16 Cerebral Cortical Plasticity: Perception and Skill Acquisition

GREGG H. RECANZONE

ABSTRACT Cerebral cortical plasticity has been demonstrated in a variety of different mammals, following a number of different peripheral and central nervous system manipulations. The reorganization of cortical representations has been implicated in the ability to acquire perceptual and motor skills throughout normal life. This chapter presents evidence from a variety of studies which indicates that cortical plasticity occurs in normal, intact animals and humans, and that these changes in representations are correlated with changes in both motor skills and sensory perceptions.

One of the central goals in neuroscience, particularly in cognitive neuroscience, is to determine the neuronal mechanisms that generate perceptions. Very little is known about how action potentials transmitted throughout the nervous system allow individuals to perceive the complex world around them, to compare this representation of the world to past experience, and to initiate behaviors to achieve goals (e.g., eating, drinking, rest, lively conversation). Although both animal and human studies indicate that the cerebral cortex is integral in processing complex stimuli, very little is known of this structure beyond the presumed relevance of particular areas for specific functions. Although much knowledge has been gained over the past decades on how the individual neurons in a limited number of cortical areas respond to different stimuli, it is still unclear how these responses participate in perception.

While it may be agreed by many that the cerebral cortex is necessary for some perceptions, there is less consensus on how the cerebral cortex is actually functioning to create these perceptions. Further, one of the basic tenets of psychological studies since the late 1800s has been that individuals will improve at virtually any task with continued practice. It was presumed by James (1890) that this improvement in performance was made possible by a change, or "plasticity," of the "organic materials" of the central nervous system.

The first real insights into how such changes could be manifest in the cerebral cortex came from studies examining the effects of peripheral nerve injuries on cortical "maps," or representations of the sensory surface, in adult mammals (see Kaas, 1991, and chapter 15). The term *plasticity* is used to describe this capacity to change cortical representations in adults. In such studies denervation, or extensive behavioral use of a restricted sensory surface, results in a change in the central representation of that sensory surface. These results are consistent with the earliest reports of cerebral cortical function performed at the turn of the 20th century by Sir Charles Sherrington and colleagues. Their studies of the motor cortex of monkeys and great apes indicated that movement representations in the motor cortex could be altered over the course of several minutes, and that this effect was reversible (Graham Brown and Sherrington, 1912).

Several other studies have shown that cortical representations most likely reflect the stimulus history of the sensory surface being represented. For example, the cortical representation of the ventral body surface is larger in nursing rat mothers than in non-nursing female rats (Xerri, Stern, and Merzenich, 1994). The selective stimulation of two whiskers either experimentally (DeLacour, Houcine, and Talbi, 1987) or by trimming all but two adjacent whiskers (Armstrong-James, Diamond, and Ebner, 1994) results in many more neurons within the somatosensory cortex responding to both of the two whiskers. In primates, surgical fusion of two digits results in a zone of cortex in area 3b in which neurons have receptive fields that cross the suture line and respond to parts of both fused digits, in contrast to the normal situation where 3b neurons rarely, if ever, respond to stimulation of two digits (Allard et al., 1991; see also Merzenich et al., 1987). Finally, Jenkins and colleagues (1990) showed that training monkeys to attend to stimulation on the tip of one or two fingers results in an increased representation of the stimulated fingertips compared to the unstimulated fingers. Similar kinds of short- and long-term plasticity have been observed in the visual cortex as well as in human sub-

---

GREGG H. RECANZONE Center for Neuroscience and Section of Neurobiology, Physiology, and Behavior, University of California at Davis, Calif.

jects performing visual psychophysical tasks (see Gilbert et al., 1996; Gilbert, 1998).

These experiments provide evidence that cortical plasticity is not necessarily a response to the peripheral injury, but can also occur by changing the stimulation pattern across the skin. This finding further suggests that practice at a particular behavioral task, which generally results in an improvement in performance, would similarly be reflected by a change in the cortical representations of the relevant sensory or motor components of the task. For example, it could be reasoned that the increased representation of the ventral surface of the rats (Xerri, Stern, and Merzenich, 1994) or the fingertips of the monkeys (Jenkins et al., 1990) results in better perceptual acuity over that skin surface for that animal. The rest of this chapter will draw on selected examples from a variety of different experimental methodologies to address the central question: Are changes in cortical representations a reflection of normal cortical processes that underlie the ability to acquire new skills and behaviors?

Cortical plasticity and changes in perception invoked by classical conditioning paradigms

Early studies on the effects of classical conditioning on the response properties of neurons in the central auditory system have shown that there is a clear change in the functional tuning properties of neurons throughout the central auditory system. Some of the earliest examples are derived from studies in which awake adult rats were implanted with a series of electrodes that recorded the activity of spatially restricted neurons throughout the brain stem, thalamus, and cortex (Olds et al., 1972; Disterhoft and Stuart, 1976). In these experiments, neuronal activity was recorded during a period in which one of two different tones was presented or a food pellet was dispensed over the course of the first day. There was no temporal relationship between the tone and the food delivery, and thus no association between the two would be expected to be formed (pseudoconditioning). On the second day, however, one of the two tones always preceded the pellet delivery, while the other tone never preceded a food reward (conditioning). In these studies, after the conditioning period, the amount of activity of cortical neurons increased in response to the tone paired with the food delivery. This increase could be extinguished by returning to the pseudoconditioning procedure, now called extinction, where the tones and food delivery were no longer correlated (Disterhoft and Stuart, 1976). Similar kinds of effects were also observed in the noncortical regions as well, particularly the posterior thalamus and pretectal regions. Much smaller differences were noted in the main ascending auditory subcortical regions, the inferior colliculus and the medial geniculate body of the thalamus (Disterhoft and Stuart, 1976).

A similar series of studies using a mild electrical shock to the forepaw as the unconditioned stimulus and the pupillary dilation reflex as the unconditioned response have extended these findings in the cat. The change in the response properties of neurons is more rapid in the auditory cortex than in the cochlear nucleus (Oleson, Ashe, and Weinberger, 1975). These changes are not, however ubiquitous throughout the central nervous system. Comparison of the conditioning effects of multiple-unit activity within the medial, ventral, and dorsal subdivisions of the auditory thalamus, the medial geniculate body (MGB), showed that neuronal responses changed only in the medial subdivision, and not in the ventral or dorsal regions of the MGB (Ryugo and Weinberger, 1978). This result is interesting in that the ventral division of the MGB has the anatomical connections and response properties consistent with those of a thalamic relay or lemniscal nucleus, whereas the medial division is more consistent with a lemniscal adjunct or nonspecific function.

