Motor skill training and strength training are associated with different plastic changes in the central nervous system

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Jensen, Jesper Lundbye, Peter C. D. Marstrand, and Jens B. Nielsen. Motor skill training and strength training are associated with different plastic changes in the central nervous system. J Appl Physiol 99: 1558–1568, 2005. First published May 12, 2005; doi:10.1152/japplphysiol.01408.2004.—Changes in corticospinal excitability induced by 4 wk of heavy strength training or visuo-motor skill learning were investigated in 24 healthy human subjects. Measurements of the input-output relation for biceps brachii motor evoked potentials (MEPs) elicited by transcranial magnetic stimulation were obtained at rest and during voluntary contraction in the course of the training. The training paradigms induced specific changes in the motor performance capacity of the subjects. The strength training group increased dynamical and isometric muscle strength by 31% \((P < 0.001)\) and 12.5% \((P = 0.045)\), respectively. The skill learning group improved skill performance significantly \((P < 0.001)\). With one training bout, the only significant change in transcranial magnetic stimulation parameters was an increase in skill learning group maximal MEP level \((MEP_{max})\) at rest \((P = 0.02)\) for subjects performing skill training. With repeated skill training three times per week for 4 wk, \(MEP_{max}\) increased and the minimal stimulation intensity required to elicit MEPS decreased significantly at rest and during contraction \((P < 0.05)\). In contrast, \(MEP_{max}\) and the slope of the input-output relation both decreased significantly at rest but not during contraction in the strength-trained subjects \((P < 0.01)\). No significant changes were observed in a control group. A significant correlation between changes in neurophysiological parameters and motor performance was observed for skill learning but not strength training. The data show that increased corticospinal excitability may develop over several weeks of skill training and indicate that these changes may be of importance for task acquisition. Because strength training was not accompanied by similar changes, the data suggest that different adaptive changes are involved in neural adaptation to strength training.

There is now increasing evidence suggesting that plastic changes in the primary motor cortex play an important role in skill acquisition. Motor skill learning has thus been demonstrated to be associated with anatomical and physiological changes within the primary motor cortex in primates and nonprimate animals \((31–33, 41, 53, 65)\). In humans, neuroimaging techniques and transcranial magnetic stimulation (TMS) have demonstrated that motor skill training induces changes in the organization of movement representations in the primary motor cortex in the form of expansion and increased excitability of the cortical representation of specific muscles (or movements) involved in the tasks \((10, 11, 17, 27, 30, 35, 43–45, 47, 48)\).

In contrast to skill acquisition, nonskill training or passive motor training is mainly reported to elicit no or only minor changes in excitability \((35, 45)\). For instance, Plautz et al. \((50)\) demonstrated in squirrel monkeys that movement repetition in the absence of motor skill acquisition was not sufficient to produce changes in cortical representational organization. On the basis of these findings, learning thus seems to be a prerequisite or an important factor in driving cortical representational plasticity related to motor experience. To fully acknowledge this hypothesis, however, it remains to be elucidated which aspects of motor experience relate to motor learning or how motor learning is to be defined.

Little is known about the neuronal mechanisms involved in the increased neuronal drive in the early stages of strength training, although it has been suggested that increased cortical drive to the spinal motoneurons may be of importance \((1)\). Strength increments arise as a consequence of numerous factors, but in many ways it would make sense to consider strength training as a kind of motor learning process. As reviewed by Carroll et al. \((8)\), strength training relates to motor learning because of the fact that athletes learn to produce muscle recruitment patterns associated with optimal performance of the specific task. It is thus likely that strength training in parallel with motor learning can lead to improved muscular coordination. Considering this, it would be reasonable to assume that similar plastic changes in the primary motor cortex as reported for acquisition of new motor tasks are also involved in the improved ability to generate force in the early stages of strength training.

Rempe et al. \((53)\) demonstrated in the rat that training of skilled reaching movements involving either a progressive increase of the maximal load (strength) or a control condition induced a similar degree of plastic changes in the motor

IN THE WORLD OF SPORTS MOST disciplines require some degree of both strength and motor skill for the athlete to be successful, and athletes often use a combination of resistance training and skill learning to optimize their performance. Whereas plastic changes in the central nervous system are well documented in relation to acquisition of new skills \((59, 61)\), such neural adaptations are generally reported mainly to take place in the initial stages of strength training \((21)\), and their significance for the increased strength compared with the well-documented muscular changes is still debated \((8, 16, 18, 20, 36)\).

plasticity; corticospinal tract; transcranial magnetic stimulation; skill learning; detraining

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cortical movement representations. This finding indicated that the observed plasticity related to the development of skilled movements rather than increased muscle strength per se (64).

