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Superior tactile performance and learning in professional pianists: evidence for meta-plasticity in musicians

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Abstract

Musician's brains constitute an interesting model for neuroplasticity. Imaging studies demonstrated that sensorimotor cortical representations are altered in musicians, which was assumed to arise from the development of skilled performance. However, the perceptual consequences of the cortical changes remain elusive. Here we ask whether cortical reorganization induced by professional musical skill training is paralleled by the evolution of other, unrelated perceptual abilities. We therefore studied psychophysically tactile spatial acuity as an indirect marker of cortical changes in professional pianists and non-musician control subjects using a simultaneous two-point discrimination paradigm. We show that long-lasting piano practising resulted in lower spatial discrimination thresholds in comparison to non-musicians. In musicians, individual discrimination thresholds were linearly correlated with the daily training duration, indicating a direct link between tactile acuity and the degree of piano practising. To investigate whether the superior acuity in pianists is subject to further improvement, we used a Hebbian stimulation protocol of tactile coactivation known to improve spatial tactile acuity. Three hours of coactivation further reduced their discrimination thresholds. The coactivation-induced gain in pianists was significantly larger in comparison to control subjects and correlated with the years of heavy daily practising (>3 h/day), but not with the total years including casual playing. Our results suggest that despite already high-level performance in pianists, Hebbian learning was more effective in musicians than in controls. This implies stronger capacities for plastic reorganization and points to enhanced learning abilities implicating a form of meta-plasticity in professional pianists.

Introduction

Many lines of evidence suggest that alterations of afferent input statistics resulting from altered use, stimulation and practise play a crucial role for the induction of cortical plasticity (Merzenich *et al*., 1988; Elbert *et al*., 1997; Recanzone, 2000; Dinse & Merzenich, 2002; Kilgard *et al*., 2002). In fact, imaging studies showed that continuous and long-lasting practise of sensorimotor skills, which is paralleled by an intensification of sensory inputs, resulted in defined expansions of cortical representational areas, as described for blind Braille readers and musicians (Pascual-Leone *et al*., 1993; Elbert *et al*., 1995; Pantev *et al*., 1998; Sterr *et al*., 1998; Rauschecker, 2001). Recently, grey matter differences between pianists and non-musicians extending from the premotor region to the primary somatosensory cortex and into the anterior parietal lobe have been described (Gaser & Schlaug, 2003). In contrast, studies in humans (Liepert *et al*., 1995) and animals (D'Amelio *et al*., 1996; Jürgens & Dinse, 1997; Coq & Xerri, 1999) provided clear evidence that reduced use, and thus altered and reduced input statistics, cause a reduction of cortical representational areas. In addition, many studies have demonstrated that plastic cortical changes can be evoked by variation of input statistics alone without involving cognitive or attentional mechanisms, provided the statistics are sufficiently altered (Diamond *et al*., 1993; Wang *et al*., 1995; Godde *et al*., 1996, 2000; Liepert *et al*., 1999; Pleger *et al*., 2001; Watanabe *et al*., 2001; Dinse & Böhmer, 2002; Dinse & Merzenich, 2002; Dinse *et al*., 2003a,b).

While MEG and EEG studies demonstrated that musicians have altered cortical representations (Elbert *et al*., 1995; Pantev *et al*., 1998; Münte *et al*., 2001; Rauschecker, 2001; Schlaug, 2001; for review, see Münte *et al*., 2002), the specificity of these reorganizational changes remains to be clarified. In our view, 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, that we believe might be more appropriate, neural changes result in a widespread modification of the entire sensory processing. In this case, extensive consequences in terms of perceptual and behavioural abilities are to be expected that must generalize widely beyond the trained skill. In other words, is a training-induced improvement paralleled by other perceptual changes, either positive or negative, that are manifested independently from the trained performance?

Here we show that skill-induced behavioural improvement as found in professional pianists is paralleled by other perceptual changes not directly related to the specific demands of piano playing. We provide psychophysical evidence that pianistic skills are accompanied by the development of additional perceptual abilities that appear to be based on an enhancement of specific learning capabilities.

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Materials and methods

We tested 14 professional piano players (21–27 years old, nine female, five male). In addition, 16 non-musicians (13 male, three female) with a mean age of 25 years served as controls.