More recent studies have expanded these observations by defining the response properties of single neurons to both conditioned and a series of nonconditioned stimuli (Diamond and Weinberger, 1986; Bakin and Weinberger, 1990; see Weinberger, 1995, 1998). In these paradigms, the responses of single neurons to a series of tone pips at different frequencies are recorded, and then one frequency is chosen to be the conditioned stimulus. A short time after the tone elicits the conditioned response (20–45 paired trials), the response of the neuron to the series of tone pips is again recorded. An example of a typical result is shown in figure 16.1 for neurons recorded in the secondary and ventral ectosylvian auditory cortical fields (Diamond and Weinberger, 1986). This figure is derived from the neurons that were the most sharply tuned for frequency. In most of these cells studied, there was an increase in the response to the tone paired with the foot shock (labeled 0 on the *x*-axis), with very little increase for other frequencies. This increase was reversed by a period of extinction, when the tone was presented in the absence of the foot shock for 20 trials (figure 16.1).

A similar result was shown in the guinea pig primary auditory cortex (Bakin and Weinberger, 1990), in which many neurons changed their frequency-tuning profile to respond best to the paired frequency (figure 16.2). In this paradigm, by choosing a paired frequency that was slightly different from the best frequency of the neuron, there was an increase in the response to the paired frequency and a parallel decrease in the response to the preconditioning best frequency, resulting in a shifted

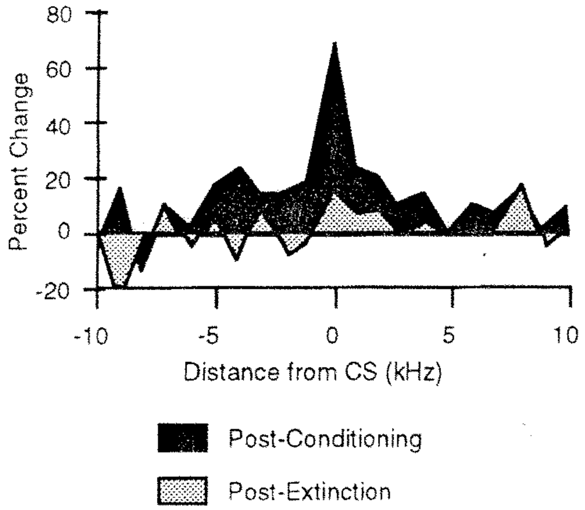


FIGURE 16.1 Changes in the activity of auditory cortical neurons following a classical conditioning paradigm. The dark area denotes the percent change in the responses of the neurons as a function of the difference in frequency from the conditioned stimulus (CS) between the preconditioning and postconditioning conditions. The shaded area denotes the change in response between the preconditioning and postextinction conditions. Note that the greatest change occurred at the CS frequency. (Adapted from Diamond and Weinberger, 1986.)

tuning profile for the neuron. This type of change in the tuning profile of the single neuron has also been shown to last for up to eight weeks after training (Weinberger, Javid, and Lapin, 1993). These results indicate that there is an expansion of the representation of the paired frequency that parallels the acquisition of the conditioned response (see Weinberger, 1998). This is expected, given that the perception of the stimulus would surely change from one that has no behavioral relevance to one that signals that a foot shock is imminent.

Similar studies in the MGB have shown that the ventral division (MGBv), which contains the most sharply frequency-tuned neurons and is considered to be the major relay nucleus, does not show the same type of plasticity (Ryugo and Weinberger, 1978). However, the medial division (MGBm), which has more broadly tuned neurons and projects to the primary auditory cortex and other cortical areas, does show a type of plasticity very similar to that of the auditory cortex (Ryugo and Weinberger, 1978; Edeline and Weinberger, 1992). These results suggest that there are two parallel pathways within the auditory system, one which is largely immune to such conditioning effects, and the other which likely mediates the cortical plasticity observed following classical conditioning (for a more complete description of this topic see Weinberger, 1998).

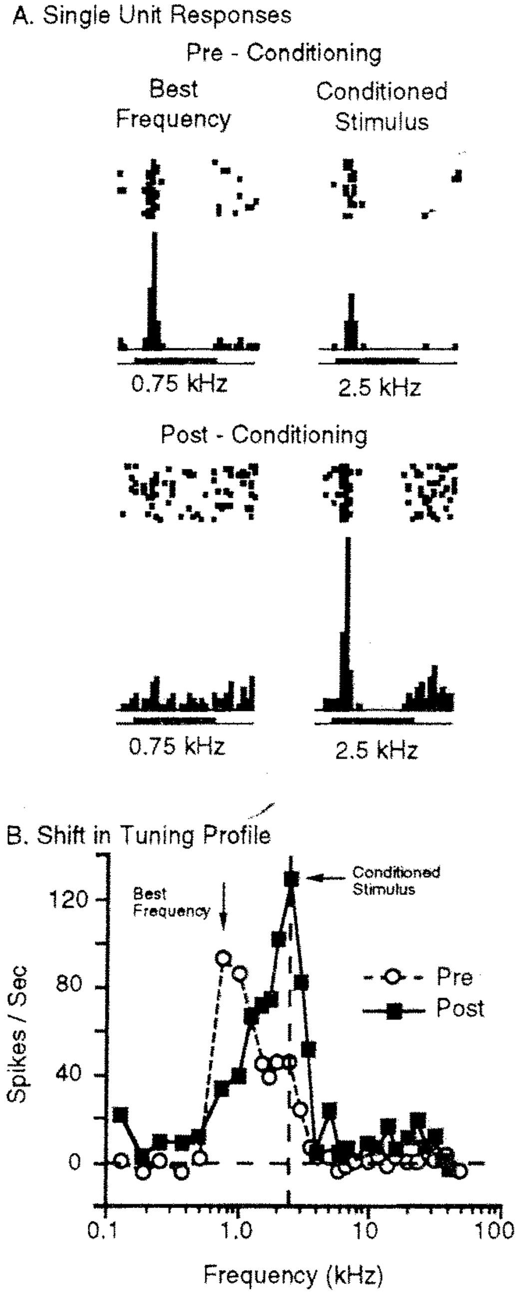


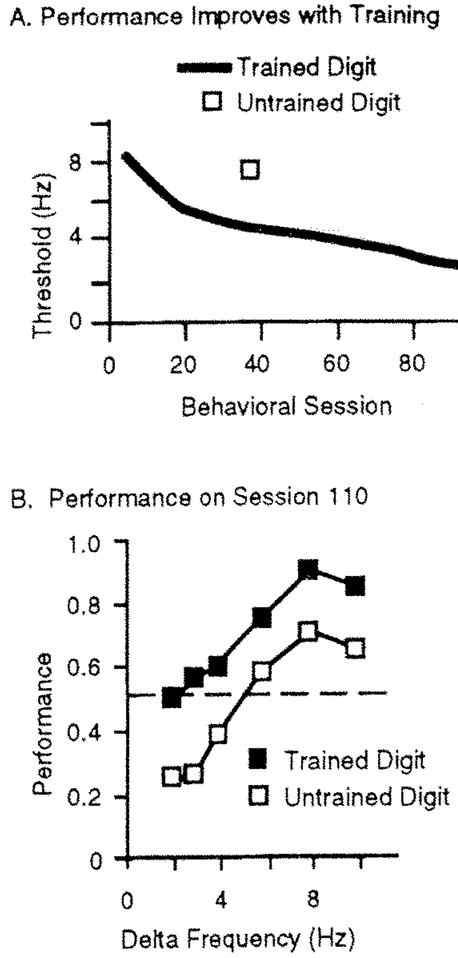
FIGURE 16.2 Change in the response profile of a single auditory cortical neuron following conditioning. (A) Rasters and peristimulus time histograms (PSTHs) of the response to the best frequency of the neuron (0.75 kHz, left) and the frequency of the conditioned stimulus (2.5 kHz, right) before (top) and after (bottom) the conditioning protocol. (B) The complete tuning profile tested before (open circles) and after (closed squares) the conditioning protocol. Note that the postconditioning best frequency of this neuron is now at 2.5 kHz. This shift resulted from an increase in the response to the CS frequency and a decrease in the response to the previous best frequency. (Adapted from Weinberger, 1998.)

