HIGHLIGHTED TOPIC | Neural Changes Associated with Training

Changes in muscle coordination with training

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Carson, Richard G. Changes in muscle coordination with training. J Appl Physiol 101: 1506–1513, 2006. First published August 3, 2006; doi:10.1152/japplphysiol.00544.2006.—Three core concepts, activity-dependent coupling, the composition of muscle synergies, and Hebbian adaptation, are discussed with a view to illustrating the nature of the constraints imposed by the organization of the central nervous system on the changes in muscle coordination induced by training. It is argued that training invoked variations in the efficiency with which motor actions can be generated influence the stability of coordination by altering the potential for activity-dependent coupling between the cortical representations of the focal muscles recruited in a movement task and brain circuits that do not contribute directly to the required behavior. The behaviors that can be generated during training are also constrained by the composition of existing intrinsic muscle synergies. In circumstances in which attempts to produce forceful or high velocity movements would otherwise result in the generation of inappropriate actions, training designed to promote the development of control strategies specific to the desired movement outcome may be necessary to compensate for protogenic muscle recruitment patterns. Hebbian adaptation refers to processes whereby, for neurons that release action potentials at the same time, there is an increased probability that synaptic connections will be formed. Neural connectivity induced by the repetition of specific muscle recruitment patterns during training may, however, inhibit the subsequent acquisition of new skills. Consideration is given to the possibility that, in the presence of the appropriate sensory guidance, it is possible to gate Hebbian plasticity and to promote greater subsequent flexibility in the recruitment of the trained muscles in other task contexts.

Activity-dependent coupling, the composition of muscle synergies, and Hebbian adaptation, are discussed with a view to illustrating the nature of the constraints imposed by the organization of the central nervous system (CNS). In the present review, consideration will be given to the nature of some of the constraints on muscle coordination and to the means by which their influence may be either ameliorated or consolidated by training. The emphasis will be on a small number of core concepts that are perhaps infrequently considered in this domain, rather than on a general coverage of neural adaptations to resistance training, for which a number of comprehensive reviews exist already (e.g., Ref. 18).

ACTIVITY-DEPENDENT COUPLING

Brain activity during functional movement tasks. During goal-directed movements, synchronization (coherence in the 2- to 14-Hz range) of the electromyogram (EMG) and cortical activity registered by high-density electroencephalography (EEG) is widely expressed across multiple motor and premotor areas (e.g., Ref. 17). These and related observations suggest that the transsynaptic spread of coherent activity through the motor network is an integral aspect of its function (cf. Ref. 54). Indeed, it is now apparent that activity-dependent coupling between neuronal oscillators is a generic characteristic of the brain. Importantly, the potential for activity-dependent cou-
pling is to a large extent independent of the underlying (structural) pattern of interconnections present between groups of neurons, and it is contingent primarily on their respective levels of activity (45, 46).

A body of evidence now exists to support the proposition that the required degree of muscle activation determines the distribution of brain activity associated with a functional movement task. The area of primary motor cortex that is activated increases with the rate of movement (4, 43, 51), and there is a close relationship between levels of motor output and the functional magnetic resonance imaging–registered brain activity present both in motor–function-related cortical fields and across the entire brain (16). Examination of the relationship between EEG-derived motor activity–related cortical potentials and voluntary muscle activation suggests that the magnitude of the signal recorded from sensorimotor cortex and supplementary motor area is contingent on the intensity of the contraction (48, 49). After the administration of repetitive transcranial magnetic stimulation, which increases the amplitude of motor potentials evoked subsequently in the target muscle by single–pulse transcranial magnetic stimulation, there occurs a corresponding increase in the excitability of corticospinal projections to other muscles of the same limb. This spread of reactivity appears to be mediated by intracortical mechanisms, in particular by changes in the excitability of interneurons mediating intracortical inhibition (36). Thus increases in the excitability of specific regions of motor cortex, whether induced by changes in the required level of muscle activation or by electromagnetic stimulation, lead to widely distributed alterations in cortical reactivity.