Personal data

Handedness was assessed using the Edinburgh inventory (Oldfield, 1971). By means of a questionnaire, information about the biography of the pianists was obtained, in particular about the duration of daily practising for the time the pianists played more than 3 h a day, the age at which they began piano playing, as well as the age at which they practised regularly more than 3 h a day. All subjects tested in this study were right-handed. Pianists began piano playing at an average age of 7.3 ± 1.4 years. They played their instrument for a mean period of 15.8 ± 2.5 years. They did heavy practising, defined as playing more than 3 h a day, for a mean period of 7.0 ± 3.9 years. Average daily practising was 3.4 ± 1.6 h. Non-musician controls were matched with regard to the educational and socioeconomic background of the professional piano players. None of the controls played an instrument for hobby or was an extensive typewriter. Given the overwhelming reign of computers, all controls had a variable history of using computer keyboards.

Two-point discrimination

In the first experiment, intended to measure the spatial discrimination ability, discrimination thresholds of the index fingers (IFs) of each hand were measured in a two-alternative forced-choice simultaneous spatial two-point discrimination task, as described previously (for details of testing, see Godde *et al.*, 2000; Pleger *et al.*, 2001; Dinse *et al.*, 2003b). To obtain a stable baseline performance, we tested the right IF in five consecutive sessions over several days [sessions 1–5 (s1–s5)]. At session 5 (s5), the thresholds of the left IF were additionally tested. Previous experiments had shown that the effect of task familiarization developing over the first sessions on the right IF transfers completely to the left hand (Godde *et al.*, 1996, 2000; Pleger *et al.*, 2001; Dinse *et al.*, 2003b).

Seven pairs of needles (diameter 200 μm) with separation distances between 0.7 and 2.5 mm in 0.3-mm steps were used. For controls, zero distance was tested with a single needle. The needles were mounted on a rotatable disc that allowed switching rapidly between distances. To accomplish a rather uniform and standardized type of stimulation, the disc was installed in front of a plate movable up and down. The arm and fingers of the subjects were fixated on the plate and the subjects were then asked to move the arm down. The down movement was arrested by a stopper at a fixed position above the needles. The test finger was held in a hollow containing a small hole through which the finger came to touch the needles approximately at the same indentations in each trial. Each distance was presented 10 times in randomized order, resulting in 80 single trials per session. The subjects had to decide immediately after touching the needles if he or she had the sensation of one or two tips by answering 'one' or 'two'. After each session, individual discrimination thresholds were calculated. The summed subject's responses ('1' for one tip and '2' for two tips) were plotted against the tip distance as a psychometric function and were fitted with a logistic regression method (SPSS version 10.01). Thresholds as a marker for individual tactile performance were taken at that point at which 50% correct responses were reached (Fig. 2A). For both groups, thresholds derived during s5 were taken as 'baseline' or 'precondition', and were used for further analysis. Previous analysis had shown that s5 provides a reliable estimate of a subject's performance because of the little variability observed during s3–s5 (Godde *et al.*, 1996, 2000; Pleger *et al.*, 2001; Dinse *et al.*, 2003b). Re-evaluating the data using mean thresholds averaged over several sessions (s3–s5) revealed similar results (not shown).

Coactivation

In a second series of experiments, we applied a simultaneous tactile coactivation protocol to the right IF. The coactivation protocol was the same as in our previous studies (Godde *et al.*, 2000; Pleger *et al.*, 2001; Dinse *et al.*, 2003b). The basic idea behind this design was to coactivate a large number of receptive fields on the tip of the IF in a Hebbian manner in order to strengthen their mutual interconnectedness (Hebb, 1949).

