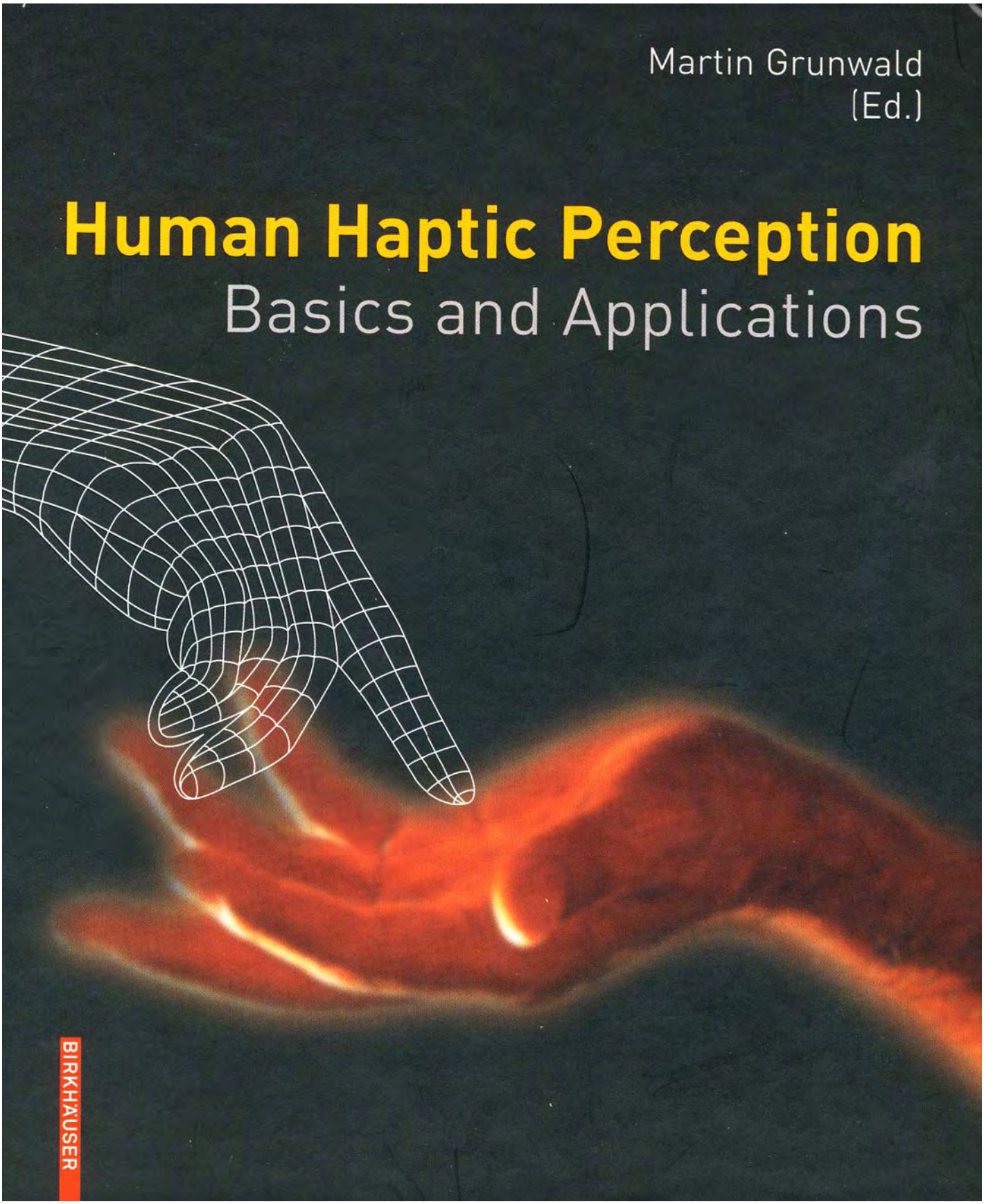

H.R. Dinse C. Wilimzig T. Kalisch
Learning in Haptic Perception

Learning effects in haptic perception

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Introduction

Human haptic perception is not a constant, but subject to manifold modifications throughout lifespan. Major determinants are development and aging as well as alterations following injury and compensatory brain reorganization. While during early development haptic perception is refined due to maturation and experience, haptic perception during aging deteriorates due to many factors, not all of them fully understood. Besides these lifespan factors, it is common wisdom that haptic perception and skills in general improve through practice (Fig. 1), see also [1]. Perceptual learning involves relatively long-lasting changes to an organism's perceptual system that improve its ability to respond to its environment and are caused by this environment. In case of Blinds or in Musicians, both characterized by superior haptic perception, improvement is assumed to be due to use-dependent or experience-dependent neuroplasticity mechanisms. In any case, enhanced haptic perception is due to learning processes occurring in brain areas devoted to processing of haptic information. Modeling these processes not only contributes to a better understanding of perceptual learning, but also of cortical processing constraints present under baseline conditions.

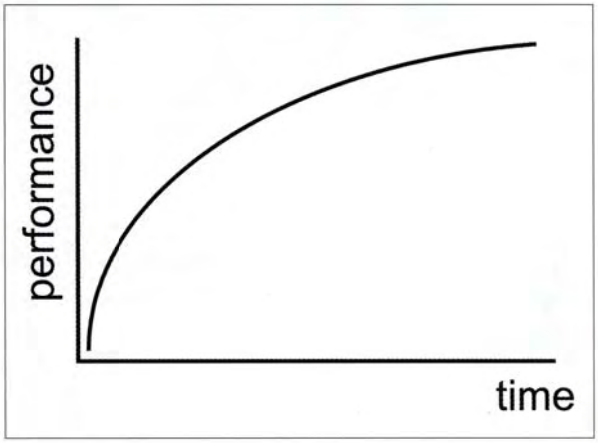


FIGURE 1. TIME COURSE OF IMPROVEMENT OF SKILLS OVER TIME.
Note rapid gain during the very early phase of practicing, while later additional improvement develops much slower indicating different mechanisms (see text).

Hierarchy of tactile-haptic performance

Gibson [2] defined the haptic system as "*The sensibility of the individual to the world adjacent to his body by use of his body*". The haptic perceptual system includes the peripheral receptors and is closely linked to the movement of the body. Many people have emphasized that haptic perception is closely linked to the concept of active touch. In our studies on haptic learning we refer to the idea of a hierarchy of tasks and task complexities that differentially involves in a graded way influences from the periphery, cortical processing with differing amount of cognitive demand, and tasks including motor aspect such as fine motor performance. Haptic learning can target specific tasks without necessarily altering the entire hierarchy. The investigation of either connected or unrelated aspects of tactile and haptic performance can help to unravel underlying mechanisms of haptic performance.

TABLE 1. HIERARCHY OF TACTILE – HAPTIC-SENSORIMOTOR PERFORMANCE

Test	Peripheral	SI cortex Low cognitive	SI + higher areas High cognitive	sensorimotor action
	touch threshold Nerve cond. velocity	spatial discrimination two-point acuity hyperacuity gratings, dot pattern localization	recognition of known or arbitrary objects letters Braille characters	reaction times tapping peg board grasping grip strength
		everyday or arbitrary textures surfaces	symmetry shapes faces heights or widths	
		temporal discrimination frequency interval		

Dependence of haptic perception and learning on skin accessibility

The crucial role of skin coverage of the finger tips on tactile and haptic sensations and motor execution has been addressed in many studies. Figure 2 summarizes a comparison of different tasks performed in young adults and healthy elderly demonstrating that skin coverage severely impairs tactile function, however, in a highly task-dependent way. Moreover, the susceptibility is age-dependent, where some tasks such as two-point discrimination suffer little, while haptic object recognition suffers dramatically (Kalisch and Dinse, unpublished data, cf. also [3]). Remarkably, also motor performance depends on intact skin sensitivity. Recording of finger movement in expert touch typists under anesthesia of the right index fingertip increased typing errors of that finger seven-fold [4]. These studies emphasize that maximal tactile-haptic performance requires unrestricted skin access. However, little is known how prolonged skin coverage and training under coverage conditions as is the case in surgeons alter dependence of haptic performance from coverage.