Electron microscopy of the ventral spinal cord showed that rats training power reaching had a significantly greater density of synapses onto spinal motor neurons than both a normal reaching group and a nonreaching control group, which led to the suggestion that strength training is supported by spinal cord synaptogenesis (64).

The only study that has addressed the issue of supraspinal adaptations to strength training in human subjects observed a decrease rather than an increase in corticospinal excitability in relation to strength training index finger abduction (7). Isolated finger abduction may, however, have little relevance to normal strength training, which often involves complex exercises involving large proximal muscle groups in combination with distal muscle groups, as is seen in biceps curl. We thus speculate that “normal” strength training involving more complex muscle recruitment patterns and a more prominent role of muscular coordination may have the potential to induce learning-related phenomena in the central nervous system.

In the present study, we used TMS to investigate whether 4 wk of strength training of the biceps brachii (BB) muscle is associated with increased excitability of corticospinal projections to the muscle. Similar measurements were also made in relation to the acquisition of a difficult motor task requiring precise control of elbow joint movements. We found that increased corticospinal excitability was only observed in relation to acquisition of the difficult motor task, whereas 4 wk of strength training that increased the dynamical strength of the biceps muscle by 31% caused a depression of corticospinal excitability at rest. A significant correlation between the changes in corticospinal excitability and motor performance was only observed for the skill-trained subjects.

METHODS

Participants

The experiments were performed on 24 healthy volunteers (11 women, 13 men) with an average age of 25 ± 5 yr. All subjects gave their written, informed consent to the experimental procedures, which were approved by the local ethics committee. The study was performed in accordance with the Declaration of Helsinki. All subjects were right-handed according to the Edinburgh Handedness Inventory (42), and no volunteers had any history of neurological disease.

The subjects were randomly allocated to three groups, two different motor training groups and a control group (n = 8, 5 men and 3 women) that did not train but participated in all testing procedures. Motor training consisted of either strength training (n = 8, 4 men and 4 women) or visuomotor skill learning (n = 8, 4 men and 4 women). There were no age differences between the three groups.

General Organization of the Study

Thirteen training sessions were performed by the participants over a 4-wk training period. At the beginning of the training period, after 2 wk, and at the end of the training period, each volunteer participated in a longer lasting experimental session. These experimental sessions involved 1) strength tests evaluating the maximal voluntary dynamic and isometric elbow flexor muscle strength of the subjects, 2) an electrophysiological testing procedure involving peripheral electrical nerve stimulation and TMS at rest and during tonic contraction, 3) one training session of either motor skill training or strength training, and 4) repeated measures of TMS and peripheral electrical nerve stimulation after training. This experimental design aimed at investigating short-term adaptations to training defined as the effect of a single training session as well as long-term adaptations to training defined as the effect of training 2–4 wk. For every testing and training procedure involved in the study, subjects were familiarized with the equipment and the measuring procedures on separate occasions before data sampling. Six months after completion of the training, it was possible to retest four of the subjects in the skill learning group to investigate reversibility of the training-induced phenomena. At this occasion, TMS and peripheral electrical nerve stimulation were applied.

Strength Tests

At the beginning of the testing procedure, the subjects’ maximal dynamic muscle strength was determined as one-repetition maximum (1 RM) biceps curl and the maximal isometric muscle strength was determined as the peak torque of a maximal voluntary contraction (MVC). For the 1 RM test, the subjects were standing in a standardized position at a custom-made biceps curl bench. Before the test, subjects performed a warm-up procedure and received instructions in how to perform unilateral biceps curl. During the test, the subject was handed a submaximal weight and performed one extension-flexion cycle of the elbow joint with the forearm supinated. As this task was completed, the load increased progressively until failure of the biceps curl occurred. 1 RM was determined as the highest load at which the task was fulfilled. In all tests, the subject performed 5–8 trials with increasing load depending on maximal strength.