Coactivation was applied at a mean stimulation frequency of 1 Hz consisting of randomized interstimulus intervals between 300 and 1000 ms. Pulses were recorded on tape and were played back via portable tape recorders allowing unrestrained mobility of the subjects during coactivation. To apply the coactivation, a small solenoid (Ø 8 mm) was mounted on the tip of the right IF in order to transmit the tactile stimuli to the skin. The solenoid allowed simultaneous stimulation of the skin portions of the index finger under the solenoid leading to coactivation of all receptive fields within this area(see Vega-Bermudez & Johnson, 1999 for an estimate of receptive field sizes of the human index finger). According to these data, receptive fields within 8 mm of the tip of the index finger overlap partially or are non-overlapping. Coactivation stimuli were applied at supra-threshold intensities. Duration of coactivation was 3 h, while all subjects resumed their normal day's work. Coactivation was applied after the fifth measurement of discrimination thresholds (s5 = 'pre' or 'baseline' condition). Assessment of discrimination performance of the test finger (right IF) was repeated about 20 min after termination of coactivation ('post-condition') in order to investigate how far a Hebbian-based learning protocol is able to further improve discrimination performance in pianists. In addition, the IF of the left hand was also tested after coactivation applied to the right IF in order to exclude unspecific side-effects to the contralateral non-stimulated hand.

Statistical analysis

All psychophysical data were statistically analysed by using repeated measures, univariate ANOVA or Student's two-sided paired *t*-test.

Results

All subjects achieved a stable baseline performance, as estimated from repeated assessment of thresholds over five consecutive sessions [repeated measures ANOVA s1–s5 (pianists), $F_{4,32} = 0.784$; $P = 0.544$; repeated measures ANOVA s1–s5 (non-musicians), $F_{4,60} = 0.386$; $P = 0.818$]. In contrast to non-musician controls, highly trained pianists had significantly lower discrimination thresholds on the tip of their IFs of each hand (two-sided *t*-test, $P < 0.001$ for both hands in comparison to non-musician controls, Figs 1, 2A and B). A gender analysis for highly trained pianists revealed no differences in tactile discrimination performance (univariate ANOVA for s5, $F_{1,12} = 0.953$; $P = 0.348$ for the right IF; univariate ANOVA, $F_{1,12} = 3.616$; $P = 0.08$ for the left IF). Mean thresholds were 1.14 ± 0.35 mm for the right IF and 1.11 ± 0.52 mm for the left IF as compared with 1.59 ± 0.20 mm and 1.63 ± 0.12 mm (right and left IF) of the control group, indicating higher spatial acuity in pianists. However, discrimination performance in musicians was more variable across subjects in comparison to non-musicians, as indicated by the large standard deviations (cf. Fig. 1). We therefore hypothesized that the superior perceptual capacity of each individual pianist might be related to the extensive sensory and motor training associated with piano practising.

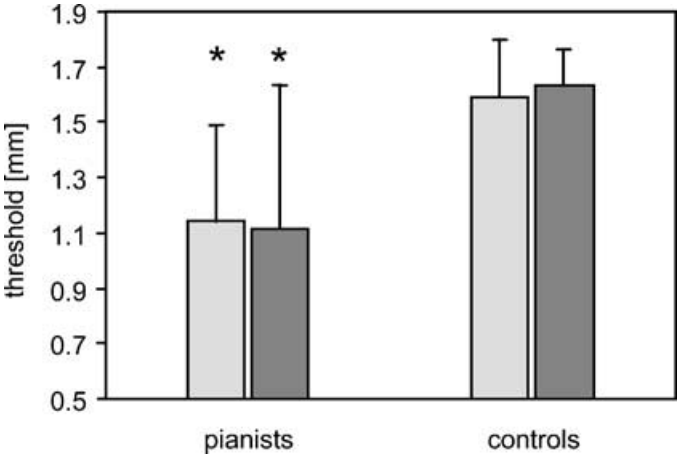

FIG. 1. Differences in discrimination thresholds of pianists and non-musicians control subjects. A comparison of the mean discrimination thresholds of the right (light grey) and left IF (dark grey) for professional pianists (left) and non-musicians (right) revealed significant lower tactile discrimination performance of the right and left IF in musicians (see asterisks), indicating a higher spatial acuity for both hands in comparison to non-musician control subjects (two-sided t-test right IF: $P < 0.001$; two-sided t-test left IF: $P < 0.001$).