Synergies. The essence of coordination is the formation of “structural units”: groups of elements united in relation to a common goal (20). In this regard, it is evident that natural tasks seldom involve a single classically defined motoneuron pool and its motor units. More often a group of muscles or motor units will be involved. Synergies are defined operationally as mechanisms employed by the CNS to coordinate groups of motor units or muscles into functional assemblies (e.g., Ref. 55). Although muscle synergies appear to represent an elegant solution to the problem posed by the multiple degrees of freedom that characterize the output of the human motor system, their implementation necessarily requires that the motor centers in the brain instantiate highly organized patterns of facilitation and inhibition that are spatially, temporally, and functionally discrete and are tailored to the specific requirements of the task at hand.

The cortical representations of muscles overlap broadly (e.g., Refs. 25, 30), and activity in each region of cortex thus has the potential to influence the projections to a wide distribution of motor units. This is depicted schematically in Fig. 1 (top). The complex connectivity that exists between multiple frontal motor areas (37) also points to means by which interference may occur between the cortical representations of the focal muscles recruited in a movement task and brain circuits that do not contribute directly to the required movement (24, 44). In so much as purposeful action requires the focal recruitment of muscles in the context of a specific synergy, factors such as elevations in the rate of movement, which increase the distribution of cortical reactivity, have the capacity to disrupt coordination. Indeed, it has been proposed previously that the potential for interference between functionally proximal areas of the cerebral cortex is contingent on the degree to which these areas are activated (29) and that it is by this means that the efficiency with which motor actions can be generated dictates the stability of coordination (10).

Variations in the efficiency of motor actions. How is the construct of “efficiency” to be understood? For the present purposes it can be said to reflect the relationship between the level of task contingent activity in the cortical motor network and the consequential alterations in muscle force (cf. Ref. 23). Unit changes in the firing rate of the corticomotoneuronal cells that innervate the flexor muscles of the upper limb result in

![Diagram](image-url)

Fig. 1. Activity (Σ) in the region of cortex of cortex that projects to the focal muscles recruited in a movement task has the potential to influence brain circuits that do not contribute directly to the required movement (α, β, and χ). In the top row, the level of activity in the region of cortex of cortex (Σ) and the consequential levels of activity that are induced in the other brain areas (α, β, and χ) are represented by the intensity of the shading (deeper shading indicates greater activity). In the middle row, the relationship between the level of task contingent activity in the cortical motor network (Σ) and the consequential alterations in muscle force (i.e., the efficiency of the motor action) is represented before (A) and after (B) a period of training that increases the force-generating capacity of the skeletal muscle. After training, there is a reduction in the level of task contingent cortical activity that is required to achieve a specific movement outcome. In the bottom row, the corresponding levels of activation in the brain circuits that do not contribute directly to the required movement (α, β, and χ) are shown directly. EMG, electromyogram.
greater increases in torque than equivalent changes in the firing rate of cells that project to the extensor muscles (15). This is also consistent with the observation that a smaller proportion of flexor motor units must be activated to produce a given level of force (53). It can thus be said that the flexor muscles of the upper limb generate motor actions more efficiently than the extensor muscles. It is notable, therefore, that tasks that require synchronization of flexion movements with an external stimulus are performed in a more consistent fashion than otherwise equivalent tasks in which extension movements are emphasized (11, 13).

It follows from this line of reasoning that acute or chronic alterations in the efficiency with which motor actions are generated should have a corresponding impact on the quality of coordination. In this regard, it has been shown that alterations in the lengths of muscles, such as those that arise from changes in the posture of the limb, result in changes in the level of force that is generated for a given neural input (e.g., Ref. 21), and correspondingly, manipulations of posture have both predictable and reliable effects on the stability with which sensorimotor coordination tasks can be performed (11, 13). Of greater relevance in the present context is the observation that chronic changes in the strength of specific muscles, induced by a program of resistance training, also have a reliable influence on the stability of sensorimotor coordination. Carroll et al. (6) reported that increases in the strength of the muscles that extend the index finger lead to enhancement of the execution of a task that required that the extension phase of rhythmic movements be made in time with the beat of an auditory metronome. Typically, the performance of such tasks becomes highly variable, and the required pattern of coordination is compromised as the frequency of movement is increased. After 4 wk of focal resistance training, however, there was a distinct increase in the frequency at which the task could be performed in an accurate and stable fashion (6).