Pharmacological studies suggest that acetylcholine (ACh) plays a key role in modulating the change in cortical neuronal responsiveness. Application of ACh at the recording electrode can alter the response of the neuron to specific frequencies (McKenna, Ashe, and Weinberger, 1989). Iontophoresis of acetylcholine paired with the presentation of a tone can result in an increase in the response of the neurons, similar to the effects seen with tone and shock pairings (Metherate and Weinberger, 1990). Similarly, direct stimulation of the nucleus basalis, which contains the neurons that release ACh in the cerebral cortex, shortly after the onset of a tone results in a similar enhancement of the neuronal response to the paired tone in both anesthetized animals (Bakin and Weinberger, 1996) and awake animals (Bjordahl, Dimyan, and Weinberger, 1998), and also results in a greater area of primary auditory cortex that responds to the paired tone (Kilgard and Merzenich, 1998). These data together indicate that (1) cortical responses can be altered over a very short time course and can be long-lasting, (2) these modifications presumably reflect a change in the perception of the stimulus, and (3) neuromodulatory elements facilitate, and may well be required, to effect such changes.

Cortical plasticity following operant conditioning

A direct test of the hypothesis that cortical representational plasticity reflects changes in perception and skill acquisition was conducted in the somatosensory cortex of adult owl monkeys. In the normal owl monkey, there is a topographically well-organized map of the contralateral hand in the primary somatosensory cortical area 3b. These experiments entailed training monkeys to perform a tactile discrimination task using only a small skin area of a single finger, measuring the improvement in performance at this task over the course of several weeks of training, and then relating this performance to the cortical representation of the small skin area used in the task.

Adult monkeys were trained to remove their hand from a tactile stimulator when they detected that the frequency of the stimulus increased from the standard of 20 Hz (Recanzone, Jenkins, et al., 1992). Initially, monkeys were only able to discriminate stimuli that were at least 5 Hz greater (i.e., 25 Hz). In the early phases of training, the thresholds decreased rapidly, followed by a longer and slower period of improvement during the subsequent weeks until these monkeys were ultimately able to discriminate differences in frequency of only 1–2 Hz. It is likely that the initial, rapid period of improvement is reflecting the ability of the monkeys to generalize to all stimulus frequencies and to develop the most effective "strategy" in performing the task (Recanzone, Jenkins, et al., 1992). When tested on an adjacent finger on two or three occasions throughout the period of extensive practice on a different finger, the thresholds reflected the rapid improvement component, but did not improve significantly during subsequent sessions (see figure 16.3).


A. Performance Improves with Training

B. Performance on Session 110

FIGURE 16.3 Improvement in performance measured during the performance of a tactile frequency discrimination task. (A) Schematic of the behavioral data where the threshold rapidly decreased during the first few training sessions, and was then followed by a much slower and progressive decrease in threshold with training. Open symbols denote the thresholds measured for the adjacent finger taken at three different time points over the course of the study. (B) Psychometric functions for both the trained (closed squares) and untrained (open squares) fingers taken the day before the electrophysiological experiment began. (Adapted from Recanzone, Jenkins, et al., 1992.)

The representation of the trained skin, as well as the same skin regions on nontrained fingers of the same and opposite hands, was then defined in cortical area 3b (Recanzone, Merzenich, et al., 1992). One striking difference was the increased area of representation of the trained skin when compared to similar, untrained skin surfaces (figure 16.4A). A second major difference was that the receptive fields on the trained skin surfaces were much larger than those on the untrained skin (figure 16.4B). A third major difference was in the responses of the cortical neurons to the same vibratory tactile stimulation that was used in the behavioral task (Recanzone, Merzenich, and Schreiner, 1992). As would be expected by the larger representation in gen-