Perceptual learning in haptic perception

Although training and practicing plays a crucial role mediating improvement of skills, perceptual learning is not achieved by a unitary process [5, 6]. Psychophysicists have distinguished between relatively peripheral, specific adaptations and more general, strategic ones [7–9], and between quick and slow perceptual learning processes [10]. Cognitive scientists have distinguished between training mechanisms driven by feedback (supervised training) and those that require no feedback, instead operating on the statistical structure inherent in the environmentally supplied stimuli (unsupervised training). In any case, perceptual learning exerts a profound influence on behavior because it occurs early during information processing and

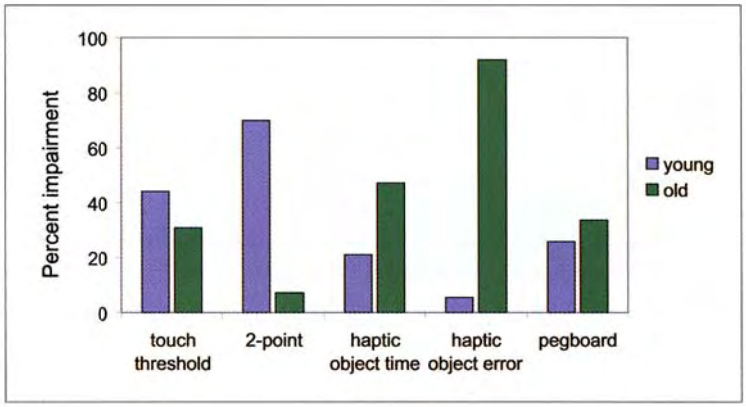


FIGURE 2. EFFECT OF SKIN COVERAGE ON HAPTIC PERFORMANCE
Shown is the task- and age-dependent impairment (percent difference compared to uncovered fingers) evoked by covering the fingers of young and elderly subjects with a rubber glove for various tactile, haptic and motor tasks.

thus shifts the foundation for all subsequent processes.

While there is a considerable amount of literature on perceptual learning of sensory and motor abilities, much less is known about training-based enhancement of haptic skills.

Time scales of perceptual learning

Practice-induced improvement can occur on many different time scales. For example, in some tasks, a few trials are sufficient to drive improvement. In other situations, performance improves only after weeks or months of practicing. What remains to be clarified are conditions that require either short- or long-term training. Also, under which conditions do improvements saturate. It has been suggested that one notable source of human inefficiency is that, unlike the ideal observer, human learning relies more heavily on previous decisions resulting in no learning on trials following a previous incorrect decision [11].

In studies of long-term training over weeks and months, one typically finds an early phase of rapid improvement followed by a second phase of much slower learning (cf. Fig. 1). It has been suggested that the early phase represents task understanding and the development of an appropriate strategy, while the second phase of improvement is due to selective and specific changes in cortical processing [12]. This view is consistent with the observation that gain obtained during the first phase is unspecific and transfers easily to other sites, whereas the gain accumulated during the second phase is highly specific to the trained condition. For an elaborated account of this assumption for visual perceptual learning see [13].

General rules in perceptual learning

An important question in evaluating studies of perceptual learning is how do we know what to learn? In other words, how does a neural system know which information is behaviorally relevant and which is not? There must be mechanisms that gate what is learned (i.e., to control what aspects are allowed and what aspects are restricted).

Mechanisms in perceptual learning (according to [5]):

- By *attention weighting* perception becomes adapted to tasks and environments by increasing the attention paid to important dimensions and features.
- By *imprinting*, processing mechanisms are developed that are specialized for stimuli or parts of stimuli.

Box 1.

How much daily training is needed for learning an auditory frequency and temporal-interval discrimination task was investigated by varying the number of training trials per day (360 or 900 trials per day for 6 days). Improvement on frequency discrimination required more than 360 trials of training while learning on temporal-interval discrimination occurred within the 360 training trials with additional daily practice having resulting no further improvement [14]. In another study, improvement in human localization (eight-alternative forced-choice with feedback) performance of a target randomly sampled from four elongated Gaussian targets with different orientations and polarities was observed within four trials lasting less than 1 min. Comparing human learning to an optimal Bayesian algorithm it was found that human learning was slower and incomplete with respect to the optimal algorithm [11]. Short-term practicing effects were also addressed in a haptic object recognition task, where subjects performed three consecutive sessions lasting between 10–30 min. Subjects improved for both time needed to complete the task and for numbers of incorrect recognitions by about 15% independent of age and gender [15].

- By *differentiation*, stimuli that were once indistinguishable become psychologically separated.
- By *unitization*, tasks that originally required detection of several parts are accomplished by detecting a single constructed unit representing a complex configuration.

Specificity

Perceptual learning is often characterized by a high specificity to stimulus parameters such as location or orientation of a stimulus with little generalization of what is learned to other locations or to other stimulus configurations. Selectivity and locality of this type implies that the underlying neural changes are most probably occurring within early cortical representations that contain well-ordered topographic maps to allow for this selectivity.

Transfer

In addition, a transfer of the newly acquired abilities is often considered an important marker of that processing level at which changes are most likely to occur: Limited generalization is taken as evidence for high locality of effects in early representations. In contrast, transfer of learned abilities is taken as evidence for the involvement of higher processing levels as is often observed in task and strategy learning [12, 16–19]. However, as summarized below, transfer and generalization is highly task-specific.

Feedback and reinforcement

Feedback provides valuable information about the correctness of performer's responses during learning. Correct feedback conditions in a Vernier discrimination task yielded a larger improvement of performance than manipulated and no feedback conditions. However, providing feedback that was uncorrelated to the performer's responses prevented learning [20]. On the other hand, studies of perceptual learning for hyperacuity found that even within-session learning occurs without feedback [21]. One explanation that perceptual learning can occur in the absence of external reinforcement is that internal reinforcement can serve as a learning signal. For instance, stimuli that are highly discernable can serve as a template that subjects can use to assess stimuli in more difficult conditions. It has been suggested that fast-learning studies often do not require feedback but that slow-learning protocols do [22]. According to recent fMRI (functional magnetic resonance imaging) data,

the caudate nucleus responded to positive and negative feedback during perceptual learning in a manner analogous to its processing of extrinsic affective reinforcers indicating that this region may be a critical moderator of the influence of feedback on learning [23].

Attention and motivation

One way in which perception becomes adapted to tasks and environments is by increasing the attention paid to perceptual dimensions and features that are important [5, 24]. This view is well in accordance with recent models of visual attention that assume that efficient stimulus processing relies on an interaction between sensory (controlled) and executive (controlling) processes [25–27]. Within this framework, motivation might reflect an important factor for establishing robust perceptual representation even when conditions are sub-optimal or not efficiently controllable by executive functions [28–29]. For an unifying account about the role of modulators of perceptual learning see [30, 31].