Are such changes in the stability of behavior mediated by trained induced alterations in the efficiency with which motor actions are generated? One direct consequence of resistance training appears to be an increase in the gain of the corticospinal pathway (8). After a training intervention of 4-wk duration, the level of input to the spinal motoneurons that is associated with a particular degree of muscle activation or joint torque is lower than that present before training (see also Ref. 27). In so much as there has been a modification of the relationship between the level of activity in the cortical motor network that is directly related to that specific task and the corresponding muscle force, a change in efficiency can thus be inferred.

Recent reports that the corticomotoneuronal synapse exhibits plasticity, and is subject to short-term modulation in response to voluntary activity (19, 40), raise the possibility of that chronic adaptations at this synapse may be induced by high-intensity training. It is perhaps more typical, however, to think of the changes in strength induced by resistance training in terms of intramuscular adaptations in contractile properties. In short, resistance training-mediated changes in protein mass and the [myosin heavy chain (MHC) isoform] composition of skeletal muscle fibers alter (i.e., increase) their intrinsic capacity to generate force in response to efferent neural drive. Certainly factors that (acutely) decrease the force-generating capacity of the peripheral musculature, such as muscle fiber damage induced by eccentric contractions require corresponding increases in cortical motor network activity to bring about equivalent behavioral outcomes (14). It seems reasonable to suppose therefore that, by virtue of the fact that there is a commensurate decrease in the descending efferent drive required to bring about an equivalent movement outcome (see Fig. 1), increases in the force-generating capacity of skeletal muscle fibers will result in a reduction of task contingent activity in the cortical motor network and thus in diminished interference mediated by activity-dependent coupling. As a result of training-induced intramuscular adaptations, therefore, the processes of instantiating task specific synergies in the motor centers of the brain, and the muscle coordination to which these synergies give rise, will be more robust than when before training muscle force was generated with lower efficiency.

THE COMPOSITION OF MUSCLES SYNERGIES

Stability and adaptability. To appreciate the potentially beneficial effects of increases in strength in complex natural tasks, it is necessary to also consider the context in which muscle actions are performed. Tasks encountered in daily living seldom involve a single muscle. The potential contribution of an increase in strength in a particular muscle, or group of muscles, to the performance of a particular movement task is constrained by the composition of the synergy within which the muscles are activated. Intrinsic synergies are conceived of as protogenic (literally, formed at the beginning) muscle recruitment patterns that generate our basic repertoire of movements. For example, rhythmic flexion and extension of the wrists require the alternating recruitment of muscles that have mechanically opposed lines of action. These movements are supported by neural circuitry that promotes the reciprocal activation of anatomical (as opposed to functional) agonist and antagonist muscles [e.g., flexor carpi radialis (FCR) and extensor carpi radialis (ECR)]. Abduction-adduction movements of the wrists can be brought about only via control strategies that inhibit the expression these protogenic muscle recruitment patterns (2, 9). Although the radial wrist extensor (ECR) and flexor (FCR) behave as classical antagonists during flexion and extension movements, they are activated together during abduction of the wrist. Although control regimes sufficient to generate rhythmic abduction-adduction movements can be instantiated in most circumstances, when task demands are increased, for example, by increasing the required rate of movement, reciprocal activation of the flexors and extensors becomes dominant as the more robust intrinsic synergies are expressed (31). Despite the fact that many muscle systems are characterized by intrinsic synergies, these patterns of activation do not necessarily always result in the most effective solution to task demands defined in an occupational or recreational setting (12).