To test this assumption, we correlated the mean discrimination threshold of the right and left IF with the daily training duration of each pianist. A linear correlation analysis (Pearson) revealed a significant relationship between mean discrimination thresholds and the amount of daily training for both fingers (right IF: $r = -0.789$, $P = 0.001$; left IF: $r = -0.799$, $P = 0.001$, Fig. 3), supporting the idea

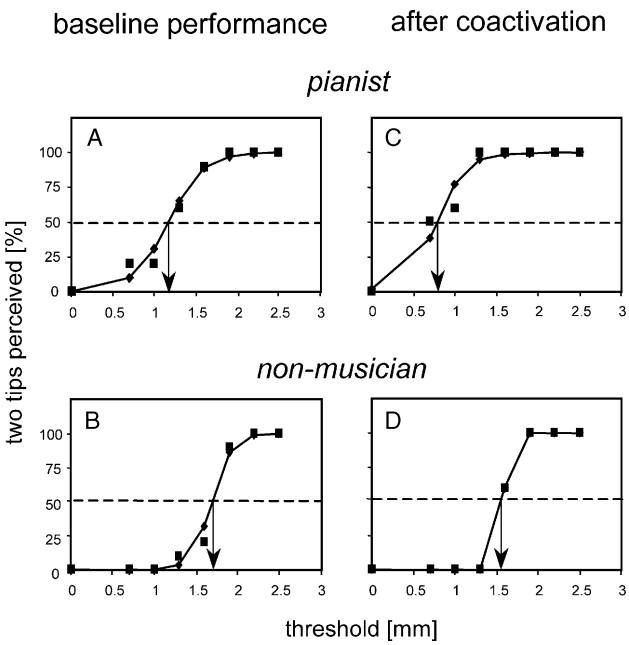

FIG. 2. Individual psychometric functions illustrating differences in discrimination behaviour (right IF) for a pianist (A) and a non-musician (B). Correct responses in percent (squares) are plotted as a function of separation distance together with the results of a logistic regression (black lines with diamonds). Fifty percent level of correct responses is indicated (dashed line) together with resulting thresholds (arrows). After coactivation, there is a distinct shift in the psychometric functions towards lower separation distances for the pianist (C) as well as the control subject (D), however, the gain in performance is larger in the pianist than the non-musician control (coactivation-induced gain 0.38 mm vs. 0.18 mm).

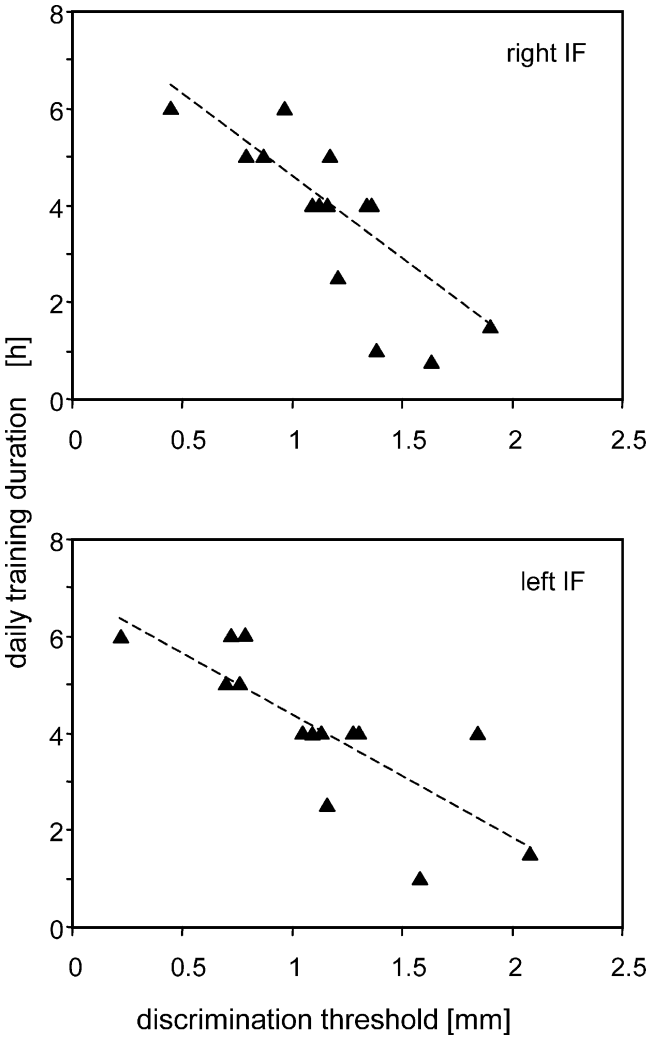

FIG. 3. Linear correlation analysis between the daily training duration and the discrimination thresholds of the right and left index finger (IF), respectively, indicating a close relation between individual perceptual performance and the amount of daily piano practising.

that the improved discrimination performance was due to the extensive daily piano practising. No significant correlations were found for the number of years of piano playing or for the age at which piano playing had started (Table 1).