External and internal noise

According to different theories practice improves discrimination by enhancing the signal, diminishing internal noise or both. This question has been studied mostly in the visual domain where signal strength and noise has been systematically varied. Data suggest that mechanisms of perceptual learning may rely on a combination of external noise exclusion and stimulus enhancement *via* additive internal noise reduction [32–33].

Magnitude of learning-induced changes

The amount of improvement of haptic performance depends on time (cf. Fig. 1). As discussed above, during the early phase subjects often improve dramatically, while the gain accumulated later in training saturates. Typical values of improvement are in the range of 10–25% compared to baseline conditions. It should be emphasized that the percent changes observed during haptic learning are several fold smaller than the typical alterations accompanying the decline of age-related haptic performance at high age.

Neural representation of learning

In search of a neurobiological basis of perceptual learning, recent studies have shown that skill acquisition is associated with selective plastic reorganizational changes in the cortical representations of those body parts that received stimuli during perceptual learning. Recanzone and co-workers were the first to demonstrate alterations of cortical sensory processing developing during perceptual learning [41]. They showed that tactile frequency discrimination training in monkeys over many sessions leads perceptually to a reduction of the discrimination threshold and cortically to an expansion of the maps in somatosensory cortex that represent the used finger. Most important, this study showed that there was a linear correlation between the individual amount of perceptual improvement induced by the training and the individual amount of cortical map expansion [41]. These data imply that cortical map size is a reliable predictor of the individual performance. This form of adult sensory plasticity has now been observed in all sensory systems including auditory, somatosensory and visual areas.

Since perceptual learning involves plasticity in the primary sensory cortices, the outcome of learning can be visualized not only in animal models, but also in human subjects using functional magnetic resonance imaging or high-resolution EEG. Pleger and co-workers [42, 43] and Dinse and co-workers [44] demonstrated that the amount of tactile discrimination improvement correlated with the amount of enlargement of the somatosensory hand representation (cf. Fig. 3). Thus, tactile learning paradigms provide a 'window' through which fundamental mechanisms of perceptual learning can be investigated. By this it becomes possible to evaluate the efficacy of perceptual learning independently on two levels: psychophysically and in terms of brain organiza-

Box 2.

In the tactile domain, Sathian and co-workers [34] provided evidence that practice-related improvement is highly specific for properties of the stimulus used in training. They reported substantial interdigital transfer of practice effects for discrimination of gratings varying in either spatial parameter and also for spatial acuity-dependent discrimination of grating orientation. Although tactile learning was task specific as shown in other sensory systems, there was generalization across fingers, unlike visual learning, which is highly location specific. In another, so-called tactile hyperacuity task, subjects had to discriminate a row of three dots in which the central dot was offset laterally from a row without such offset. Performance at the right index fingerpad improved with practice, which transferred completely to the left index finger demonstrating intermanual transfer [35]. To study tactile interval discrimination, subjects were trained for 900 trials per day for 10–15 days. Learning at the trained base interval generalized completely across untrained skin locations on the trained hand and to the corresponding untrained skin location in the contralateral hand. There was partial generalization to untrained base intervals similar to the trained one, but not to more distant base intervals. Interestingly, learning with somatosensory stimuli generalized to auditory stimuli presented at comparable base intervals [36]. These results demonstrate temporal specificity in somatosensory interval discrimination learning that generalizes across skin location, hemisphere, and modality.

The ability to detect the symmetrical or asymmetrical characteristics of individually presented plastic non-representational shapes was tested over 4 days. This brief training led to improved performance as indicated by a decrease in scanning time and number of identification errors. However, learning depended on form parameters of symmetry and the type of scanning strategy used to explore a stimulus [37]. These data suggest that perceptual experience plays a major role in the efficient pick-up and utilization of haptic information.

Fast perceptual learning was investigated with respect to the perception of the heights or widths of wielded non visible rectangular objects. In this particular task, inertial differences are the basis for perceived size differences. Variables analyzed were attunement (attending to the task-relevant inertial variable), calibration (scaling spatial extent to the task-relevant inertial variable), and exploratory behavior (wielding so as to differentiate the task-relevant inertial variable). Subjects had to perform 25 trials with a set of practice objects; those trials were followed and preceded by 18 trials with a set of test objects. Practice, with knowledge of results, improved both attunement as measured by regression of perceived spatial extent on the inertial variables, and calibration, as measured by constant and variable error. In the absence of knowledge of results only variable error improved with practice. In both conditions, however, exploratory behavior decreased in duration and complexity, as measured by recurrence quantification analysis [38]. The data revealed a substantial complexity of mechanisms involved in fast perceptual haptic learning dependent on knowledge.

The role of knowledge in haptic exploration was specifically addressed in a haptic classification task. First, haptically available object properties were assessed by means of a questionnaire. Then the hand movements executed during haptic classification of manipulable common objects were examined. Manual exploration consisted of a two-stage sequence, an initial generalized 'grasp-and-lift' routine, followed by a series of more specialized hand-movement patterns. Interestingly, the specialized movements were largely driven by the knowledge of the properties of the specific objects [39].

Healthy subjects of different age-groups (covering 20–89 years) performed a cross-modal 3D shape-matching test based on artificial, cubic objects modified according to [40], which had to be explored haptically by hand movements and afterwards allocated to visually presented samples. There was a significant decline of cross-modal visuo-haptic performance with increasing age [15]. Both parameters of the visuo-haptic test, i.e., the time to complete the test and the number of errors increased significantly with age. Furthermore the age-related decay of haptic performance was stronger in female subjects. Interestingly, the individual level of sensory hand functions (touch threshold or two-point discrimination threshold) did neither predict the age-related decrease of haptic performance, nor the gender-specific differences in haptic performance. On the other side general cognitive abilities were found a reliable indicator of visuo-haptic performance in old age to a greater extent than sensory hand functions.

