogy between perceptual learning and functional plasticity, one would expect some extra-retinal control mechanism to "gate" functional plasticity—i.e., control the adaptive state of cortical neurons. Such mechanisms play a decisive role during developmental plasticity,^{8,10,48} and presumably account for the fact that only behaviorally relevant neuronal plasticity occurs in the adult brain.⁴⁹

To test this proposal, a modified stimulus was devised (Figure 2(b)). Our results show that for observers consistently presented with two targets of which only one is relevant for task performance, learning occurs only for the task-related target.^{18,21} Although the two targets are physically identical, learning occurs independently for each target as determined by the target's relevance for task performance. However, when both targets are relevant (e.g., in a comparison, same/different, task), learning occurs for both in parallel.

Several mechanisms could underlie this nonretinal-input-determined selectivity of the learning process. For example, plasticity in mammalian visual cortex was shown to be dependent on motor and ocular activity, arousal, thalamic inputs and tonic effects of neuromodulators.^{8,10,17,48,49} Our results would suggest a much more specific, selective mechanism. Nonetheless, it is possible that the fine specificity and selectivity of the learning effect is due to retinal-input-dependent

local neuronal activation while the gating mechanisms are relatively "coarse." In a study of auditory conditioning, a convergence of specific auditory input and task-dependent ACh release has been suggested to underlie the modification of auditory information processing by experience.⁵⁴ Behavior-dependent modulation of single unit responses have been shown at several levels of visual processing.^{6,9}

Independent of the neuronal implementation, our results suggest that learning is gated by extra-retinal, task-dependent inputs. It is the combination of the specific sensory (retinal) input and the task demands may provide sufficient constraints to determine the evolution of perceptual learning and control the loci of experience-dependent plasticity. Two recent studies suggest that task demands may designate the relevant physical aspects of the stimulus and therefore determine which neurons are relevant for performance and learning.^{1,47} Learning may occur only in those neuronal assemblies that are activated by the stimulus and are, at the same time, task relevant.

LATER BUT (ALMOST) FOREVER (TWO MECHANISMS OF MEMORY)

The time course of texture discrimination learning provides more compelling, although indirect, support for the reductionistic interpretation of perceptual learning.²² In a recent study, we have uncovered two stages, possibly two processes, in the acquisition of improved perception. The first, involves fast, within session, improvement which can be affected by a limited number of trials on a time scale of a few minutes, but only if high-quality sensory input is provided. It consistently occurs only early in the very first practice session of naive observers and both its time-course and stimulus specificity profile are similar to those reported in previous paradigms of human perceptual learning.^{7,39,42} However, our results show that while the fast learning effect quickly saturates, there seems to follow a slower, time-consuming stage of learning which has not been described before (but has been recently shown to occur in several other perceptual learning paradigms²²; see also Polat and Sagi⁴¹ in this volume). This stage, underlies the emergence of a large performance gain several hours after, but not during or shortly following the practice session (latent learning phase).

Finally, once asymptotic performance was reached for a specific stimulus configuration, there is almost no forgetting. In Figure 1(b) we depict the discrimination performance of S.W. on consecutive daily sessions during September–October 1989, and her performance on a probe session 32 months later, with no training in the interval. Almost three years later most of her performance gain is retained. This is also the case for G.H., after an interval of 22 months (Figure 1(b)).

Although the relationship between fast and slow learning is unclear, they may involve different levels (stages) of visual processing. This is suggested by the finding

of different stimulus specificities for the two tasks. Only the slow, latent phase-dependent, learning—but not the fast phase improvement—is monocular and its spatial specificity is much narrower. On the other hand, only fast learning seems to be specific for target element orientation. These results imply that fast learning is mediated by later stages of visual processing. Fast learning is a process critically dependent on high-quality sensory input and may reflect the setting up of task-specific routines for solving the perceptual problem^{51,52} (for example, through a process of “adaptive filtering” which could occur at all relevant levels of processing^{6,9,34,39}). It probably involves top-down processes, presumably selecting the optimal sensory units for the performance of the task. Slow learning, however, reflects an ongoing long-term, perhaps structural, modification of basic perceptual modules; it may be implemented through the strengthening (and presumably weakening^{40,41}) of links between sensory neurons (those which respond differentially to the critical stimulus parameters) as a function of stimulus-dependent correlated activity. While the nature of the task determines which aspects of a stimulus are critical for the performance of the task, it is the interaction of the sensory input and the functional architecture of the sensory system which determines the minimal level at which these critical stimulus parameters are differentially represented in terms of neuronal responses. The Minimal Level Hypothesis predicts that at this level experience-dependent plasticity, subserving (slow) skill learning, will occur.