Because of a large similarity between the 1 RM test and the strength training paradigm, it was hypothesized that the 1 RM test could be influenced by effects of learning (28, 58). Therefore, in addition to the 1 RM test, a MVC test was used as a control to validate any training-induced alterations in the maximal strength of the subjects. For the MVC test, subjects were seated in a custom-built rigid chair and firmly strapped to an upright backrest. The elbow was flexed to 90° and the forearm was supinated and rested on a table. A nonelastic strap around the wrist was connected to a strain-gauge transducer. Subjects were instructed to perform a maximal contraction of the right arm elbow flexors by increasing the torque to maximum within a few seconds and then to exert maximal torque for 2 s, while maintaining the standardized position. Verbal encouragement and visual feedback of the torque exerted were provided. Typically four or five successive trials were performed until the peak torque did not increase any further. The peak torque recorded in either of the trials was taken as the MVC. Strength measurements were only obtained during the first and the last of the three testing sessions.

Electrophysiological Testing Procedures

After completing the strength tests, subjects were seated in an armchair for the electrophysiological testing procedure involving TMS and peripheral electrical nerve stimulation. Subjects were positioned with the head supported and the examined right arm fixed on a cushioned arm support, the shoulder joint flexed 45° and the elbow joint almost fully extended.

Data recording. Surface electrodes were used for electrical nerve stimulation and recording of electromyographic activity (EMG). EMG activity was recorded from the BB and triceps brachii muscle by nonpolarizable bipolar Ag-AgCl electrodes (1 cm², interelectrode distance 1 cm). The amplified EMG signals were filtered (band-pass, 25 Hz to 1 kHz), sampled at 2 kHz, and stored on a personal computer for offline analysis. Furthermore, the EMG was full-wave rectified, integrated, and displayed to the subject as visual feedback during tonic contraction.

TMS. Motor evoked potentials (MEPs) were evoked by TMS of the left hemisphere (contralateral) motor cortical arm area at the hot spot for activation of BB by using a magnetic stimulator (Magstim 200, Magstim) with the capability to deliver a magnetic field of 2 T for 100
Through the figure-of-eight coil (loop diameter, 9 cm; type no. 8106), the MEPs were recorded from BB and triceps brachii EMG. Before TMS stimulation, a cap with a coordinate system marked on it was placed on the subject’s head and the hot spot for activation of BB was identified through a motor cortical mapping procedure. The hot spot was identified as the coordinates in which the lowest intensity of magnetic stimulation was required to evoke a MEP of 50 μV peak-to-peak amplitude in at least three of five consecutive trials (55).

The coil was oriented and positioned with the handle of the coil pointing backward to induce posterior to anterior current flow across the primary motor cortex, and the coil was secured to ensure that the same area of the cortex was stimulated throughout the experiment. Single pulse stimuli were delivered at an interstimulus interval of 4 s. During the experiment, MEPs were displayed and averaged online for visual inspection as well as stored on a computer for offline analysis.

At first, TMS was applied at rest. Magnetic stimuli were applied at 10–15 different stimulation intensities from 0.6–2.0 of the minimal stimulation intensity required to elicit MEPs (MEPthreshold) with 10 stimulations at each intensity. The sequence of intensities was randomly varied. Responses were measured as the peak-to-peak amplitude and expressed as a percentage of the corresponding maximal M-wave (Mmax). For each stimulation intensity, responses were averaged and the peak-to-peak amplitude was plotted until a stimulus-response curve with a well-defined MEPthreshold, slope, and maximal level (MEPmax) had been obtained. Figure 1 illustrates an example of the obtained BB MEPs, their increase with stimulus intensity, and the creation of a stimulus-response curve.

After a pretraining stimulus-response curve was obtained at rest, the maximal amplitude of the integrated BB EMG was determined and a TMS stimulus-response curve was obtained during tonic contraction of BB corresponding to 5% of maximal amplitude of the integrated EMG. This procedure was followed by a training session. Immediately after training, two additional stimulus-response curves were generated during tonic contraction and at rest.