The evident potential for task-dependent modulation of muscle recruitment patterns in the context of skill acquisition indicates that there is also a certain amount of flexibility in the composition of muscle synergies (e.g., Refs. 26, 47). Yet it is apparent that the CNS maintains a balance between the facility for adaptation in response to novel task requirements and the number of parameters with respect to which variations in motor output are expressed. Programs of training that involve the
activation of muscles in ways not favored by intrinsic synergies may in principal promote flexibility in the subsequent recruitment of these muscles in other task contexts and thus enhance their functional capabilities. It is evident, however, that only a small subset of all possible muscle combinations is employed in the regulation of movement. The muscle synergies represented by these combinations appear particularly sensitive to biomechanical factors, including the force-generating capabilities of the individual muscles acting on the limb (35) and their respective muscle moment arms. Necessarily, therefore, the subspace of possible muscle combinations that can be accessed during training is highly constrained.

An illustrative example. The nature of the constraints on training that are imposed by the presence of intrinsic muscle synergies may be illustrated by a sensorimotor coordination task that at first glance may appear to lack the complexity of movements that are employed in the course of daily living. Nonetheless, it affords a clear view of principles that apply more generally. When first asked to generate rhythmic abduction-adduction movements of the index finger (about the metacarpal-phalangeal joint) in time with the beat of a metronome, most individuals exhibit involuntary spontaneous transitions to rotary motion of the finger and ultimately to flexion-extension, as the frequency of movement is increased (28). The undesired behavior arises as a direct consequence of the fact that abduction-adduction movements of the fingers can be brought about only via complex neural control strategies that must serve to inhibit the expression of basal (i.e., intrinsic) muscle synergies. An analysis of musculoskeletal anatomy suggests that the side-to-side motion of the fingers demanded by the coordination task can be brought about by the action of muscles intrinsic to the hand: the first dorsal interosseus (FDI) and the first volar interosseus (FVI). Yet muscles originating in the forearm, which act primarily to flex and extend the finger such as extensor digitorum communis (EDC) and the index finger portion of flexor digitorum superficialis (FDS), also have the potential to contribute to abduction and adduction (e.g., Ref. 52). On initial exposure to the abduction-adduction task, efferent drive is not simply directed to the interossei; the extrinsic muscles originating in the forearm are also engaged. Because most individuals are incapable of directing focal motor commands to the intrinsic hand muscles alone as the frequency of movement is increased, and the force-generating capacity of the forearm muscles is substantially greater than that of the interossei, their recruitment ultimately results in motion that is dominated by their major moment arms: i.e., flexion and extension (12).

In a recent study (12; illustrated schematically in Fig. 2), we sought to assess the patterns of muscle coordination that are implemented by the CNS, not only on initial exposure to this task but also after an intensive training period. Five sessions, each consisting of 20 trials, were conducted on successive days. In each trial, the participants attempted to produce abduction-adduction movements as the frequency of a pacing metronome was increased. EMG activity was recorded from FDI, FVI, FDS, and EDC. By the final day of the training period, the frequencies more accurately matched the required profile (i.e., abduction-adduction), and they exhibited greatly increased temporal stability than those generated during initial performance. In the early stages of training, an alternating pattern of activation in the intrinsic hand muscles (FDI and FVI) was maintained, even at the highest frequencies. In contrast, as the pace of the movements was elevated, the activity in FDS and EDC increased in overall intensity, and it became either tonic or intermittent. As training proceeded, and performance improved, alterations in muscle coordination were expressed primarily in the extrinsic muscles (EDC and FDS). These changes took the form of increases in the postural role of these muscles, shifts to phasic patterns of activation, or selective disengagement of these muscles (12). Although performance of the task improved in every instance, the fact that the nature of the adaptive change was quite distinct for the various individuals who participated in the study, corroborates the view that the suppression of intrinsic muscle synergies can only be achieved via complex, and often idiosyncratic, neural control strategies. It seems reasonable to conclude that programs of training that engage muscles in patterns of activation that are not promoted by intrinsic synergies and thus require the development of novel strategies of control, also promote flexibility in the subsequent recruitment of these muscles in other task contexts. The evidence to be considered in the following section suggests, however, that when intrinsic muscle synergies are reinforced by repetitive and stereotypical (resistance) training regimes, enhancement of the facility to recruit the trained muscles in other task contexts cannot be assumed.