The main result uncovered by following the time-course of texture discrimination learning was a latent phase of several hours duration in the evolution of superior performance, i.e., a latent phase in human learning. We have suggested the term “consolidation” for the process, presumably initiated during the practice session, which underlies the improvement of perceptual sensitivity several hours after visual experience was terminated, and results in very long-term retention. In this we follow use of the term in developmental plasticity studies; investigating developmental plasticity in the cat, several studies have documented the progression of input-dependent selectivity commitment of visual neurons hours after the termination of the visual stimulation.^{5,38} More recently, Heggelund et al. have shown, using a pharmacological paradigm, that visual cortex plasticity is a progressive, continuous process that terminates after about 22 hours.¹⁰ Finally, several behavioral paradigms of mammalian memory consolidation have shown a latent phase of several hours duration before the long-term retention of a specific skill.^{31,32} There is, therefore, reasonable ground to conjecture that slow learning reflects a functional property of basic neuronal mechanisms of learning and memory storage within the sensory (visual as well as other modalities) cortex itself. These mechanisms, subserving developmental and maturational plasticity, may have been preserved in the adult cortex, and may underlie adult perceptual skill learning.

Recently, evidence pointing to a possible role for acetylcholine in the consolidation of perceptual skill learning was provided by investigating the relationship between sleep and texture discrimination learning.²⁵ Unlike the awake state, normal sleep is parsed into discrete stages—each characterized by distinct electrophysiological and neurochemical events.¹¹ Of these, REM stage is strongly associated

with cholinergic activity.^{11,13} Experiments involving selective sleep stage deprivation showed, first, that performance has improved after a normal night's sleep. Second, REM sleep deprivation effectively abolished any performance gain during the sleep interval, while non-REM, stage 3 and 4 sleep deprivation resulted in significant improvement, comparable to that found after an undisturbed night. Finally, REM sleep deprivation was shown not to have any detrimental effects on performance when a previously well-practiced stimulus configuration was presented, as a control. On the other hand, there was a small but significant detrimental effect of stage 3-4 sleep deprivation on the previously learned (control) task. This dissociation suggests that REM deprivation affected the consolidation of the recent perceptual experience, but not perceptual performance by itself, making it unlikely that the effects we observed were nonspecific consequences of disturbed sleep. This deleterious effect of post-training REM deprivation on the consolidation of skill memory suggests the possibility that the evolution of the activity-dependent neural changes into an enduring and efficient memory trace, are acetylcholine dependent. One such mechanism, by which a cholinergic input may play a critical role in memory consolidation at the cellular level, has been proposed by Bear and Singer³; see also Juliano et al.¹⁷ and Metherate and Weinberger.³⁴

A MEMORY SYSTEM FOR SKILL LEARNING

Though going beyond the data, there is a reasonable case to be made for the reductionistic interpretation of the constraints provided by the texture discrimination learning studies, as well as other paradigms of perceptual learning. For example, that a high degree of plasticity has been preserved in the adult visual cortex. This plasticity may underlie the long-term storage of procedural knowledge. One context perceptual learning can be viewed in, is the classical procedural ("how to") vs. declarative ("what"), or the "habit" vs. memory, dichotomies.^{36,50} These dichotomies have been suggested to account for the dissociation of memories and skills in brain-damaged patients and lesioned primates. They postulate that the retention of experience entails two widely differing processes. A more cognitive, and flexible, cortico-limbic-dependent system, and a second system which is independent not only of cortico-limbic processing but also of recognition and perhaps some other types of associative memory.³⁶ This second, perhaps more primitive, system of learning is a slow learning system. Its effects are best documented within a time frame of hours and days, and it is very specific for many parameters of experience that we don't usually recognize in the normal everyday business of learning.^{24,22,36} However, assuming that "where the brain does it—it's remembered," and assuming a limited repertoire of neuronal mechanisms that mediate memory functions throughout the mammalian cortex, there is a case to be made for the possibility that not only other types of human skill learning (e.g., motor skill learning²⁴) but

perhaps the formation of some types of long-term associative memory, should show the same organizational principles.

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