**Peripheral Electrical Nerve Stimulation**

Before generation of a stimulus-response curve, maximal compound muscle action potentials of BB (maximal M-waves or Mmax) were elicited by bipolar surface electrical stimulation of the musculocutaneous nerve. A custom-built stimulator applied current to the nerve via ball-shaped electrodes fixed in the axilla with an interelectrode distance of 4 cm. The intensity of stimulation was increased from a subliminal level until there was no further increase in the peak-to-peak amplitude of the M-wave with increasing intensity. Mmax was determined by using this procedure before the generation of

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**Fig. 1.** Transcranial magnetic stimulation (TMS) procedure and generation of stimulus-response curves. When transcranial magnetic stimulation is applied over the motor cortex, contraction of contralateral muscles may be elicited because of activation of corticospinal cells and spinal motoneurons (A). B: typical surface EMG recordings of motor evoked potentials (MEPs) of the biceps brachii (BB) obtained in a subject resting (left) and exerting a voluntary tonic contraction of 5% of maximum voluntary contraction integrated EMG (right). Responses to stimuli of increasing strength are aligned. For each stimulating intensity, a sequence of 10 stimuli (<0.25 Hz) was delivered and the peak-to-peak amplitudes of the elicited MEPs were averaged and normalized to the corresponding maximal M-wave (Mmax). When all mean MEP amplitudes are plotted against stimulation intensity, a stimulus-response curve is obtained (C). Each stimulus-response curve is characterized by a set of parameters including minimal stimulation intensity required to elicit MEPs (MEPthreshold), peak slope, maximum level of MEP amplitude (MEPmax), and stimulus intensity at which the MEP amplitude size is 50% of MEPmax (S50). Before training, 2 stimulus-response curves were obtained at rest and during a tonic contraction, and immediately after training 2 additional stimulus response curves were obtained during tonic contraction and at rest. For comparison, all stimulation intensities were normalized to the individual pretraining motor threshold of the baseline test.
every stimulus-response curve (54) by application of TMS. The purpose of this procedure was to normalize the TMS data to the corresponding individual $M_{\text{max}}$, thereby making it possible to compare the different test sessions.

**Strength Training**

The strength training group performed heavy-load strength training of the dominant right arm elbow flexors three times per week for 4 wk. Training sessions never took place on consecutive days. During training, subjects were seated in an armchair with the right arm positioned on an arm support, the shoulder joint flexed, and the forearm supinated. This position was chosen to match the strength training paradigm anatomically and kinematically in the sense that only simple elbow flexion-extension movements were allowed. Because of the setup, flexion was caused by eccentric contraction of the elbow flexors whereas extension primarily was caused by eccentric contraction of the same muscles.

For the skill training, a purpose-build computer program was used. The position of the elbow joint was measured by a SG110 twin axis elbow goniometer (Biometrics) and displayed as a circular cursor on a computer screen in front of the subject. On the screen, a series of six figures were presented in a randomized order, each of them sketching a different series of combinations of flexion and extension movements. The cursor automatically moved from the left to the right at a velocity that was predetermined for each screen paradigm. Subjects were able to control the vertical movement of the cursor by varying the position of the elbow joint, thereby tracking the presented figures as precisely as possible. During extension of the elbow, the cursor moved to the bottom of the screen, whereas during flexion the cursor moved to the top of the screen. Figure 2 illustrates the different screen figures presented to the subjects. Time over the screen varied between 1.88 and 3.14 s, and the range of movement varied between the six different figures as well. After 2 wk of training, two additional screen figures were introduced to ensure maximal attention to the task. For this purpose, all training sessions were also monitored by a supervisor. Each training session consisted of four sets of 4-min continuous tracking with 1 min of rest in between the sets.

During the first, fifth, ninth and thirteenth training session, goniometer data were digitally sampled at 2,000 Hz with a QNX real-time analog-to-digital capturing system for calculation of performance. For each set of 4 min, training goniometer data were averaged for each screen figure and superimposed on the optimal track. Motor performance was quantified as the total distance between the performed and the optimal track in 10 different points.

**Data Processing**

Measures of corticospinal excitability include, among other parameters, MEP amplitudes, $M_{\text{threshold}}$, and stimulus-response curves (14, 54). To characterize the stimulus-response function, the stimulus-response curve data were quantified through several procedures. The data of each curve were fitted with a three-parameter sigmoid function