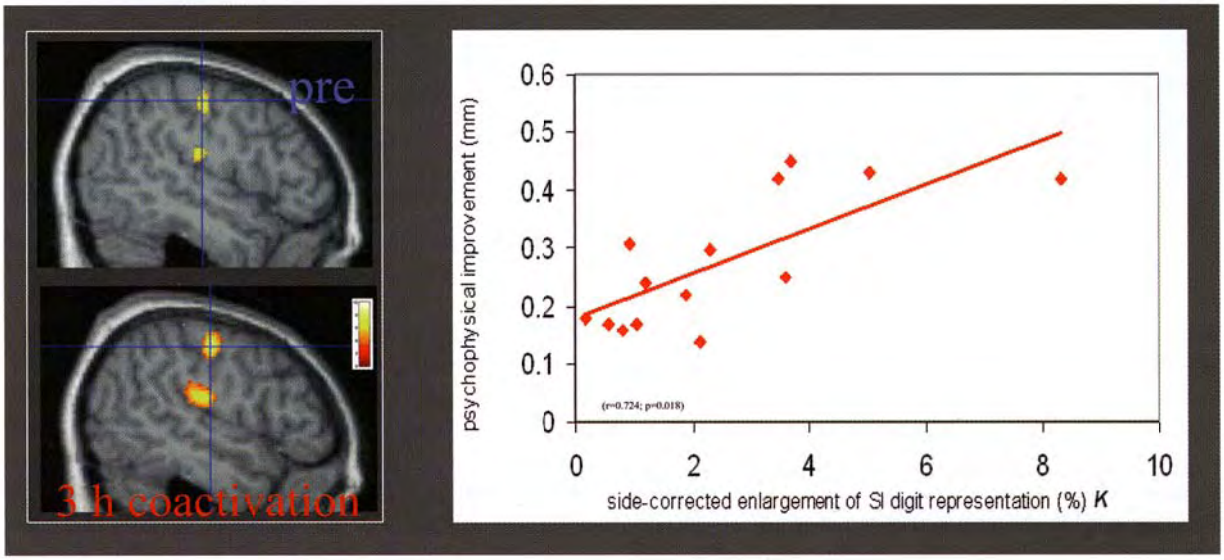


FIGURE 3. SINGLE SUBJECT COACTIVATION EFFECT ON CORTICAL MAPS

(A): BOLD (blood oxygenation level dependent) signals detected pre- and post coactivation in the contralateral SI in the postcentral gyrus, and in the contralateral SII in the parietal operculum above the Sylvian fissure. Comparing pre- with post-coactivation fMRI sessions revealed enlarged activation and increased BOLD signal intensity in SI and SII (secondary somatosensory cortex) representing the coactivated IF (index finger). These changes of BOLD signals recovered 24 h after coactivation (not shown). Linear correlation analysis between perceptual and cortical changes in SI (Pearson) revealed that psychophysical improvement correlated with the size of cortical map expansion indicating a causal relation (B). To express the coactivation effect on BOLD signals of the contralateral SI, the corresponding number of activated voxels per cluster were used to calculate $K=((right_{post}-right_{pre})-(left_{post}-left_{pre}))/right_{pre}$. *"K" was positively correlated with changes in psychophysical thresholds ($r=0.744$; $p=0.002$). Modified according to [43], with permission from* Science.

Box 3.

A recent neuroimaging study addressed the question of whether sensory cortical regions support retrieval of perceptual knowledge. Semantic decisions that indexed tactile, gustatory, auditory, and visual knowledge specifically activated brain regions associated with encoding these sensory experiences. Retrieval of tactile knowledge was specifically associated with increased activation in somatosensory, motor, and premotor cortical regions. In contrast, decisions involving flavor knowledge increased activation in an orbitofrontal region previously implicated in processing semantic comparisons among edible items. Perceptual knowledge retrieval that references visual and auditory experiences was associated with increased activity indistinct temporal brain regions involved in the respective sensory processing [45]. These results indicate that retrieval of perceptual knowledge relies on brain regions used to mediate sensory experiences with the referenced objects.
Individual differences in regional brain volumes modified by the effects of age and sex on the acquisition of a perceptual-motor skill in healthy adults were studied in subjects performing five five-trial blocks of a mirror-drawing task on three separate days. Index of performance was time to completion and number of errors committed. All participants improved with practice, but younger adults performed better than their older counterparts, and women performed better than men. Four brain regions – lateral prefrontal cortex, hippocampus, cerebellar hemispheres and the caudate nucleus – were analyzed. All regional volumes were negatively associated with age. Larger lateral prefrontal cortex was associated with better performance on the mirror drawing task, and this link was stronger in the older participants and was strengthened at the later stages of learning. Larger caudate was related to better performance, especially at later learning, among men, but among women the link was evident only during early learning. Thus, mirror-drawing represents a task that evokes activation which is highly dependent on age, gender and skill level [46].

tion offering a unique way to quantify and visualize learning processes.

Role of intensified or reduced use

Continuous and long-lasting practice of sensorimotor skills results in defined expansions of cortical representational areas as described for blind Braille readers and musicians [47–53]. As a consequence, their tactile and haptic performance becomes better.

While MEG and EEG studies demonstrated that musicians have altered cortical representations, there is still controversy about the specificity of these reorganizational changes. There are two possibilities: These changes are highly specific in the sense that they allow for improvement of the trained motor or perceptual skill only, i.e., the neural changes arising from skill training are assumed to have little consequences for information processing beyond that skill. In an alternative scenario, neural changes result in a widespread modification of the entire sensory processing. In this case, extensive consequences in terms of perceptual and behavioral abilities are to be expected that must generalize beyond the trained skill. There seem to be no simple answers as both has been found in sensory and motor domain suggesting some modality-specificity of this form of adaptation.

While there is agreement that use is a major factor driving plasticity of cortical processing and cortical maps thereby driving the development of outstanding sensorimotor skills, little is known how periods of disuse affect cortical representations and parallel perceptual performance in humans.

Box 4.

To address this question, the impact of about 3 weeks of immobilization of finger and hand due to cast wearing was investigated. Cast wearing significantly reduced the use of the immobilized limb, which was associated with a severe loss of tactile acuity and a reduced BOLD (blood oxygenation level dependent) response of cortical representational maps of the immobilized finger. In contrast to these maladaptations, compensatory effects on the left, healthy hand were observed: the frequency of use was substantially enhanced, and in case of right-hand immobilization, the perceptual performance of the left, healthy hand became even superior in comparison to healthy controls. About 2 weeks after cast removal, perceptual and cortical changes were fully reversible; however, enhanced tactile acuity of the healthy hand persisted [54]. The results demonstrate that disuse as occurring under the everyday-life situation of cast wearing impairs tactile performance and functional brain organization on a time scale of days. Accordingly, the concept of use-dependent plasticity can be extended into maladaptive regimes under conditions of disuse.

Role of passive stimulation

It is now clear that in addition to training, practice and experience, i.e., intensified or reduced use perceptual performance can also be improved by passive stimulation (i.e., through the statistics of the input) on a time scale of only a few hours or less. According to recent behavioral studies perceptual learning of visual motion can occur as a result of mere exposure to a subliminal stimulus, without external reinforcement, the subject actively attending to a task, or the motion-stimulus being a relevant feature of the particular task [55–58]. The coactivation paradigm developed by Dinse and co-workers induces improvements of tactile and haptic performance, and results in cortical reorganization thereby adding an important alternative for inducing perceptual changes without training [31, 42–44, 59–72].

In order to explain this effectiveness it has been suggested that all these types of learning occur through similar processes. Namely that the key to learning is that sensory stimulation needs to be sufficient to drive the neural system past the point of a learning threshold [31]. Factors such as reinforcement or motivation appear to play a permissive role, but optimizing sensory inputs by implementing specific high-frequency or burst-like stimulation, which are known to induce synaptic plasticity in brain-slice preparations, can also serve to boost responses that normally are insufficient to drive learning past this learning threshold.

Coactivation

Utilizing the knowledge about brain plasticity accumulated over the last years [61, 74], it has been suggested that specific stimulation protocols can be designed through which it becomes feasible to change purposefully brain organization and thus perception and behavior. Based on this concept, we have developed a so-called coactivation protocol, through which we can enforce localized activation pattern in the brain [42–44, 59, 60, 65]. Coactivation follows closely the idea of Hebbian learning [75]: Synchronous neural activity, which is regarded instrumental to drive plastic changes, is generated by the simultaneous tactile 'co-stimulation'. Coactivation leads to an improvement of tactile acuity and an expansion of corresponding cortical maps. The amount of perceptual gain resulting from this procedure linearly correlates with the amount of cortical reorganization and sug-

Box 5.