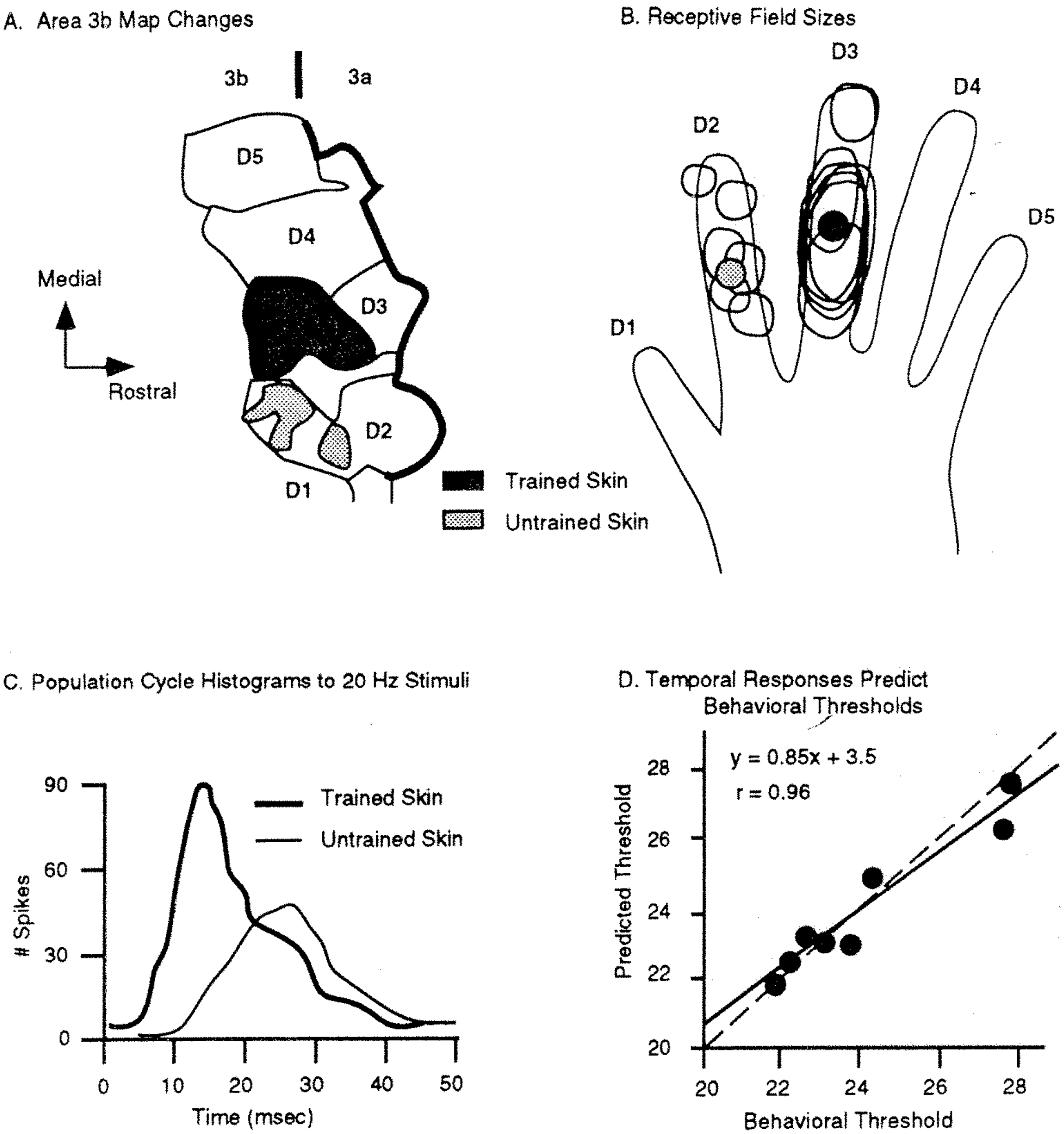


FIGURE 16.4 Changes in cortical representations of trained and untrained skin regions in monkeys trained at a tactile discrimination task. (A) The cortical area of representation of the trained (black) and adjacent, untrained (shaded) skin regions. (B) Representative receptive fields recorded for each of these fingers. The circles show the region of skin stimulated during the task for the trained (filled) and untrained (shaded) fingers. (A and B adapted from Recanzone, Merzenich, et al., 1992.) (C) Population cycle histograms taken from all locations that responded to stimulation of the trained and untrained skin surfaces in a single monkey. These cycle histograms were obtained by combining the action potentials for all stimulus cycles excluding the first across all cortical locations. Bin size is 1 millisecond. The heavy line shows the responses to stimulation of the trained skin site; the thin line shows the responses to stimulation of the adjacent skin site. (D) Regression analysis between the measured behavioral threshold for both trained and untrained digits as a function of the predicted threshold based on differences in the population cycle histograms between the standard and test frequencies. The solid line shows the best-fit regression line; the dashed line shows perfect correlation. (C and D adapted from Recanzone, Merzenich, and Schreiner, 1992.)

eral, there was a greater number of neurons that responded to stimulation on the trained finger when compared to untrained monkeys or to other fingers on the same hand. Although the responses of the neurons at each cortical location were very similar to stimulation of the trained and untrained fingers, when the responses were pooled across the population of area 3b neurons, there was an increase in the temporal fidelity of the responses to these behaviorally relevant stimuli (figure 16.4C). This increased fidelity was strongly correlated with the behavioral performance of both trained and untrained digits (figure 16.4D). The large representations of the trained skin and the correlated activity across neurons to the same stimulus frequencies indicate that the population of cortical neurons became highly selective in their responses and responded synchronously to the same behaviorally relevant tactile input. As the monkey continued to practice the task over weeks of daily sessions, there was presumably an increase in this population encoding of the stimulus frequency, which resulted in better information on the stimulus frequency and therefore improved performance at the task.

The same result was subsequently found in the primary auditory cortex in monkeys trained to perform an acoustic frequency discrimination task (Recanzone, Schreiner, and Merzenich, 1993). Monkeys performing a similar type of behavioral task showed a progressive improvement in their ability to discriminate small differences in the frequency of sequentially presented acoustic stimuli (figure 16.5A). When the frequency representation was defined in these monkeys, there was a clear increase in the cortical area of representation of the behaviorally relevant stimuli (figure 16.5B, C) compared to controls that were either engaged in the task using a different standard frequency or were untrained in any task. This increased representation was similarly closely correlated with the improved performance and increased frequency discrimination acuity.

In both the somatosensory and auditory experiments, it was found that attention to either the tactile or auditory stimulus was required for the cortical changes to occur. In monkeys that received the same tactile stimulus but were performing the auditory discrimination task, changes were observed in the auditory cortex but not in the somatosensory cortex. Similarly, monkeys that received the same auditory stimuli while performing the tactile task showed changes only in the somatosensory cortex but not in the auditory cortex. These results strongly suggest that attending to the stimuli (and thereby activating neuromodulatory circuits such as ACh) is necessary to change the cortical representations, and presumably to effect a change in the percep-

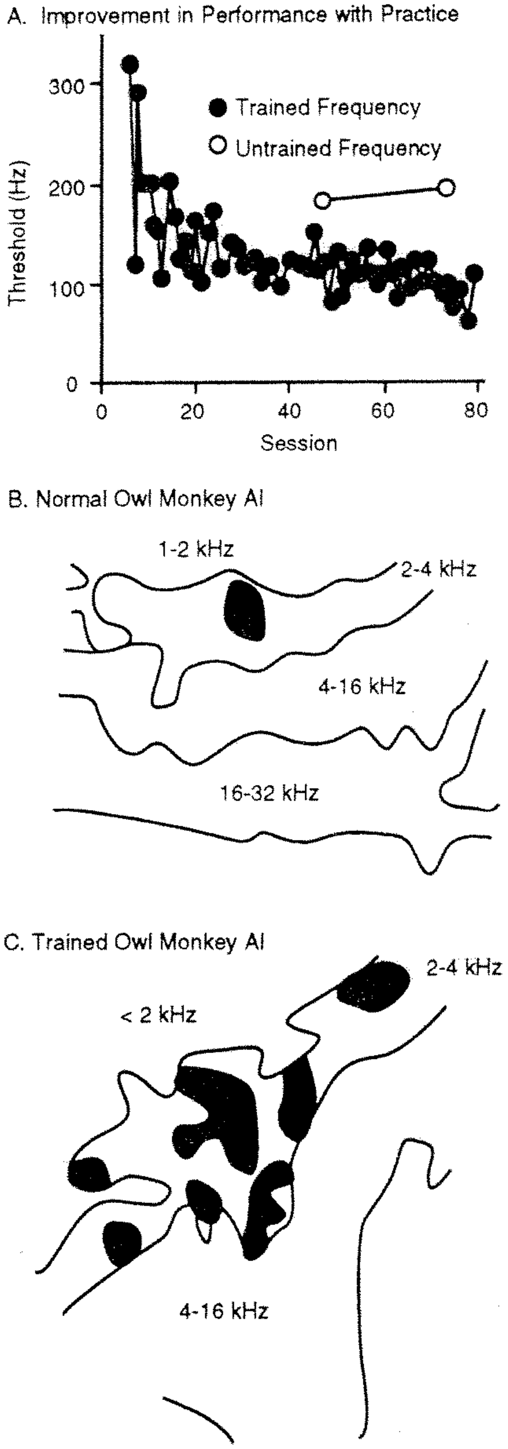


FIGURE 16.5 Auditory frequency discrimination training. (A) Behavioral threshold as a function of session for one monkey. Solid symbols show the threshold measured for the trained frequency. Open symbols show the threshold measured for a different frequency that was only tested on two, widely interspersed, sessions. (B) The region of primary auditory cortex in an untrained monkey that contained cells with a characteristic frequency in the range used in the behavioral task (black regions). (C) Similar map of primary auditory cortex in a monkey trained to discriminate the same frequency shown in B. (Adapted from Recanzone, Merzenich, and Schreiner, 1993).