$$\text{MEP}(s) = \frac{\text{MEP}_{\text{max}}}{1 + e^{m(S - S_{50})}}$$

where $S$ is stimulus intensity, $\text{MEP}_{\text{max}}$ represents the maximum MEP defined by the function, and $m$ is the slope parameter of the function. $S_{50}$ is the stimulus intensity at which the MEP amplitude size is 50% of $\text{MEP}_{\text{max}}$. This equation has previously been referred to as an analog of the Boltzmann equation and has been used to fit data points by the Levenberg-Marquard algorithm (6, 7, 14, 29, 54). From this analysis, the maximal amplitude of the stimulus-response curve $\text{MEP}_{\text{max}}$ was obtained. Furthermore, every curve was characterized by the slope parameter of the function and the $M_{\text{threshold}}$. The slope was calculated for the steepest part of the curve (i.e., at $S_{50}$), indicating the maximal increase of MEP amplitude with increasing stimulator intensity. Because the $M_{\text{threshold}}$ is not an explicit parameter of the equation and cannot be directly derived, it was calculated by using linear regression analysis. The data points on the steepest part of the curve were fitted by a straight-line regression formula ($y = a + bx$) and the baseline activity ± 1 SD were included in another linear regression. $M_{\text{threshold}}$ was then calculated as the intercept between these two regression lines.

For comparison and to be able to pool group data, all stimulus intensities were normalized to the resting or tonic $M_{\text{threshold}}$ of the individual stimulus-response curves obtained pretraining on the day of the first training session. Normalization to $M_{\text{threshold}}$ of the initial test was preferred because an analysis based on this procedure could detect whether stimulus-response curves were shifted left or right as a
consequence of training. It has previously been demonstrated that the sigmoidal function parameters can be obtained reliably in testing sessions conducted on different days (9).

Statistics

Before statistical comparison, all data sets were tested for normal distribution by a Kolmogorov-Smirnoff test. Changes in maximal strength and motor skill performance were tested by using paired t-tests for each of the three groups.

The stimulus-response curve parameters $\text{MEP}_{\text{threshold}}$, $\text{MEP}_{\text{max}}$, slope, and $S_{50}$ were analyzed by comparing pre- and postraining values in each of the three testing sessions. Resting and contraction values were analyzed separately for each of the three groups by paired t-tests, and a criterion of $P < 0.05$ was used. Significant $P$ values are marked with an asterisk.

Long-term adaptations to training were investigated by comparing postraining data from the three testing sessions with repeated-measures ANOVA. For multiple-comparison analysis, Tukey’s test was used for all pairwise comparisons between the group mean responses. Data are presented as means ± SE unless reported otherwise. Correlation between changes in the neurophysiological parameters and changes in motor performance capacity was tested using the Pearson’s product-moment correlation test.

RESULTS

Changes in Muscle Strength and Motor Performance

At the end of the training period, the strength training group displayed a significant improvement in both maximal isometric and dynamic muscle strength. After 4 wk of strength training, the group average maximal dynamic strength increased significantly by 31.2% from 10.5 ± 2 to 13.8 ± 1.8 kg ($P < 0.001$). MVC also increased significantly by 12.5% from 21.9 ± 2.7 to 24.8 ± 2.3 N•m ($P = 0.045$). The maximal dynamic as well as isometric muscle strength of the skill learning group and the control group remained unaltered. Skill learning group mean 1 RM was 12.9 ± 1.7 before and 12.9 ± 1.9 kg after the training period, whereas MVC was 25.1 ± 2.5 before and 24.7 ± 2.6 N•m after training. 1 RM in the control group decreased slightly from 12.4 ± 1.6 to 12.2 ± 1.6 kg. MVC in the control group was 21.6 ± 2.5 N•m before training and 21.7 ± 2.2 N•m after the training. These results imply that the strength training paradigm caused significant improvements of the subjects’ maximal muscle strength. Neither the skill learning paradigm nor the experimental procedures induced changes in the maximal strength of the subjects.

The level of performance was tested in the subjects in the skill learning group during the first, fifth, ninth, and thirteenth training sessions that the long-term improvement of motor performance capacity over the 4 wk was highly significant ($P < 0.001$), which is also evident from Fig. 4.

TMS Measurements

The TMS measurement aimed at investigating both short-term and long-term adaptations to the motor training paradigms. None of the control group measurements showed any significant changes during the whole period. The measurements from the control group will therefore not be considered further.

Short-term adaptations to training. Figure 5 illustrates measurement before and after one training session at rest and during tonic contraction on the day of the first, the seventh, and the final training session. Because only the skill learning group subjects exhibited any significant short-term changes in response to single training sessions, only the results of this group are illustrated.