There have been many reports according to which prolonged and unattended stimulation is ineffective to drive plastic changes. Pairing of sensory stimulation with electrical stimulation of the Nucleus basalis (NB) has been shown to result in reorganization of cortical maps, however, simple sensory stimulation alone without NB stimulation was ineffective [73]. These apparent discrepancies can be settled in the light of the observation that simple (i.e., small field) prolonged passive stimulation had no effect on discrimination abilities, and that more massive, 'coactive' stimulation was required for plasticity [43, 65, 31]. Accordingly, in order to be effective, the passive stimulation has to include specific constraints such as high-frequency, burst-like stimulation described above.

gests a causal relation (Fig. 3), [31, 42–44, 62, 64, 65]. Coactivation-induced improvement of tactile acuity is quite large (15–20%), whereas gain after years of practice in musicians was in a range of 20–25% [65].

Technical aspects

To apply coactivation, a small device consisting of a small tactile stimulation device is taped to the tip of a finger. The device allows stimulation of the skin portions underneath thereby coactivating the receptive fields within this area of approximately 1 cm^2 (Fig. 4). In the standard version, coactivation is applied for 3 h using stimuli drawn from a Poisson process at interstimulus-intervals between 100 to 3,000 ms with an average stimulation frequency of 1 Hz and a pulse duration of 10 ms. Pulse trains required to drive the solenoid were stored on MP3-player, permitting unrestrained mobility of the subjects during coactivation.

In order to optimize coactivation to maximize effectiveness we have developed a number of protocols (Patents DE) such as employing electrical stimulation, multifinger coactivation [72], and high-frequency stimulation [69, 70], the latter allows to drive changes in 20 min only. Other options include combination with transcranial magnetic stimulation [67], drugs [44, 63, 71], or repeated applications (unpublished) that potentiate the effects of coactivation. In Figure 5 the effects of different coactivation protocols on magnitude and stability of evoked tactile improvement are summarized.

Other passive methods

Coactivation is not the only form of unattended activation-based learning. Under the assumption that simultaneously applied coactivation induces synchronous neural activity at a cortical site selected by the location of tactile stimulation, we went one step further and short-cut the sensory pathway. To this end we applied so-called high-frequency (5 Hz) transcranial magnetic stimulation (TMS) from outside the scull directly to selected brain areas in order to induce synchronous activity. Applying 20 min of 5 Hz TMS over the finger representation of SI lead to similar changes as observed after coactivation. These changes were paralleled by an expansion of the cortical finger representation and an increase of cortical excitability in SI (primary somatosensory cortex) and recovered after about 2–3 h [76, 77]. These findings demonstrate that meaningful improvement of perceptual performance can even be obtained by specific (high-frequency) stimulation of brain areas from outside the scull. Most notably, this intervention does not leave the cortical processing in a disorganized state, but on the

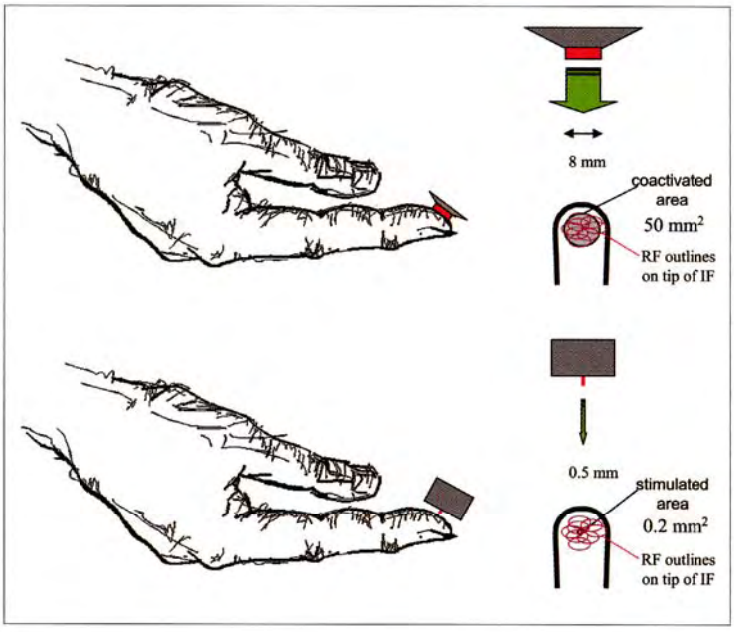


FIGURE 4. APPLICATION OF COACTIVATION
A. A small solenoid with a diameter of 8 mm is mounted on the tip of the right index finger (IF) to coactivate the receptive fields representing the skin portion under the solenoid (50 mm²). B. Control protocol to demonstrate the requirement for 'co-activation'. Application of a so-called single-site stimulation: A small device consisting of only one tiny stimulator (tip diameter 0.5 mm) is mounted on the tip of the right IF to stimulate a single 'point' (0.8 mm²) on the skin. Duration of stimulation is 3 h. Reprinted with permission from Neuron *[43].*

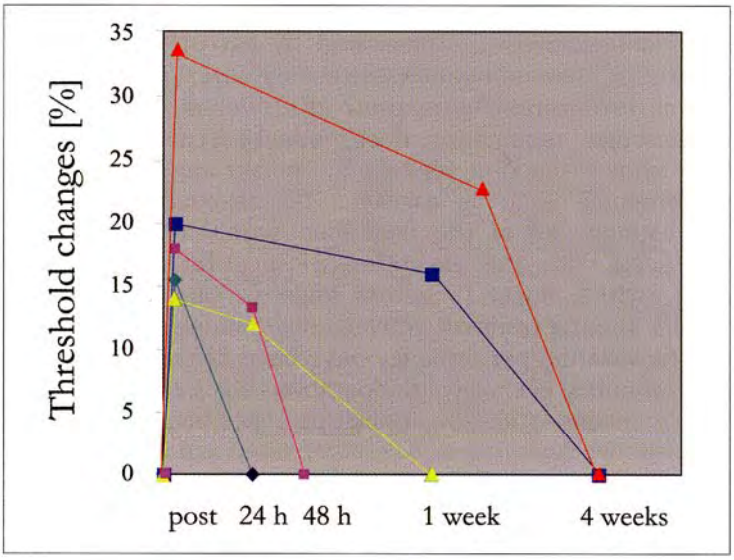


FIGURE 5. TIME COURSE OF IMPROVEMENT (PERCENT DIFFERENCE COMPARED TO BASELINE CONDITIONS) OF TACTILE ACUITY FOR VARIOUS COACTIVATION PROTOCOLS
Dependent on the refinement of the protocol used, induced changes are comparable in magnitude to changes observed in subjects undergoing heavy schedules of training. Repeated application of coactivation over many days stabilizes the improvement. Green: 1-finger coac [43], pink: 5-finger coac [72], yellow: 20 min high-frequency [69], blue: 5-finger 20 min high-frequency [unpublished], red: 5-finger 20 min high-frequency, repeated every 3 days [unpublished].

contrary leads to the emergence of a different, yet organized and meaningful behavior, as indicated by the improvement of discrimination performance.

Wide-range effectiveness of coactivation

Central to coactivation is that it does not require training of particular tasks, which makes coacti-

vation-induced improvements task-independent. Therefore, testing for tactile acuity does not imply that acuity is in some way specific to coactivation. On the contrary, we assume that coactivation alters the entire way of neural processing related to tactile and haptic information. Consequently, one can expect that coactivation not only affects two-point discrimination thresholds, but basically all tasks related to tactile, haptic and sensorimotor processing. To test this assumption, we initiated a more comprehensive study in which we looked for a number of haptic tasks beyond two-point discrimination (Tab. 2).