We now asked whether the superior spatial discrimination performance in pianists reflects a lower limit in spatial acuity or whether thresholds were subject to further improvement by learning. Based on the Hebbian principle (Hebb, 1949), according to which simultaneity plays a key role in mediating changes of synaptic plasticity, we have introduced a learning protocol based on tactile coactivation (Godde *et al.*, 1996, 2000; Pleger *et al.*, 2001; Dinse *et al.*, 2003b). When this protocol is applied to the tip of the right IF for 3 h, the cortical representation of the right IF undergoes rapid reorganization, which is paralleled by an improvement of spatial discrimination performance (Godde *et al.*, 2000; Pleger *et al.*, 2001, 2003; Dinse *et al.*, 2003b). Applying the coactivation protocol in pianists to the right IF for 3 h revealed a further reduction of discrimination thresholds (Fig. 2A and C). We found a coactivation-induced gain in performance of 28% from 1.14 to 0.82 mm, whereas in non-musicians the improvement was only 12% (two-sided t-test: $P = 0.02$; Fig. 4). A gender analysis for pianists

TABLE 1. Pearson correlation coefficients for different parameters describing tactile acuity and learning efficacy in relation to the practising schedule

Parameter and statistic	Baseline	Post coactivation	Gain, baseline–post coactivation (%)	Gain, baseline–post coactivation (difference)
Daily practising (h)				
Pearson *r*	−0.789	−0.6253	0.3223	0.3074
P-value	0.001*	0.0168*	0.2611	0.2850
Began piano playing (age years)				
Pearson *r*	0.4193	0.4658	−0.3737	−0.2743
P-value	0.1356	0.0932	0.1881	0.3426
Total years playing (years)				
Pearson *r*	0.4168	0.2446	0.2171	0.3118
P-value	0.1381	0.3993	0.4560	0.2779
Began playing >3 h (age years)				
Pearson *r*	−0.2493	−0.3842	0.5354	0.5113
P-value	0.3900	0.1750	0.0485*	0.0616†
Playing >3 h (years)				
Pearson *r*	−0.0948	−0.2215	0.5110†	0.4580
P-value	0.7472	0.4466	0.0619	0.0995

*$P < 0.05$, significant two-sided correlations; †$P < 0.1$, correlations suggesting a trend only, two-sided).

revealed no significant differences regarding their individual gain in tactile performance (univariate ANOVA: $F_{1,12} = 1.498$; $P = 0.244$). However, in all subjects, the left IF remained unchanged after the coactivation protocol, confirming the local nature of coactivation-induced changes with no indications for generalization across hands [repeated measures ANOVA pre-post coactivation: $F_{1,13} = 0.125$; $P = 0.729$ (pianists); $F_{1,15} = 1.518$; $P = 0.237$ (non-musicians)]. Again, linear correlation analysis revealed a significant correlation between post-thresholds and daily hours of piano practising ($r = -0.625$; $P = 0.01$, Table 1) with no correlations of post-thresholds with the number of years of piano playing ($r = 0.244$; $P = 0.399$) or with the age that piano playing had started ($r = 0.465$; $P = 0.093$). In contrast, the individual coactivation-induced gain was correlated with the number of years of extensive (>3 h per day) piano playing ($r = 0.535$; $P = 0.048$), and with the age that extensive piano playing had started ($r = 0.511$; $P = 0.062$, Table 1), with no correlation for the total of years of casual playing <3 h per day. These results indicate that pianists that practised for many years for more than 3 h a day showed the largest coactivation-induced learning, while pianists that started later and practised more than 3 h a day benefited less from coactivation.