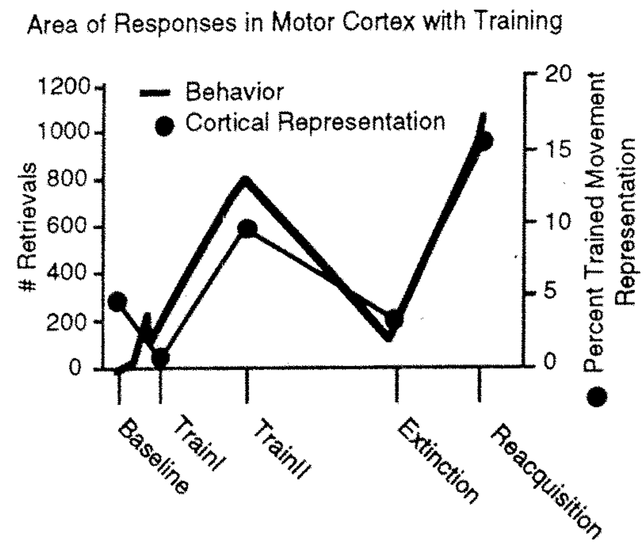


FIGURE 16.6 Changes in motor cortical areas of representation with training. The number of successful pellet retrievals (heavy lines, left *y*-axis) is an indicator of the ability of the monkey to obtain the pellet. The area of representation of the relevant movements in the task (finger flexion and wrist extension) as a percent of the hand representation in the motor cortex is shown as the thin line and solid circles. This monkey went through five different phases of training, extinction, and reacquisition. The cortical area of representation of the relevant movements parallels the monkey's ability to perform the task. (Adapted from Nudo et al., 1996.)

tion, although this assumption was not tested in these animals.

Other studies in the motor cortex show a similar pattern of results. Motor cortical maps can be derived by electrically stimulating the deep cortical layers with small currents (10–30 μA) and observing the elicited movements. Several studies on the motor cortex of squirrel monkeys indicate that the cortical representation of motor movements is related to the ability of the monkey to perform simple motor tasks. For example, there are differences in the organization of the hand representations in the primary motor cortex in individual monkeys, with the representation of the dominant hand being larger and more spatially complex than the representation of the nondominant hand (Nudo et al., 1992), presumably reflecting the greater use and dexterity of the dominant hand. Monkeys trained to make a set of specific movements, whether rotation about the wrist or movement of the wrist and fingers, had a greater representation of the practiced movements (Nudo et al., 1996). The changes in the cortical representations of these movements closely followed the behavioral ability of the monkey to retrieve the pellet, which is based primarily on the dexterity of the movement (figure 16.6). These data showed that the motor cortical representations are plastic and can change over time in the adult animal and that these changes reflect the acquisition and degradation of the monkey's motor skills during the course of the experiments.

Cortical plasticity demonstrated in human subjects

Functional imaging techniques applied to human subjects have been valuable tools in investigating cortical plasticity in human subjects and indicate that cortical reorganization with training, as seen in the animal experiments, occurs in the human cortex as well. For example, humans who are practiced string players (violin, cello, or guitar) have greater cortical activation (based on MEG dipole strength) from stimulation on the fingertips of their left hands than people who do not play an instrument (Elbert et al., 1995).

Changes in cortical representations that relate to changes in the ability to perform a motor task have also been demonstrated in human subjects (Karni et al., 1995; see also Karni et al., 1998). In this study, the amount of activity in the motor cortex was defined using functional magnetic resonance imaging (fMRI) while the subjects made one of two matched, mirror-reversed sequenced finger movements (e.g., pinkie–middle–ring–index–pinkie). These subjects then practiced only one of these two sequences for 10–20 minutes each day. Over the course of several weeks the speed with which the sequences were performed increased, and the number of errors decreased. When the subjects were scanned again after training, there was more activation of primary motor cortex for the practiced sequence compared to the unpracticed sequence in each subject tested (figure 16.7). This result is predicted by the monkey experiments described earlier (Recanzone, Jenkins, et al., 1992; Recanzone, Merzenich, et al., 1992; Recanzone, Merzenich, and Schreiner, 1992; Recanzone, Schreiner, and Merzenich, 1993; Nudo et al., 1996), where the increased cortical areas of representation were correlated with an improvement in performance at a perceptual or motor task.

A second area of interest has focused on cortical plasticity in blind individuals who read braille. The previously discussed animal work predicts that these individuals would have increased representations of their braille-reading finger pads compared to either sighted or non-braille-reading controls. Evidence to support this hypothesis has been obtained using both scalp-evoked potentials and transcranial magnetic stimulation of the sensorimotor cortex of blind and control human subjects (Pascual-Leone and Torres, 1993; Pascual-Leone et al., 1993). These experiments have shown that there is an increase in the representation of the finger

Increased Response Area in Motor Cortex with Training

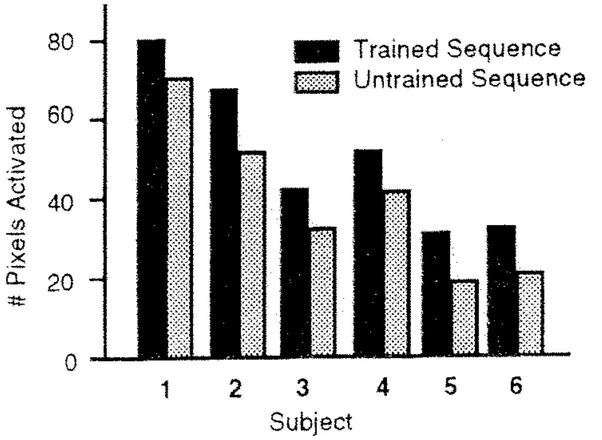


FIGURE 16.7 Motor cortex activation during a practiced and nonpracticed finger-tapping task. These data show the extent of motor cortex that was activated during the performance of the practiced sequenced finger-movement task (solid bars) compared to a similar but unpracticed sequence (stippled bars). Each subject showed an increase in the number of pixels activated within motor cortex for the practiced task. (Adapted from Karni et al., 1995.)

muscles most used during braille reading in motor cortex, and a greater activation of the sensorimotor cortex during stimulation of the fingertips used during braille reading. Interestingly, subjects who have been blind since infancy or early childhood also commonly have an activation of visual cortex during braille reading (Sadato et al., 1996) that does not occur in sighted individuals. This intriguing result suggests that the neurons in the cerebral cortex are not only capable of altering their responses within a given modality but can also change the modality of their responses if altered experiences occur early enough during development (see also chapter 7).