In fact, consistent with these assumptions, coactivation leads to a remodeling of a wide range of tactile, haptic and even sensorimotor tasks (Tab. 2). Also consistent, both improvement and impairment is induced. The only parameter not affected by coactivation is touch threshold, which, according to Table 1, represents the most peripheral parameter. In contrast, of all parameters tested all have been affected by coactivation: tactile acuity (as measured by two-point or grating discrimination), frequency discrimination, localization, dot-pattern discrimination, haptic object recognition, decision making (multiple choice reaction times) and sensorimotor performance such as assessed by pegboard. Interestingly, all of the described parameters improved with the exception of localization tasks (within finger or across fingers). Similar results about a trade-off between discrimination and localization performance have been demonstrated under everyday-life conditions for blind Braille readers [50, 78], indicating that this is not coactivation-related, but rather represents a typical property.

Cellular studies suggest that there might be only a few, basic mechanisms that control synaptic transmission. In particular, the N-methyl-D-aspartate (NMDA) receptor has been implicated in synaptic plasticity [79–81]. In order to demonstrate that coactivation is mediated by established plasticity mechanisms, we tested its dependency on NMDA receptor activity. We found that memantine, a substance known to block selectively NMDA receptors [82], eliminates coactivation-induced learning, both psychophysically and cortically [44]. These data show that coactivation-induced perceptual learning and associated cortical changes are controlled by basic mechanisms known to mediate and modulate synaptic plasticity. More generally, these data demonstrate that by using specific drugs the outcome of coactivation can be further amplified.

Table 2. Joint changes of tactile-haptic-sensorimotor performance after coactivation

Task/parameter	effect of coactivation
touch threshold	no effect
two-point discrimination	+
Localization	-
finger mislocalization	-
frequency (flutter) discrimination	+
reaction times	+
Braille sign recognition	+
fine motor movements (finger–hand)	+
haptic object recognition	+
every day life performance	+

Musicians

The potential of coactivation is not limited to young adult subjects, but has been applied in musicians and elderly subjects, whose performance is already altered.

In professional pianists, tactile performance was significantly superior to that found in non-musician controls indicating that piano players benefit from their daily routine by developing significantly reduced tactile discrimination thresh-

Box 6.

Surprisingly, despite the better baseline performance coactivation resulted in an even higher gain of tactile acuity. While the baseline performance correlated well with the duration of daily piano practicing, the coactivation-induced improvement was correlated with the number of years of extensive piano playing [68]. These findings imply stronger capacities for plastic reorganization in pianists, and points to enhanced learning abilities. This kind of meta-plasticity suggests that extensive piano practicing alters somatosensory information processing and sensory perception beyond training specific constraints. The data also suggest that the potential of coactivation applies also in subjects characterized by high-level baseline performance. Support for enhanced learning capabilities comes from a recent study employing paired associative stimulation (PAS), which consists of an electric median nerve stimulus repeatedly paired (200 times at 0.25 Hz) with a TMS pulse over the hand motor area. Musicians showed a wider modification range of synaptic plasticity than no-musician controls, which suggests that Musicians regulate plasticity and excitability with a higher gain than normal [83].

olds, although piano playing is little related to tactile acuity abilities. Therefore, the question was whether there is room for further improvement.

Age

In contrast, elderly subjects are characterized by a significant decline of tactile, haptic and sensorimotor abilities. However, this decline is not irreversible, but treatable through various measures (Fig. 6).

The typical approach to ameliorate age-related changes is to subject elderly to intense schedules of training and practicing, and there is no doubt about the effectiveness of training-based intervention even at high age [84–88]. However, since many elderly suffer from restricted mobility, additional and alternative approaches are needed which supplement and enhance, or even replace conventional training procedures.

Taken together, these results show that age-related decline of perception and behavior can at least be ameliorated. This is important as it implies that age-related loss of mechanoreceptors appear to play a minor role in mediating and maintaining tactile and haptic function.

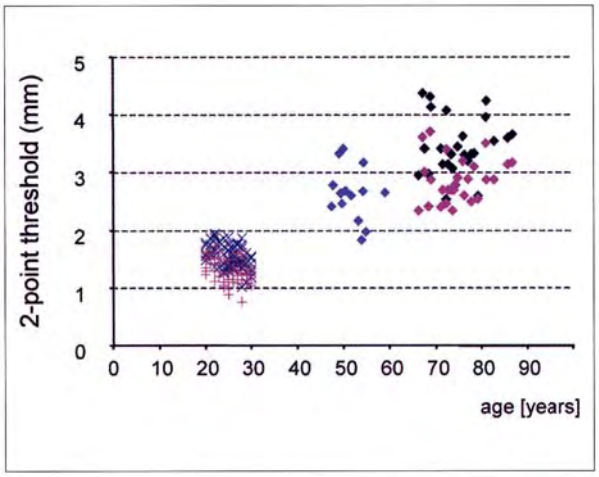


Figure 6. Tactile two-point discrimination thresholds of the tip of the right index finger as a function of age (total of 120 subjects)
After coactivation (pink symbols), thresholds of the coactivated subjects (young control group and group of elderly) were significantly reduced. Coactivation-induced improvement in the group aged 66–86 was several-fold stronger in magnitude as compared to the young subject. As a result, after coactivation thresholds of the elderly resembled those found in the subjects 47–55 years old. Reprinted with permission from Annals of Neurology *[66].*

Box 7.

To show that the age-related impairment of tactile acuity can be ameliorated by coactivation, we studied discrimination thresholds in healthy subjects aged 66–86 years. We found that 3 h of coactivation reduced two-point thresholds in aged subjects similar as described above for young adults. In this way, tactile acuity of a 80 year old subject comes to match that typically found at an age of 50 [66, 89]. However, the lowest thresholds in elderly after coactivation were still above thresholds typically observed in young subjects. Further experiments are therefore required to clarify if the performance observed after coactivation represents the lowest limit in acuity that can be reached by elderly given the anatomical and morphological changes accumulating over age, or if discrimination thresholds can be further reduced using more refined intervention methods. Recent data from a study on tactile acuity in elderly blind subjects revealed the maintenance of very low discrimination threshold even at high age [90], which supports the notion that tactile acuity in elderly can be preserved at a level typically found in young subjects under conditions of heavy regular practicing.

There have been alternative attempts to interfere with the age-related decline of sensory capacities. For example, the addition of noise can improve the ability to transfer reliably information, a phenomenon known as stochastic resonance. Electrical noise stimulation to the hand of elderly subjects lowered touch thresholds [91], while noise stimulation to the foot improved sway parameters in young and elderly subjects [92]. While stochastic resonance affects thresholds by enhancing inputs otherwise subthreshold, coactivation most likely alters the modes of neural processing due to specific changes of synaptic efficacy and synaptic connections [42–44]. Taking a pharmacological approach, a recent report showed enhanced encoding of motor memories in elderly adults, up to levels present in younger subjects, by restoring dopaminergic function in the elderly subjects through administration of a single oral dose of levodopa [93].

Trade-offs and interdependence

One of the hottest questions in learning is whether the enhancement of one ability occurs on the cost of others. In other words, is there a trade-off between abilities we gain while others are lost at the same time? A related question addresses the putative interdependence between various tasks. Both aspects are interesting because they allow insight into constraints of cortical processing (cf. Modeling).