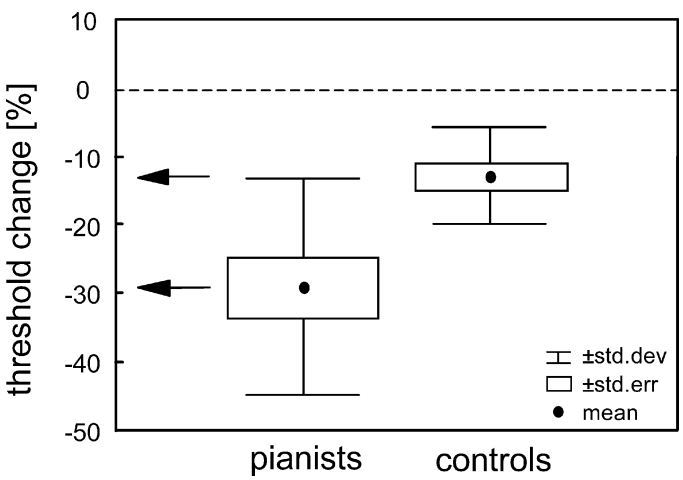

FIG. 4. Percentage changes of spatial discrimination thresholds of the right IF after coactivation. The coactivation protocol induced a significant reduction of discrimination thresholds in pianists (two-sided *t*-test, $P < 0.0001$) as well as in non-musicians (two-sided *t*-test, $P < 0.0001$). However, the mean percentage improvement in tactile discrimination abilities was significantly higher in pianists as compared with control subjects (two-sided *t*-test, $P = 0.02$), indicating a stronger capacity for plastic reorganizational changes induced by a Hebbian learning protocol.

Discussion

From a number of human studies, the musician's brain has been suggested to constitute a perfect model for neuroplasticity in auditory and motor domains (Schlaug, 2001; for review see Münte *et al*., 2002). However, less is known about adaptational processes in somatosensory systems as a consequence of extensive piano practising. We therefore studied altered sensory tactile perception in pianists as an indirect measure for the outcome of use-dependent cortical plasticity.

Our results show that spatial tactile acuity in professional pianists is significantly higher compared with a non-musician control group. The significant correlation of their individual thresholds with the daily practising duration suggests that the superior performance is related to their musical abilities (cf. Ericsson *et al*., 1993; Gaser & Schlaug, 2003). Piano playing *per se* has little to do with the aspect of tactile acuity, except for the case that professional playing is based on extreme usage of the fingers. In contrast, the enhanced discrimination abilities in blind Braille readers can be explained by the unusual and extensive use of the fingers to gather fine-scale spatial tactile information (Van Boven *et al*., 2000; Goldreich & Kanics, 2003). In fact, the acquisition of Braille reading is assumed to result particularly from extensive training of spatio-temporal events on the reading finger (Pascual-Leone & Torres, 1993; Van Boven *et al*., 2000; Goldreich & Kanics, 2003). Combined, our results demonstrate that professional piano players benefit from their daily routine by developing significantly reduced tactile discrimination thresholds, although piano playing in contrast to Braille reading is less obviously related to tactile acuity abilities.

To explain the lower thresholds in pianists, we assume that the intensive practising routine alters the input statistics for the fingertips. As a result, synaptic efficacy is modified, which in turn drives cortical reorganization. All these changes then alter the way in which sensory information is processed in somatosensory cortex leading, among others, to a lowering of spatial discrimination thresholds.

In the second series of experiments, we attempted to further improve the discrimination performance in pianists by a Hebbian learning protocol. Synchronous neural activity, which is believed to play a key role in driving plastic changes, was generated by coactivating a

restricted skin portion of the tip of the right IF (Godde *et al*., 1996, 2000; Pleger *et al*., 2001; Dinse *et al*., 2003b). In somatosensory cortex of adult rats, coactivation resulted in selective and reversible reorganization of receptive fields and cortical maps (Godde *et al*., 1996). To show that coactivation, which also alters the statistics of the tactile input, has perceptually meaningful implications, we recently assessed spatial tactile discrimination performance in human subjects before and after coactivation as a marker of plastic reorganization, which revealed a reversible lowering of thresholds (Godde *et al*., 2000). Combining fMRI measurements or measurements of somatosensory-evoked potentials with tactile discrimination assessment revealed a close correlation between the amount of coactivation-induced perceptual improvement and the degree of individual cortical reorganization (Pleger *et al*., 2001, 2003; Dinse *et al*., 2003b). Here we used the coactivation protocol to show that pianists had not reached their lower acuity limits. Mechanoreceptor density in the skin has been assumed to be related to two-point discrimination performance (Johansson & Vallbo, 1979). We are not aware of data suggesting that receptor density is altered in musicians. Consequently, our finding that discrimination thresholds in pianists were lower and could be further reduced by coactivation supports the view that their overall performance is likely to be mediated and determined by plastic adaptations of cortical processing dynamics rather than peripheral constraints such as receptor density.