In the skill learning group, there was a significant effect of the first training session. At rest, the MEPs were generally facilitated after training, and this was reflected in a significant increase of $\text{MEP}_{\text{max}}$ (pretraining = 3.89 ± 0.8% of $M_{\text{max}}$ to postraining = 6.03 ± 0.91% of $M_{\text{max}}$; $P = 0.02$). As an effect of training, the $\text{MEP}_{\text{threshold}}$ seemed to decline and the slope seemed to increase; none of these alterations were, however, significant. $S_{50}$ remained unchanged. The same pattern of changes was seen on the day of the seventh and the last training sessions (Fig. 5, B and C). However, none of these changes were significant. The short-term effect of training thus seemed to be largest in response to the first training session.

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The same tendencies as those seen at rest were evident during tonic contraction. As shown in Fig. 5, D, E, and F, MEPmax also tended to increase after training during tonic contraction. However, none of the changes after training were significant in any of the three testing sessions. Strength training did not induce any significant short-term changes in the TMS stimulus-response curves.

**Long-term adaptations to training.** The long-term adaptations to training are defined as the differences that occur when comparing the pretraining values obtained in the baseline test, the 2-wk test, and the 4-wk test. The adaptations that occurred after 2 and 4 wk of training are illustrated in Fig. 6.

For the skill learning group, MEPmax at rest increased from $3.9 \pm 0.8$ to $6.9 \pm 1.5\%$ of $M_{\text{max}}$ after 2 wk ($P = 0.04^*$) and $6.8 \pm 1.1\%$ of $M_{\text{max}}$ after 4 wk of training ($P = 0.046^*$). MEPthreshold decreased from $48.7 \pm 4.8\%$ of maximal stimulator output in the baseline test to $42.5 \pm 5\%$ after 2 wk ($P = 0.07$) and $41.2 \pm 5.1\%$ after 4 wk ($P = 0.03^*$). No other parameters exhibited any significant changes.

MEPmax also increased during tonic contraction in response to training [from $33.2 \pm 4.3\%$ of $M_{\text{max}}$ to $52.5 \pm 10.6\%$ ($P = 0.04^*$] after 2 wk and $50.2 \pm 10\%$ after 4 wk of training ($P = 0.07$). MEPthreshold decreased from $32.7 \pm 1.4\%$ of maximal stimulator output initially to $29.5 \pm 2\%$ after 2 wk ($P = 0.16$) of training and $28.1 \pm 1.5\%$ after 4 wk of training ($P = 0.04^*$). No other parameters exhibited any significant changes during tonic contraction.

For the strength training group, there was no change of MEPmax at rest after the first 2 wk of training. After 4 wk of training, however, MEPmax decreased significantly from the initial $6.5 \pm 1.4$ to $3.8 \pm 1.5\%$ of $M_{\text{max}}$ ($P = 0.01^*$). The slope of the stimulus-response curves decreased from $0.24 \pm 0.07$ to $0.17 \pm 0.06$ after 2 wk of training ($P = 0.11$) and to $0.11 \pm 0.04$ after 4 wk of strength training ($P < 0.01^*$). Similar...
changes were observed during tonic contraction; these changes did not, however, reach a statistically significant level.

Detraining

It was possible to test four of the eight subjects in the skill training group again 6 mo after they had completed the training period. The results from the four subjects are illustrated in Fig. 7. As can be seen, MEP$_{\text{max}}$, MEP$_{\text{threshold}}$, and the slope of the recruitment curve were almost similar to the measurements before the training. Because of the small number of subjects the data were not subjected to a statistical analysis. The material was also too limited to determine a difference in the performance of the task at the three occasions (before training, after training, and 6 mo after training).

Correlation Analysis

The correlation analysis using the Pearson product moment correlation test showed a significant correlation between the long-term changes in the skill learning group TMS parameters and the motor performance (skill) of the subjects. The correlation analysis of the measurements obtained at rest (A, C, E) and during tonic contraction (B, D, F) showed a correlation coefficient of $R = 0.431$ ($R^2 = 0.186$) and $P = 0.006^*$ for skill and MEP$_{\text{max}}$, whereas the analysis of skill and MEP$_{\text{threshold}}$ showed a correlation coefficient of $R = 0.486$ ($R^2 = 0.236$) and $P = 0.001^*$. In contrast to skill learning, there was no correlation between the neurophysiological changes and the increase of maximal strength observed in the strength training group.