In tactile perception the answer is clear: When subjects improve their tactile discrimination abilities (i.e., to perceive two closely spaced stimuli as two), this develops on the costs of localization performance, i.e., to accurately tell the position of a stimulus on the skin. Interestingly, both types of changes evolve without altering touch thresholds, which imply a trade-off between localization and discrimination on the one hand, but independence of both parameters from touch threshold on the other hand. Another example comes from haptic exploration, where haptic recognition is poorly associated with tactile acuity, but correlated with measures of non-verbal intelligence (Raven matrix [15]). In Figure 7 the joint dependences under baseline conditions are summarized for touch threshold, two-point discrimination and haptic object recognition revealing a complete lack of correlations. These findings imply that there exist cortical processing modes that cannot be optimized in parallel. In this view, the average performance encountered in an individual performer reflects most likely a sort of a balanced compromise trying to achieve optimal, but not maximal performance. Through perceptual learning it is possible to further enhance certain skills, but not all, resulting in a parallel improvement of some skills on the cost of impairment of others.

How that can be explained in terms of cortical processing is described in the next paragraph.

Modeling tactile learning

There is now compelling evidence that cortical population activity provides the most promising bridging between behavior on the one hand, and neural activity on the other hand [94–96]. To understand tactile spatial discrimination performance and its alterations during learning we provided a general framework using a mean field approach [97] (Fig. 8). In this approach, cortical population activity within cortical maps is modeled with a Mexican hat interaction of short-range excitation and longer-range inhibition [98, 99]. Within such a representation tactile stimulation evokes either single peaks of activation coding for the subjective experience of a single point on the skin while bimodal distributions are read out for two-points.

In the cortex the skin surface of the finger is represented as a topographically organized, two-dimensional map in which neighboring stimuli evoke neighboring peaks of activation of populations of neurons. In a simplified one-dimensional version, two neighboring inputs are represented along a one-dimensional cut through the two-dimensional topographic map.

Influence of lateral inhibition on discrimination and localization performance

In the model, stimulation at a single site evokes single peaks of activation coding for the subjective experience of a single point, while simultaneous stimulation at two sites (like in two-point discrimination experiments) evokes two peaks, which are read out for perceiving two points. It has been shown experimentally that for large distances two peaks of activation interact only weakly, while lateral inhibition leads to substantial suppression for shorter separations [100].

In contrast, localization refers to the ability to precisely read out the location of monomodal

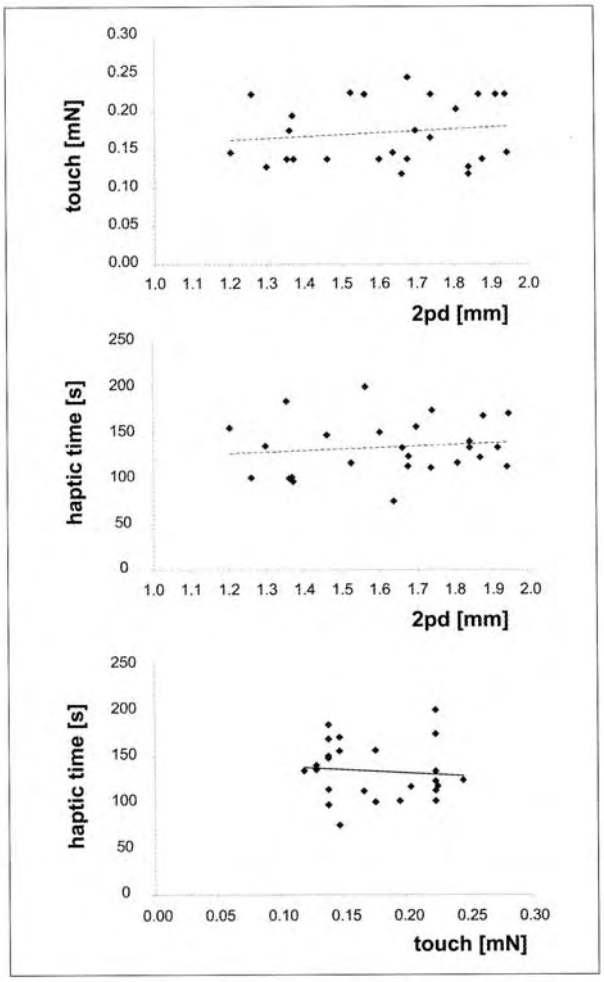
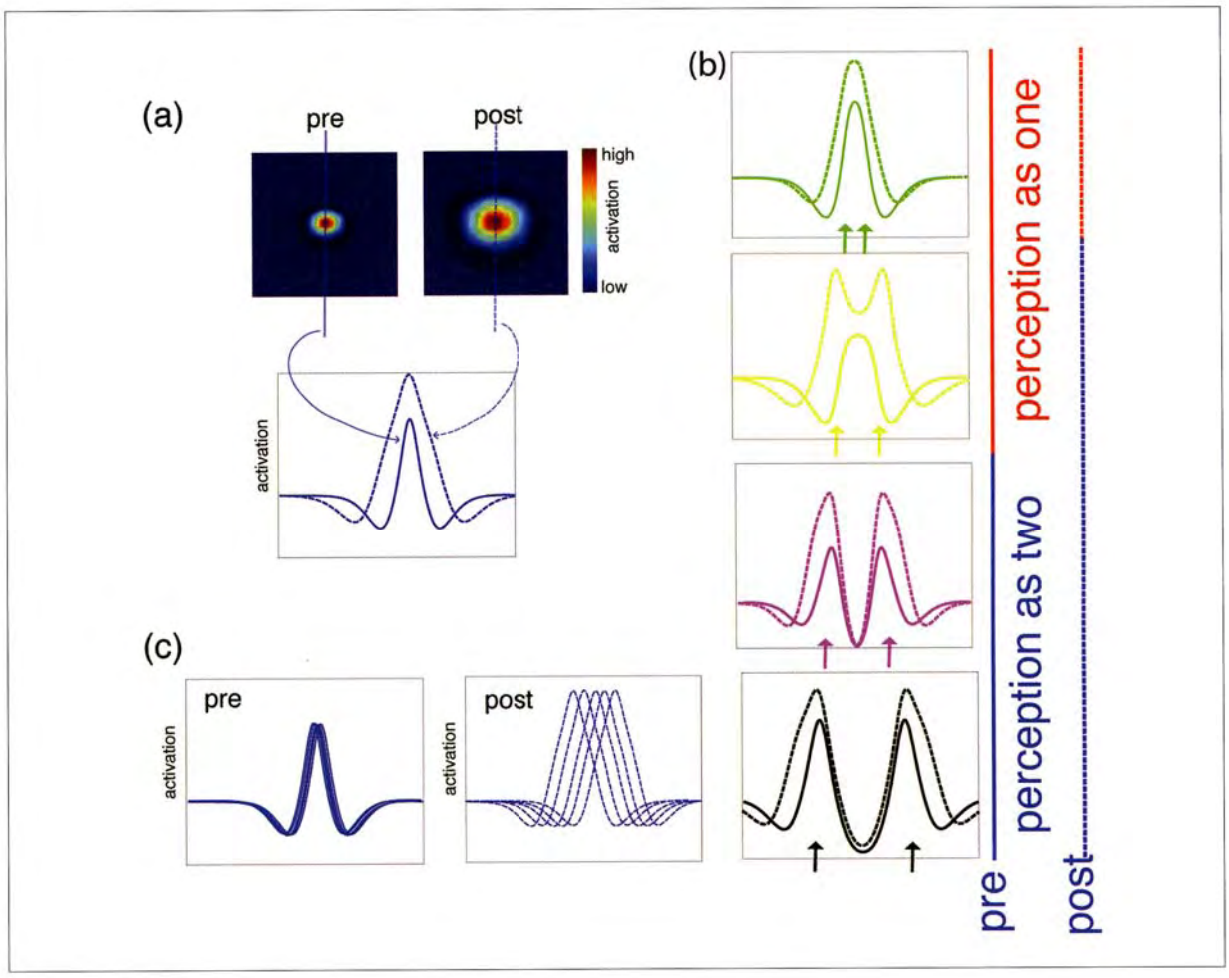