In the coactivation protocol, cortical reorganization is driven in a task-free manner by manipulating the input statistics, without invoking training or cognitive factors. Similar to the lines of arguments provided in the context of piano playing, the Hebbian coactivation protocol is likely to modify synaptic efficacy between and within the cortical neuron pool representing the IF; for an account showing that dendritic spikes mediate a form of synaptic potentiation that does not require postsynaptic action potential firing in the axon, see Golding *et al*., 2002. As a chain of changes following coactivation, we suggest that the simultaneous activation on the skin of the IF alters synaptic transmission at a cortical level, which results in an enlargement of the finger representation in SI and SII (Pleger *et al*., 2001, 2003; Dinse *et al*., 2003b). Unfortunately, at present, little is known how cortical map changes translate to changes of perceptual parameters. According to these data, enlargement of cortical territory was associated with a lowering of spatial discrimination thresholds (Pleger *et al*., 2001, 2003; Dinse *et al*., 2003b), implying that coactivation leads to major changes of sensory information processing. Because of the passive, task-free nature of the coactivation protocol, there is little reason to assume that two-point discrimination is the sole parameter affected. In particular, a fundamental change in the way tactile information is processed does not rule out that some aspects of tactile information processing might become worse. According to unpublished data, the coactivation protocol affects many parameters of tactile perception. For example, while tactile acuity improves, localization abilities on the coactivated IF become impaired, with no changes in touch threshold (unpublished data). Evidence for a trade-off between localization and discrimination was also provided in a study of Braille readers (Sterr *et al*., 1998). Conceivably, enhanced spatial discrimination might emerge in parallel to impaired localization. For a detailed discussion of attention and the influence of stimulus numbers on passive learning and cortical reorganization, see Pleger *et al*., 2001. It should be emphasized that the same lines or arguments hold for the impact of piano playing on tactile processing. While not tested so far, we would expect that other parameters than two-point discrimination such as localization will be altered as well in highly trained musicians.

At a cellular level, metaplasticity is induced by synaptic or cellular activity, but it is not necessarily expressed as a change in the efficacy of normal synaptic transmission. Instead, metaplasticity is evident from a change in the ability to induce subsequent synaptic plasticity, such as long-term potentiation or depression (Abraham & Bear, 1996). Thus, metaplasticity is a higher-order form of plasticity related to the phenomenon of 'learning to learn'. Recently it was demonstrated that metaplasticity might in fact involve alterations in *N*-methyl-D-aspartate receptor functions (Philpot *et al*., 2003). Findings pointing to metaplasticity in humans have recently been demonstrated after amputation-induced reorganizations (Knecht *et al*., 1998).

To explain the enhanced learning capabilities in pianists, we suggest two non-exclusive possibilities. It is conceivable that *N*-methyl-D-aspartate receptor functions are altered in pianists due to the prolonged and sustained practising that, at a very general level, involve an unusually extensive processing of touch information. Alternatively, piano practising could lead to enlarged cortical finger representations. As a result, more cortical area and thus more processing resources, i.e. more synapses, are subject to modifications by the Hebbian coactivation, thereby increasing learning capacities. Such mechanisms might be similar to those proposed recently for fast and slow perceptual and motor learning (Karni, 1996).

Despite the already high-level performance in pianists, the Hebbian stimulation protocol induced a higher gain in discrimination abilities in musicians as compared with controls (Fig. 4). This implies stronger capacities for plastic reorganization in pianists, and points to enhanced learning abilities. Interestingly, the coactivation-induced gain in performance correlated with the number of years of extensive piano playing. This kind of metaplasticity suggests that extensive piano practising alters somatosensory information processing and sensory perception beyond training-specific constraints.

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Abbreviation

IF, index finger.

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