DISCUSSION

In this study, we have demonstrated that acquisition of a visuomotor skill is associated with increased corticospinal excitability over several weeks. Strength training for a similar amount of time was in contrast associated with decreased corticospinal excitability.

Increased Corticospinal Excitability in Relation to Acquisition of a Visuomotor Task

Increased corticospinal excitability and expansion of the cortical representation of hand and finger muscles in relation to the acquisition of motor tasks is well documented (45, 46, 48). The present data demonstrate that similar changes also take place for proximal arm muscles in relation to acquisition of a visuomotor tracking task requiring precise control of the elbow flexor muscles. The excitability changes are thus not restricted to distal finger muscles, which are generally believed to receive a more significant corticospinal control than proximal muscle.
groups (52). This is of importance in relation to many forms of sports in which large proximal muscle groups are more important for the performance than the smaller distal muscle groups.

It is not possible from our study to determine the underlying physiological mechanisms responsible for the changes in corticospinal excitability. Changes in the spinal motoneurons, corticospinal neurons, subcortical neurons contacted by corticospinal tract fibers and projecting to the spinal motoneurons, as well as intracortical inhibitory and/or excitatory interneurons may be involved. However, previous studies have demonstrated that changes within the primary motor cortex are involved in the expansion of the cortical representation of the muscles as well as the increased corticospinal excitability changes demonstrated by recording of the input-output relation for the MEP as in the present study (4, 5, 9, 12–14, 23, 49, 52, 56, 57, 61). Experiments in primates and rats give strong support to this (15, 32, 40, 41, 60, 61).

Pascual-Leone et al. (45) demonstrated changes in the representation of hand muscles in the course of a 5-day training program involving acquisition of a finger motor skill, and Pascual-Leone et al. (46) added information to this study by including measurements during 28 days of training. The results demonstrated that the main improvement in the performance occurred during the first week of (quite intense) training after which the subjects continued to perform the task at a high level in the rest of the training period. The expansion of the cortical representation of the tested muscle was also mainly seen in the first week of training after which it gradually declined. We similarly found that the corticospinal excitability mainly increased within the first 2 wk of training, which was also the period where the main improvement in the performance of the task was observed. Some improvement of the performance of the task was still observed between the second and fourth weeks, but this was not accompanied by any changes in corticospinal excitability. This is in line with the idea that the increased corticospinal excitability is involved in the early acquisition of the visuomotor skill is not necessary for the skilled performance of the task as such. Convincing evidence of a crucial role of the motor cortex in early acquisition of motor skills has also been provided by Muellbacher et al. (38), who observed that the retention of motor learning could be blocked by repetitive TMS over the primary motor cortex in the early stages of learning. The exact time course of the changes in corticospinal excitability probably reflects the complexity of the task and the intensity of the training. This likely explains why the corticospinal excitability declined in the study by Pascual-Leone et al. (46) in the third and fourth weeks of training, whereas we observed no change. Evidence for a continuous reorganization in the primary motor cortex over several weeks has also been obtained in relation to the acquisition of a finger sequence learning task using brain imaging (30, 63).

Changes in Corticospinal Excitability in Relation to Strength Training

Several studies have suggested that strength training is associated with increased neuronal drive to the muscles: 1) Significant increases in strength precede muscular hypertrophy in the course of a strength training program (25, 28, 34, 39, 51). 2) “Cross education,” whereby movements contralateral to the trained limb exhibit increased strength, has been observed in a number of studies (19, 26, 37, 39). 3) Subjects who train imaginary muscle contractions have been shown to exhibit significant MVC increases (Refs. 66, 67; see, however, Ref. 24). 4) Several studies have reported increased maximal EMG recorded from the trained muscle after a period of training and used this to infer an increased neuronal drive to the muscles (2, 24, 37, 39).