HEBBIAN ADAPTATION

Neurons that fire together wire together. Although synergies represent the building blocks of our repertoire of voluntary movements, the acquisition of novel motor skills is necessarily based on their recomposition. It is clear, however, that this process requires that highly refined patterns of descending control be instantiated, to counteract protogenic muscle recruitment patterns, subject to habitual reinforcement, that might otherwise interfere with the desired movement outcome. It would be surprising, therefore, if training movements that required the activation of muscles in habitual patterns were also able to promote their flexible recruitment in other task contexts.

In 1949, Donald Hebb (22) introduced the idea that connections between cortical neurons are strengthened to the degree that they are active simultaneously.

When an axon of cell A is near enough to excite a cell B and repeatedly or persistently takes part in firing it, some growth process or metabolic change takes place in one or both cells such that A’s efficiency, as one of the cells firing cell B, is increased.

The concept that “neurons that fire together, wire together,” as depicted schematically in Fig. 3A, is now a central tenet of developmental neuroscience, and it is supported by empirical evidence that for neurons that release action potentials at the same time, there is an increased probability that synaptic connections will be formed. Associations required by the eliciting “behavioral” context are thus retained, whereas others are eliminated. By the same token, it is assumed that uncorrelated activity diminishes functional connectivity. Although these processes are thought to play an important role in cognitive and linguistic development (e.g., Ref. 39), there are circumstances in which they can lead to undesirable consequences. In extreme examples such as epilepsy, neurons that
are activated synchronously during seizures exhibit chronic adaptations such as axonal sprouting. Hebbian adaptation may strengthen the neural response that is generated by a specific input; however, this is only useful if the elicited response is appropriate to the context in which the desired behaviour will ultimately be expressed. In circumstances in which a dissimilar response would be more appropriate, Hebbian reinforcement can have deleterious consequences.

It is now generally recognized that the effectiveness with which resistance training-induced adaptations transfer to other functional tasks depends on the similarity between the muscle coordination that is consolidated through the regular performance of the training exercise and that which is required to meet movement goals that are defined in the pursuit of other activities (e.g., Ref. 41). It is anticipated that positive transfer will occur in circumstances in which the specific muscle activation patterns reinforced through training are also those required in the alternative task context. In the event that the activation patterns reinforced by training are inconsistent with those required by the target behavior, negative transfer is likely to occur. We have proposed previously that the potential for negative transfer may in principle be reduced by the implementation of specific control mechanisms mediated by the higher brain centers (7). These may include the regulation of inhibitory intracortical pathways that are believed to mediate surround inhibition in the motor system (e.g., Ref. 50).

**Invited Review**

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**The mediating role of feedback.** Although Hebbian mechanisms appear to provide a promising basis on which to account for various aspects of neural adaptation, including long-term potentiation, it is now evident that this framework is not fully sufficient to account for changes in behavior without elaboration to encompass sensitivity to outcome information. In contemporary analyses (e.g., Ref. 38), consideration has been given to the means by which an inherently Hebbian adaptive process may be guided by superordinate control schemes, based on the provision of feedback on which potential outcomes may be discriminated. The key insight in this regard, which is of particular relevance in relation to adaptations to...
training (as illustrated schematically in Fig. 3), is the recognition that, in the presence of the appropriate sensory guidance, it is possible to gate Hebbian plasticity (e.g., Ref. 42).