Experiments on human amputees further suggest that cortical plasticity can account for altered perceptions following the amputation. In many human amputee patients, there is a phenomenon known as the phantom limb (Henderson and Smyth, 1948; Cronholm, 1951; Haber, 1958) in which subjects clearly perceive their missing limb as still being attached, although they are cognitively fully aware that it no longer is. It had been suggested that the phantom limb was the result of the residual representation in the cortex of what used to respond to the arm input, following a "filling in" of the former hand representation by the face and arm representation, which is seen following amputations and deafferentation in monkeys (Merzenich et al., 1984; Pons et al., 1991). The human somatosensory cortex is functionally organized with a topography similar to that of the monkey; namely, the hand representation is bordered medially by the arm representation and laterally by the chin and jaw representation. Since there is no longer any afferent drive from the missing limb, these cortical neurons would either come to respond to adjacent, intact body regions, or would remain silent as the deafferentation was too large to overcome (see Merzenich et al., 1984).

Functional imaging studies similarly indicate that the region formerly responding to the hand now responds to stimulation of the face (Yang et al., 1994; Elbert et al., 1994; see Ramachandran, 1993). The extent of this reorganization has been shown to be correlated with the amount of pain experienced in the phantom limb (Flor et al., 1995). In a second study (Birbaumer et al., 1997), injection of local anesthetic into the region near the amputation resulted in relief of phantom limb pain in half of the subjects tested. In those subjects that had pain relief, there was a reduction in the amount of apparent cortical reorganization following the injection of the local anesthetic. Interestingly, in the subjects that did not experience any pain relief or had not experienced phantom pain previously, there was no change in the cortical representations before and after the injection of the anesthetic. This result suggests that the amount of cortex that was reorganized from formerly representing the amputated arm and hand to representing the shoulder and face in some way contributes to the phantom pain or, conversely, that phantom pain in some way results in the altered cortical representation. It will be interesting to see how these two factors are related in future experiments.

Implications of cortical plasticity and changes in perception

This chapter has reviewed evidence that changes in perceptual acuity or motor skill are the result of changes in the cortical representations of the relevant sensory or motor aspects of the task. In each of the cases of cortical plasticity there is an increased representation of the relevant stimuli. Given that the size of the cerebral cortex is fixed in the adult, this result implies that the cortical representations of some sensory surfaces or movements have necessarily decreased in order to accommodate the greater representation of other sensory surfaces or movements. This relationship has been noted primarily in animal studies where there is a clear decrease in the cortical representation of adjacent skin surfaces in the somatosensory cortex (see Jenkins et al., 1990; Recanzone, Merzenich, et al., 1992), or the adjacent frequencies in the auditory cortex (Recanzone, Schreiner, and Merzenich, 1993) or different movement representations in the motor cortex (Nudo et al., 1996). Does this result then imply that there is a decrease in performance at some other task? The lim-

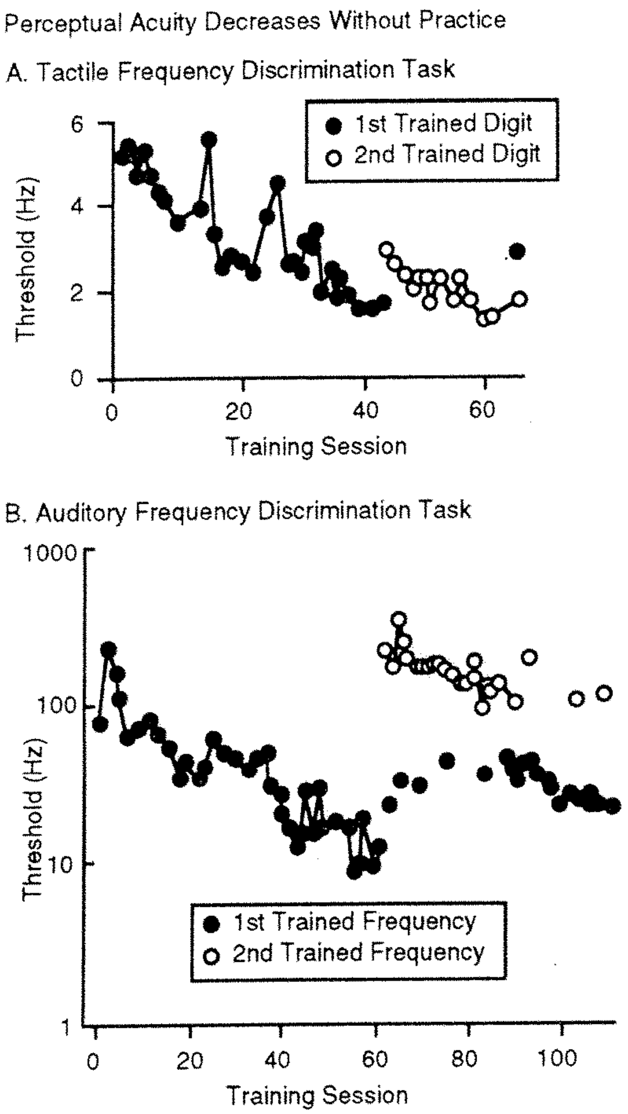


FIGURE 16.8 Changes in perceptual performance as a function of practice. Data taken from one monkey that was trained at a tactile frequency discrimination task (A) taken from Recanzone, Jenkins, et al. (1992) and one trained at an auditory frequency discrimination task (B) taken from Recanzone, Schreiner, and Merzenich, (1993). In both cases, 1–2 weeks of testing on either a different skin surface or a different frequency (open circles) resulted in an increase in threshold for the previously practiced (solid circles) skin surface or auditory frequency.

ited data available suggest that this is indeed the case; performance at one task will change the cortical representations in favor of that task at the expense of some unpracticed task. For example, there was a progressive improvement in performance with training at both a tactile frequency discrimination task or an auditory discrimination task as described previously (figure 16.8; Recanzone, Jenkins, et al., 1992; Recanzone, Schreiner, and Merzenich, 1993). If the task is changed to test a different sensory surface, after the improvement in performance at the first, there is an improvement over time in the performance for the new skin surface or frequency (open symbols, figure 16.8) and a corresponding decrease in performance at the previously trained skin surface or frequency (closed symbols, figure 16.8). A similar improvement and degradation in performance can be seen in motor tasks with a corresponding change in the cortical representation of the specific movements used in the task (figure 16.6; Nudo et al., 1996).