A few studies have also argued against any changes in neuronal drive in relation to strength training. Using twitch interpolation to evaluate the voluntary drive to the muscle has thus generally shown that subjects are able to voluntarily activate the muscle almost to its maximal capacity before training and that no or only minor changes occur in relation to strength training (3, 22, 24, 62).
A number of studies have reported various adaptations in the central nervous system in relation to strength training. Aagaard et al. (1) demonstrated significant increases of evoked H-reflex and V-wave responses during maximal contraction after 14 wk of strength training and suggested that this reflected increases in descending motor drive from higher centers leading to increased α-motoneuronal excitability. However, in the present study we found no evidence of increased corticospinal excitability either at rest or during voluntary contraction of the muscle. In line with a recent study by Carroll et al. (7), we actually observed a decrease of corticospinal excitability. In rats, Remple et al. (53) have also found that reorganization of the movement representation within the motor cortex is similar, whether the rats perform the movements against a low or a high load. There is thus no evidence that stronger muscles are related to a larger representation of the muscles in the primary motor cortex. From our study, we cannot decide whether the observed decrease in MEPmax and the slope of the input-output relation is explained by changes at a cortical or subcortical level. In the study by Carroll et al., MEPs evoked by transcranial electrical stimulation (TES) showed similar changes after strength training as MEPs evoked by TMS. Because TES is assumed to be only little influenced by cortical excitability changes, this observation favors a subcortical mechanism, although it should be pointed out that the low sensitivity of MEPs evoked by TES to cortical excitability changes mainly applies for small MEPs, whereas the changes in the MEP after strength training was mainly seen for large MEPs in the study by Carroll et al. (7) as well as in the present study. In the present study, a significant depression of the MEPs after strength training was only observed at rest.

Carroll et al. (7) observed no changes in the MEPs at rest, but only during stronger contractions, whereas we only found significant changes at rest (a decrease in MEPmax was observed also during voluntary contraction, but it did not reach a significant level; this is in all likelihood explained by the higher variability of the recordings during voluntary contraction compared with rest). This discrepancy may be explained either by the different muscles being studied (Carroll et al. studied the first dorsal interosseus muscle), differences in the training design (the subjects in the study by Carroll et al. performed 4 times 6 abduction-adduction movements against external loads 3 times per week), or the MEP measurements (Carroll et al. investigated contraction levels up to 60% of MVC). Carroll et al. suggested that the decrease in the MEP size in their study was most easily explained by changes in the firing rate of the spinal motoneurons and/or their intrinsic firing properties. The findings in the present study do not exclude that such changes may occur in relation to strength training but suggest that other changes, such as changes in the excitability of cortical and/or spinal neurons and the transmission across synaptic connections between corticospinal fibers and spinal neurons, may also occur.

We did not observe any correlation between the changes in MEPmax and the increased muscle strength in the subjects. Although this negative finding should not be overinterpreted, it does question whether changes in corticospinal excitability have any functional significance for the increased muscle strength.

Is the Ability to Generate Large Force Not a Skill?

A 4-wk strength training program is usually considered to be too short for any structural muscular changes to take place, but we cannot fully exclude that some changes did take place in the muscles in our study and thus explain at least partly the increased muscle strength in the subjects. Nevertheless, most studies agree that increased neuronal drive is manifest very soon after the onset of strength training and is responsible for the main part of the initial gain in muscle strength. Then why did we not see similar changes in the MEPs as during the visuomotor skill training? Does this imply that the initial strength gain during strength training is not explained by the neuronal adaptations involved in learning and optimizing a skill? We do not think so. There are several factors that distinguish learning the visuomotor task and “learning” to generate maximal force: 1) novelty of the task, 2) visual feedback, 3) complexity of the task, and 4) pattern of somatosensory feedback related to the training. We find it likely that changes in the MEP and expansion of the cortical area might be involved when subjects are forced to use visual feedback to improve their ability of generating force as quickly and possibly also as precisely as possible. This would be of clear relevance to most sports activities, where it is not only important to be able to generate large force, but also to do it at a precise time and with maximal precision.

In conclusion, these experiments have demonstrated that increased corticospinal excitability occurs over the course of several weeks of skill learning and that these changes seem to be closely related to the acquisition of new visuomotor skills. Such changes do not occur in relation to strength training. In contrast, strength training was associated with decreased corticospinal excitability at rest, which was not correlated to the increased muscle strength. The findings in the study thus emphasize the role of plastic changes in the corticospinal pathway in the acquisition of new motor skills but question whether similar changes play a role in possible neuronal adaptations to muscle strength training.

GRANTS

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REFERENCES

3. Allen GM, Gandevia SC, and McKenzie DK. Reliability of measurements of muscle strength and voluntary activation using twitch interpola-


