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Neural Adaptations to Resistance Training

Implications for Movement Control

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Abstract

It has long been believed that resistance training is accompanied by changes within the nervous system that play an important role in the development of strength. Many elements of the nervous system exhibit the potential for adaptation in response to resistance training, including supraspinal centres, descending neural tracts, spinal circuitry and the motor end plate connections between motoneurons and muscle fibres. Yet the specific sites of adaptation along the neuraxis have seldom been identified experimentally, and much of the evidence for neural adaptations following resistance training remains indirect. As a consequence of this current lack of knowledge, there exists uncertainty regarding the manner in which resistance training impacts upon the control and execution of functional movements. We aim to demonstrate that resistance training is likely to cause adaptations to many neural elements that are involved in the control of movement, and is therefore likely to affect movement execution during a wide range of tasks.

We review a small number of experiments that provide evidence that resistance training affects the way in which muscles that have been engaged during training are recruited during related movement tasks. The concepts addressed in this article represent an important new approach to research on the effects of resistance training. They are also of considerable practical importance, since most individuals perform resistance training in the expectation that it will enhance their performance in related functional tasks.

Muscular strength is fundamental to the successful and efficient performance of many tasks that are encountered in daily living. Strength is defined as the capacity to exert force under a particular set of biomechanical conditions. The amount of force that an isolated muscle can exert is influenced by factors such as: the number and size of muscle fibres, the orientation of fibres with respect to the line of muscle action, and the proportion of myosin heavy and light chain isoforms that are expressed within the muscle fibres.[1] However, in natural tasks individual muscles are seldom required to generate force in isolation. Rather, most movements arise from the cooperation of a number of muscles acting together as functional synergists. The amount of force that can be generated in a particular movement context is therefore determined not only by intramuscular factors, but also by the effectiveness of muscular coordination.

It is well documented in the literature that resistance training can lead to increases in muscular strength. There is a compelling body of evidence that many of the physiological adaptations that underlie increments in strength occur within the muscles themselves.[1-3] It has long been believed that resistance training is also accompanied by changes within the nervous system, that play an important role in the development of strength.[4,5-7] However, the specific sites of adaptation along the neuraxis have seldom been identified experimentally, and much of the evidence for neural adaptations following resistance training remains indirect. For example, in a recent review, Enoka[5] identified phenomena such as strength changes in the absence of substantial muscular adaptations, strength changes in the limb contralateral to the trained muscles (cross education), and specificity of strength adaptations to the training movements, as the strongest evidence that resistance training is accompanied by neural adaptations.

While it is clear that intramuscular adaptations induced during a programme of resistance training lead to strength increases by increasing the force-generating capacity of individual muscles, it is likely that neural adaptations also contribute to strength increments by enhancing the effectiveness of muscular coordination.[8-10] That is, some of the adaptations associated with resistance training may be regarded as motor learning, in so much as individuals learn to produce the specific patterns of muscle recruitment that are associated with optimal performance of the training tasks. At present, it is difficult to predict the impact that the physiological adaptations that underlie motor learning during resistance training will have upon the control and execution of functional tasks. However, in the present article, we aim to demonstrate that resistance training has the potential to alter the manner in which muscles that have been recruited during training are controlled by the central nervous system (CNS). We review a small number of experiments that provide evidence that the changes that occur within the nervous system in response to resistance training may affect patterns of muscle recruitment within a variety of movement contexts.

1. Implications for Movement Control

It is well established that resistance training results in greater increases in force-generating capacity in tasks that closely resemble the exercises performed during training than in novel tasks. That is, strength increases are somewhat specific to the tasks performed during training.[11-13] Many researchers have inferred from this concept that some of the adaptations that cause strength increases have an effect only on movements that are similar to the training tasks. However, while the principle of training specificity suggests that the adaptations within the nervous system that underlie motor learning do not greatly contribute to increases in strength when novel resistance training tasks are performed, it does not necessarily imply that the physiological changes associated with motor learning do not affect the manner in which novel movements are controlled and executed.

When resistance training influences the execution of another movement task the effect can be regarded as a ‘transfer of learning’. Transfer occurs when training for one task affects the performance or learning of a subsequent task. Positive transfer takes place if training for the original task improves performance during a subsequent task, whereas transfer is negative if training causes a reduction in performance on the transfer task. The transfer of learning has been extensively studied over the past century.[14] A number of researchers have also attempted to understand the principles that govern transfer within the context of motor learning, particularly from a behavioural viewpoint.[14,15] Much of this ‘motor learning’ research was concerned with transfer between tasks requiring considerable cognitive, as well as motor, processing.