This is not a simple "zero sum" rule in which learning one thing will necessarily result in forgetting something else; rather, it is a simple reflection of the fact that performance at unpracticed tasks is degraded over time. There are clear anatomical and functional limits to the extent of cortical reorganization and the extent at which performance at a particular task can improve. I do not suggest that continued practice at a frequency discrimination task would ultimately cause only that narrow band of frequencies to be represented across the entire extent of primary auditory cortex at the expense of all other frequencies. The ability to process acoustic information is an important and behaviorally relevant task in most mammals, and there exists a driving force to maintain that ability in spite of a competing need to perform well at a specific task. Therefore, the cerebral cortex must be continuously modifying its central representations in a delicate balance to ensure that all of the behaviorally relevant and important information processing can take place. These dynamic processes are presumably continuing throughout life (e.g., see Merzenich et al., 1991, 1993) and likely account for the normal variability seen in cortical representations of different individuals of a species (Merzenich et al., 1987) and indeed the normal variations in abilities seen across individuals such as ourselves.

ACKNOWLEDGMENTS I would like to thank L. A. Krubitzer, N. M. Weinberger, M. L. Sutter, M. L. Phan, A. R. Tice, and J. A. Langston for helpful suggestions on previous versions of the manuscript. Funding provided in part by NIH grant DC-02371, the Klingenstein Fund, and the Sloan Foundation.

REFERENCES

ALLARD, T., S. A. CLARK, W. M., JENKINS, and M. M. MERZENICH, 1991. Reorganization of somatosensory area 3b representations in adult owl monkeys after digital syndactyly. *J. Neurophysiol.* 66:1048–1058.

ARMSTRONG-JAMES, M., M. E. DIAMOND, and F. F. EBNER, 1994. An innocuous bias in whisker use in adult rats modifies receptive fields of barrel cortex neurons. *J. Neurosci.* 14:6978–6991.

BAKIN, J. S., and N. M. WEINBERGER, 1990. Classical conditioning induces CS-specific receptive field plasticity in the auditory cortex of the guinea pig. *Brain Res.* 536(1–2):271–86.

Bakin, J. S., and N. M. Weinberger, 1996. Induction of a physiological memory in the cerebral cortex by stimulation of the nucleus basalis. *Proc. Natl. Acad. Sci. U.S.A.* 93(20): 11219–11224.

Birbaumer, N., W. Lutzenberger, P. Montoya, W. Larbig, K. Unertl, S. Töpfner, W. Grodd, E. Taub, and H. Flor, 1997. Effects of regional anesthesia on phantom limb pain are mirrored in changes in cortical reorganization. *J. Neurosci.* 17:5503–5508.

Bjordahl, T. S., M. A. Dimyan, and N. M. Weinberger, 1998. Induction of long-term receptive field plasticity in the auditory cortex of the waking guinea pig by stimulation of the nucleus basalis. *Behav. Neurosci.* 112:467–479.

Cronholm, B., 1951. Phantom limbs in amputees: A study of changes in the integration of centripetal impulses with special reference to referred sensations. *Acta Psychiat. Neurological. Scand. Suppl.* 72:1–310.

DeLacour, J., O. Houcine, and B. Talbi, 1987. "Learned" changes in the responses of the rat barrel field neurons. *Neuroscience* 23:63–71.

Diamond, D. M., and N. M. Weinberger, 1986. Classical conditioning rapidly induces specific changes in frequency receptive fields of single neurons in secondary and ventral ectosylvian auditory cortical fields. *Brain Res.* 372:357–360.

Disterhoft, J. F., and D. K. Stuart, 1976. Trial sequence of changed unit activity in auditory system of alert rat during conditioned response acquisition and extinction. *J. Neurophysiol.* 39:266–281.

Edeline, J.-M., and N. M. Weinberger, 1992. Associative retuning in the thalamic source of input to the amygdala and auditory cortex: Receptive field plasticity in the medial division of the medial geniculate body. *Behav. Neurosci.* 106:81–105.

Elbert, T., H. Flor, N. Birbaumer, S. Knecht, S. Hampson, W. Larbig, and E. Taub, 1994. Extensive reorganization of the somatosensory cortex on adult humans after nervous system injury. *NeyroReport* 5:2593–2597.

Elbert, T., C. Pantev, C. Wienbruch, B. Rockstroh, and E. Taub, 1995. Increased cortical representation of the fingers of the left hand in string players. *Science* 270:305–307.

Flor, H., T. Elbert, S. Knecht, C. Wienbruch, C. Pantev, N. Birbaumer, W. Larbig, and E. Taub, 1995. Phantom-limb pain as a perceptual correlate of cortical reorganization following arm amputation. *Nature* 375:482–484.

Gilbert, C. D., 1998. Adult cortical dynamics. *Physiol. Rev.* 78:467–485.

Gilbert, C. D., A. Das, M. Ito, M. Kapadia, and G. Westheimer, 1996. Spatial integration and cortical dynamics. *Proc. Natl. Acad. Sci. U.S.A.* 93:615–622.

Graham Brown, T., and C. S. Sherrington, 1912. On the instability of a cortical point. *Proc. Roy. Soc. Lond. B* 85:250–277.

Haber, W. B., 1958. Reactions to loss of limb: Physiological and psychological aspects. *Ann. N.Y. Acad. Sci.* 74:14–24.

Henderson, W. R., and G. E. Smyth, 1948. Phantom limbs. *J. Neurol. Neurosurg. Psychiat.* 11:88–112.

James, W., 1890. *The Principles of Psychology.* vol 1. New York: Dover.

Jenkins, W. M., M. M. Merzenich, M. T. Ochs, T. Allard, and E. Guic-Robles, 1990. Functional reorganization of primary somatosensory cortex in adult owl monkeys after behaviorally controlled tactile stimulation. *J. Neurophysiol.* 63:82–104.

Kaas, J. H., 1991. Plasticity of sensory and motor maps in adult mammals. *Annu. Rev. Neurosci.* 14:137–167.

Karni, A., G. Meyer, P. Jezzard, M. M. Adams, R. Turner, and L. G. Ungerleider, 1995. Functional MRI evidence for adult motor cortex plasticity during motor skill learning. *Nature* 377:155–158.

Karni, A., G. Meyer, C. Rey-Hipolito, P. Jezzard, M. M. Adams, R. Turner, and L. G. Ungerleider, 1998. The acquisition of skilled motor performance: Fast and slow experience-driven changes in primary motor cortex. *Proc. Natl. Acad. Sci. U.S.A.* 95:861–868.

Kilgard, M. P., and M. M. Merzenich, 1998. Cortical map reorganization enabled by nucleus basalis activity. *Science* 279:1714–1718.

McKenna, T. M., J. H. Ashe, and N. M. Weinberger, 1989. Cholinergic modulation of frequency receptive fields in auditory cortex. I. Frequency-specific effects of muscarinic agonists. *Synapse* 4:30–43.