In a recent experiment conducted in our laboratory (1), we examined the impact of resistance training on the coordinated production of force by older adults. Thirty individuals completed a visually guided aiming task to a range of targets that required the precise generation of isometric torque in 2 degrees of freedom (i.e., pronation-supination and flexion-extension) about the elbow, both before and after a 4-wk training period. Groups of six participants were allocated to two progressive [40–100% maximal voluntary contraction (MVC)] resistance-training (PRT) groups, to two constant low-load (10% MVC) training groups (CLO), and to one no-training control group. Separate groups of six participants in the PRT and CLO cohorts performed training movements that required either the generation of combined flexion and supination torques or the combined extension and supination torques. These specific combinations were selected because in combined flexion and supination the biceps brachii acts as an agonist in both degrees of freedom, whereas, in flexion and pronation, this muscle is an agonist for flexion but is an antagonist with respect to pronation. It was presumed therefore that, with respect to this muscle at least, the generation of combined flexion and supination would serve to reinforce an existing synergy, whereas combined flexion and pronation would require a novel strategy of control. In each case, the training movements were guided by the provision of continuous visual feedback of the level of torque currently being applied in each degree of freedom. A critical finding was that the improvements in the performance of the visually guided aiming task exhibited by the participants who trained with low loads were more consistent than those realized by the group that had trained with progressively increasing loads. Most notably, the group that generated combined flexion and supination during training with progressively increasing loads exhibited a decrease in performance (an increase in target-acquisition time) when a pure supination movement was subsequently required in the transfer task. No such deficits were observed for the group that performed precisely the same training combination at low loads.

With regard to the flexion-supination training group, when the level of torque required was relatively low (10% MVC), the provision of visual feedback of the training movement appears to have been sufficient to engender positive transfer to the aiming task. In contrast, in circumstances in which the level of torque required by the training task was substantial (40–100% MVC), there was evidence of negative transfer. These findings are amenable to interpretation in terms of a Hebbian referenced analysis (e.g., Ref. 56). In this regard, the (flexion-supination) training task can be characterized in terms of the operation of two concurrent processes. It would be anticipated that the frequent repetition of a recruitment pattern subserved by an intrinsic muscle synergy would further consolidate functional connectivity within the corresponding neural networks (e.g., Ref. 34). In so much as the level of activity is thought to be a critical determining factor in Hebbian adaptation, the level of consolidation induced by this means is likely to have been greater for those participants who generated contractions of high, and progressively increasing, intensity than for those who applied low levels of force. A further important aspect of the

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Fig. 3. Hebbian adaptation encapsulates the premise that connections between cortical neurons are strengthened to the degree that they are active simultaneously. In the top row, 2 cells A and B that are engaged in the context of a training task are shown exhibiting synchronous spike trains. In the event that Hebbian adaptation occurs (the thickness of the arrows linking A and B denotes the strength of the synaptic connections), the functional connections between the 2 cells will be strengthened as the training progresses (A). In the event, however, that there occurs gating of Hebbian adaptation via superordinate control based on sensory guidance (B), the functional connections between cell A and cell B may not be strengthened as a consequence of training.
directed purposeful actions. The point was also made that the range of behaviors that can be generated during training is constrained by the composition of existing intrinsic muscle synergies, and Hebbian adaptation. It was argued that training-invoked variations in the efficiency with which motor actions can be generated influence the stability of coordination by altering the potential for activity-dependent coupling between the cortical representations of the focal muscles recruited in a movement task and brain circuits that do not contribute directly to the required behavior. The point was also made that the range of behaviors that can be generated during training is constrained by the composition of existing intrinsic muscle synergies. In circumstances in which attempts to produce forceful or high-velocity movements would otherwise result in the generation of inappropriate action patterns, training designed to promote the development of control strategies that are specific to the desired movement outcome may be necessary to compensate for vagaries in the force-generating capacities of the muscles engaged by intrinsic synergies. It was also shown that, in the absence of superordinate control based on sensory feedback, there exists the possibility that the functional neural connectivity reinforced by the repetitive execution of movement patterns that are supported by intrinsic muscle synergies, may be ill suited to the subsequent decomposition of these synergies, as may be required by other goals directed purposeful actions.

ACKNOWLEDGMENTS

I take this opportunity to acknowledge the contributions of Tim Carroll, Ben Barry, and Jon Shemmell, who helped shape my thinking with regard to the issues covered in the present review, and initiated some of the related experimental work that was conducted in the Perception and Motor Systems Laboratory at the University of Queensland. Appreciation is also extended to Simon Gandevia, and three anonymous reviewers, for their useful comments on a previous version of this manuscript.

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