FIGURE 7. RELATION BETWEEN THREE MEASURES OF TACTILE PERCEPTION

Touch threshold (touch, the lowest force that allows detecting the presence of a stimulus on the skin of the fingertip), spatial two-point discrimination (2pd, the critical distance at which two simultaneously presented stimuli on the skin of the fingertip are perceived as two), and haptic object recognition (haptic time, time needed to correctly identify arbitrary three-dimensional objects made from Lego® bricks). There is an overall lack of correlation between measures: Top: touch vs. two-point (Pearson, $r=0.127$, $p=0.537$*); middle: haptic recognition* versus *two-point (Pearson,* $r=0.118$, $p=0.566$*), bottom: haptic recognition* versus *touch (Pearson,* $r=0.099$, $p=0.632$*). Data from [15].*



distributions of population activation. Several approaches have been formalized how single parameters may be estimated from population distributions of activation [101]. Spatial discrimination and localization are affected oppositely by lateral interaction: Lateral inhibition reduces coexisting, ongoing activation present at other locations of the cortical population. As coexisting activation is necessary for bimodal activation profiles coding for the perception of two points strong lateral inhibition deteriorates discrimination performance. On the other hand lateral inhibition suppresses the influence of noisy fluctuations of activation leading to a subsequent reduction in the variance of the read out peak position. Thus lateral inhibition improves localization performance but decreases discrimination performance.

Influence of learning on a computational level: suppression of inhibition

There is ample experimental evidence that learning processes are mediated through a decrease of inhibitory interaction. For example, coactiva-

FIGURE 8. MODELING LEARNING INDUCED CHANGES OF CORTICAL POPULATION ACTIVITY AND ITS IMPLICATIONS FOR TACTILE PERCEPTION

a. Cortical population activity evoked by single site stimulation modeled as localized activation using a mean field approach with center-surround inhibition. Shown are a two-dimensional simulation (corresponding to a cortical activity distribution as measured by fMRI) for a pre and a post condition (a. top row) and a one-dimensional simulation (a. bottom row). For simplification we use in the following a one-dimensional model (i.e., a one-dimensional cut through cortical surface) but emphasize that all results are applicable for two-dimensional models accordingly. When the strength of inhibitory interaction is weakened through learning, the size of the cortical representation becomes larger, both for the width of the cortical area activated by the stimulus and the height of the activation (cf. pre-post).

b. For two-point stimulation (simultaneous stimulation at two sites) two spatially very close stimuli evoke a monomodal distribution of activation (green and yellow, solid lines; arrows depict location of incoming stimuli) which corresponds to the percept of one stimulus. For larger distances a bimodal distribution of activation develops, which is assumed to code for the sensation of perceiving two stimuli (magenta and black, solid lines). Note that for medium distances the two peaks of activation inhibit each other resulting in reduced maximum levels of activation (magenta), while for large distances between inputs this inhibition is reduced resulting in higher levels of activation (black). Reducing the inhibitory interaction through learning does not change the model performance for very close (green, dashed line) or very distant (black, dashed line) inputs. However, for intermediate distances the reduced inhibition allows for more co-existing activity (yellow, dashed line). As a result, activation profiles become bimodal shifting the discrimination of two separate stimuli towards smaller separation distances. The weakened inhibition is also evident in the smaller reduction in overall-level of activation for medium distances (magenta, dashed line).

c. Fluctuations in peak position, either from spontaneous noise within the neural population or from noise at the peripheral (input) level, shift the exact location of the activation peaks on a trial by trial basis (different lines refer to the model response in different trials. Strong inhibition prevents fluctuations enabling a precise read-out of the exact peak-location. After learning which reduces inhibition fluctuations increase. Using the same input and model parameters as used in a. and b., noise components integrated into the model (here: Gaussian white noise) lead to substantial scatter of the exact peak location. Due to the strong inhibitory component this scatter is weak before learning because the existing inhibition prevents influence from co-existing activation on other sites of the population of the population thus diminishing the influence of noise. After weakening the inhibitory component through learning the very same mechanisms that improve discrimination by permitting bimodal distributions (see b.) now deteriorate localization performance: Co-existing activation, in this case noisy fluctuations, lead to substantial scatter of the peak, thus making read-out of the exact peak location less precise.

tion has been shown to suppress paired-pulse inhibition in human subjects [102]. As a result, decreasing the strength of lateral inhibition in the model increases the size of the cortical representation as observed in fMRI and EEG studies [42–44, 64]. For discrimination (stimulation at two sites) the decrease in inhibitory interaction leads to bimodal activation profiles for distances that before learning evoked only single peaks, which provides a compelling explanation for the learning-induced improvement of discrimination [31, 42–44, 59–72]. In contrast, for localization reduced inhibition permits coexisting activation, which leads to a more powerful influence of noise thus deteriorating localization abilities. Combined, modeling lateral cortical interaction in population representations provides a unifying framework that explains task-specific requirements in tactile and haptic perception and their alterations evoked by perceptual learning.

Summary

Haptic perception in humans underlies a continuous remodeling resulting in altered perfor-

mance skills. Most notably, intensive practicing improves skills, while little practicing impairs perception indicating that high-level skills cannot be maintained without ongoing training. Remodeling of haptic perception occurs not only under conditions of specific task training, but also under everyday-life conditions characterized by intensive execution of more complex schedules as in Braille reading blinds, or musicians. Time scales for improvement range from seconds to years suggesting the involvement of many different mechanisms. There is a controversial discussion about the role of top-down *versus* bottom-up processes, the role of feedback, and about conditions under which no further gain can be accumulated despite ongoing training. In addition, passive stimulation procedures that fulfill requirements for inducing synaptic plasticity are similarly affective in altering human haptic perception. Because of the passive nature these approaches provide alternative therapeutic means for intervention in impaired human subpopulations. Independent of how haptic learning is evoked there is now agreement that development of skills is based upon neuroplasticity mechanisms that alter cortical processing in sensorimotor areas.

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Important websites

The Haptics Community Web Site:
http://haptic.mech.northwestern.edu/

Haptics-L: The electronic mailing list for the international haptics community:
http://www.roblesdelatorre.com/gabriel/hapticsl/

The wiki of the international community of scholars studying perceptual learning:
http://www.perceptuallearning.org/

The Perceptual Learning mailing list:
http://cogmod.osu.edu/mailman/listinfo/plearn

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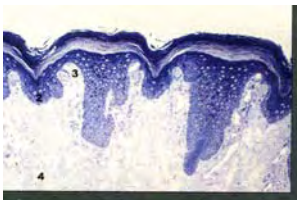

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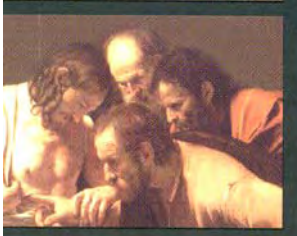
Human Haptic Perception
Basics and Applications



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