Merzenich, M. M., K. A. Grajski, W. M. Jenkins, G. H. Recanzone, and B. Peterson, 1991. Functional cortical plasticity: Cortical network origins of representations changes. *Cold Spring Harbor Symp. Quant. Biol.* 55:873–887.

Merzenich, M. M., R. J. Nelson, J. H. Kaas, M. P. Stryker, W. M. Jenkins, J. M. Zook, M. S. Cynader, and A. Schoppmann, 1987. Variability in hand surface representations in areas 3b and 1 in adult owl and squirrel monkeys. *J. Comp. Neurol.* 258:281–296.

Merzenich, M. M., R. J. Nelson, M. P. Stryker, M. S. Cynader, A. Schoppmann, and J. M. Zook, 1984. Somatosensory cortical map changes following digital amputation in adult monkey. *J. Comp. Neurol.* 224:591–605.

Merzenich, M. M., C. Schreiner, W. M. Jenkins, and X. Wang, 1993. Neural mechanisms underlying temporal integration, segmentation, and input sequence representation: Some implications for the origin of learning disabilities. *Ann. N.Y. Acad. Sci.* 682:1–22.

Metherate, R., and N. M. Weinberger, 1990. Cholinergic modulation of responses to single tones produces tone-specific receptive field alterations in cat auditory cortex. *Synapse* 6:133–145.

Nudo, R. J., W. M. Jenkins, M. M. Merzenich, T. Prejean, and R. Grenda, 1992. Neurophysiological correlates of hand preference in primary motor cortex of adult squirrel monkeys. *J. Neurosci.* 12:2918–2947.

Nudo, R. J., G. W. Milliken, W. M. Jenkins, and M. M. Merzenich, 1996. Use-dependent alterations of movement representations in primary motor cortex of adult squirrel monkeys. *J. Neurosci.* 16:785–807.

Olds, J., J. F. Disterhoft, M. Segal, C. L. Kornblith, and R. Hirsh, 1972. Learning centers of rat brain mapped by measuring latencies of conditioned unit responses. *J. Neurophysiol.* 35:202–219.

Oleson, T. D., J. H. Ashe, and N. M. Weinberger, 1975. Modification of auditory and somatosensory system activity during pupillary conditioning in the paralyzed cat. *J. Neurophysiol.* 38:1114–1139.

Pascual-Leone, A., A. Cammarota, E. M. Wassermann, J. P. Brasil-Neto, L. G. Cohen, and M. Hallett, 1993. Modulation of motor cortical outputs to the reading hand of braille readers. *Ann. Neurol.* 34:33–37.

Pascual-Leone, A., and F. Torres, 1993. Plasticity of the sensorimotor cortex representation of the reading finger of braille readers. *Brain* 116:39–52.

PONS, T. P., P. E. GARRAGHTY, A. K. OMMAYA, J. H. KAAS, E. TAUB, and M. MISHKIN, 1991. Massive cortical reorganization after sensory deafferentation in adult macaques. *Science* 252:1857–1860.

RAMACHANDRAN, V. S., 1993. Behavioral and magneto encephalographic correlates of plasticity in the adult human brain. *Proc. Natl. Acad. Sci. U.S.A.* 90:10413–10420.

RECANZONE, G. H., W. M. JENKINS, G. T. HRADEK, and M. M. MERZENICH, 1992. Progressive improvement in discriminative abilities in adult owl monkeys performing a tactile frequency discrimination task. *J. Neurophysiol.* 67:1015–1030.

RECANZONE, G. H., M. M. MERZENICH, W. M. JENKINS, K. A. GRAJSKI, and H. A. DINSE, 1992. Topographic reorganization of the hand representation in cortical area 3b of owl monkeys trained in a frequency discrimination task. *J. Neurophysiol.* 67:1031–1056.

RECANZONE, G. H., M. M. MERZENICH, and C. E. SCHREINER, 1992. Changes in the distributed temporal response properties of SI cortical neurons reflect improvements in performance on a temporally based tactile discrimination task. *J. Neurophysiol.* 67:1071–1091.

RECANZONE, G. H., C. E. SCHREINER, and M. M. MERZENICH, 1993. Plasticity in the frequency representation of primary auditory cortex following discrimination training in adult owl monkeys. *J. Neurosci.* 13:87–103.

RYUGO, D. K., and N. M. WEINBERGER, 1978. Differential plasticity of morphologically distinct neuron populations in the medial geniculate body of the cat during classical conditioning. *Behav. Biol.* 22:275–301.

SADATO, N., A. PASCUAL-LEONE, J. GRAFMAN, V. IBANEZ, M. P. DEIBER, G. DOLD, and M. HALLETT, 1996. Activation of the primary visual cortex by Braille reading in blind subjects. *Nature* 380:526–528.

WEINBERGER, N. M., 1995. Dynamic regulation of receptive fields maps in the adult sensory cortex. *Annu. Rev. Neurosci.* 18:129–158.

WEINBERGER, N. M., 1998. Physiological memory in primary auditory cortex: Characteristics and mechanisms. *Neurobiology of Learning and Memory* 70:226–251.

WEINBERGER, N. M., R. JAVID, and B. LEPAN, 1993. Long-term retention of learning-induced receptive-field plasticity in the auditory cortex. *Proc. Natl. Acad. Sci. U.S.A.* 90:2394–2398.

XERRI, C., J. M. STERN, and M. M. MERZENICH, 1994. Alterations of the cortical representation of the rat ventrum induced by nursing behavior. *J. Neurosci.* 14:1710–1721.

YANG, T. T., C. C. GALLEN, V. S. RAMACHANDRAN, S. COBB, B. J. SCHWARTZ, and F. E. BLOOM, 1994. Noninvasive detection of cerebral plasticity in adult human somatosensory cortex. *NeuroReport* 5:701–704.

THE NEW COGNITIVE NEUROSCIENCES

Second Edition

Michael S. Gazzaniga, *Editor-in-Chief*

Section Editors:
Emilio Bizzi
Ira B. Black
Colin Blakemore
Leda Cosmides
Gregory J. DiGirolamo
Stephen M. Kosslyn
Joseph E. LeDoux
Willem J. M. Levelt
J. Anthony Movshon
Michael I. Posner
Pasko Rakic
Daniel L. Schacter
Edward E. Smith
John Tooby
Endel Tulving

A BRADFORD BOOK
THE MIT PRESS
CAMBRIDGE, MASSACHUSETTS
LONDON, ENGLAND

This book was set in Baskerville by Publication Services, Champaign, Illinois, and was printed and bound in the United States of America.

Library of Congress Cataloging-in-Publication Data

The new cognitive neurosciences / Michael S. Gazzaniga,
editor-in-chief.
p. cm.
"A Bradford book."
Rev. ed. of: The cognitive neurosciences. c1995.
Includes bibliographical references and index.
ISBN 0-262-07195-9 (hc : alk. paper)
1. Cognitive neuroscience. I. Gazzaniga, Michael S.
II. Cognitive neurosciences.
QP360.5.N4986 1999
153–dc21 98-52869
CIP