In the present article, we attempt to understand the impact of resistance training on the performance of a wide range of transfer tasks in terms of the physiological adaptations that accompany training. We argue that resistance training has the capacity to cause adaptations to many neuromuscular elements that are involved in the control and execution of movement, and is therefore likely to affect performance during a wide range of movement tasks. Our reasoning is based on the classic work of Thorndike and Woodworth[16] who stated that 'spread of practice occurs only where identical elements are concerned in the influencing and influenced function' (page 249). The degree and direction (i.e. whether transfer is negative or positive) of transfer from resistance training to other tasks is determined by the interaction of the various neuromuscular adaptations associated with training, and the characteristics of the transfer tasks. Figure 1 depicts a simplified model that illustrates how 2 independent neuromuscular adaptations could interact to affect the performance of a particular movement task. In reality, it is certain that transfer from resistance training to other movements will depend on the interaction of more than 2 forms of adaptation. The challenge for future researchers is to determine the precise nature of the neuromuscular adaptations that accompany resistance training, and to identify patterns of interaction among these adaptations for various classes of movement.

1.1 Individual Muscles

In a recent experiment, we sought to establish whether resistance training has the capacity to influence the activation patterns of muscles that are

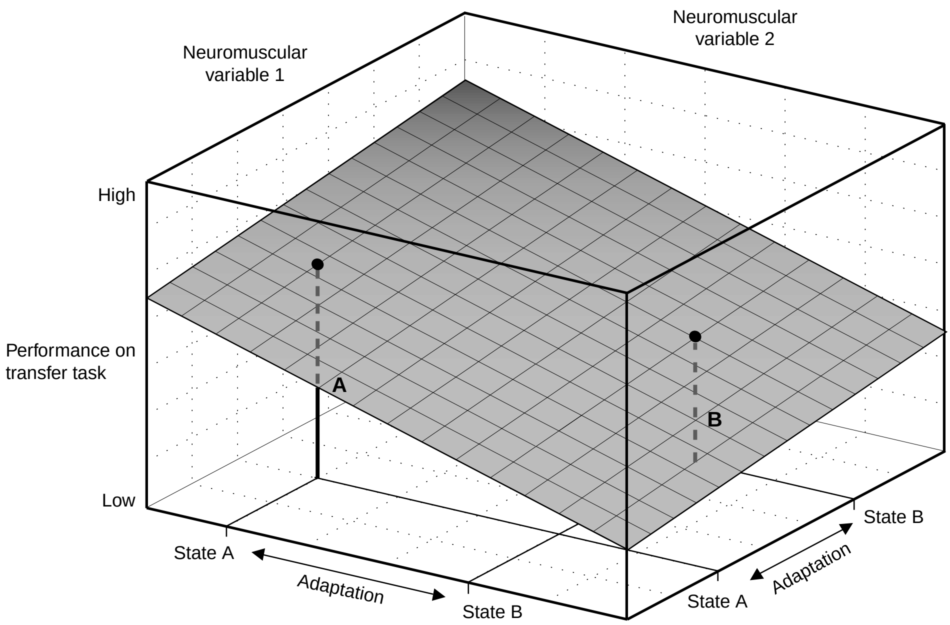

Fig. 1. A simplified model that illustrates how a linear interaction between 2 neuromuscular variables could affect performance on a hypothetical transfer task. The vertical coordinate of each point on the shaded surface specifies the level of performance on the transfer task. The 2 neuromuscular variables can adapt independently, but performance is determined by the interaction between their adaptive states. For example, the model depicts that adaptation of neuromuscular variable 1 in the direction from state A to state B increases the level of performance on the transfer task when the state of neuromuscular variable 1 remains constant. In contrast, an isolated adaptation of neuromuscular variable 2 in the direction from state A to state B reduces the level of performance on the transfer task. In this hypothetical case, the overall influence on performance as the state of the system changes from state A to state B is negative. Thus, transfer is negative despite that fact that neuromuscular variable 1 adapts in a manner that has a positive influence on the performance of the transfer task.

recruited during training when they are engaged in tasks requiring more complex muscular coordination. We assessed the impact of resistance training for the index finger extensor muscles on the performance of a difficult sensorimotor coordination task.[17] The task required participants to synchronise flexion and extension movements of the index finger with an auditory pacing signal. The frequency of the pacing signal increased over time. Training that increased isometric finger strength enhanced performance on the finger coordination task. The improvements in performance were also accompanied by changes in the manner in which the trained muscles were recruited. More specifically, the finger extensors were recruited in a more consistent fashion during the coordination task after the programme of resistance training. That is, the variability in the timing, amplitude and duration of muscle activity was reduced.

These results confirm that the neuromuscular adaptations that are induced as a consequence of resistance training have the capacity to alter the manner in which trained muscles are activated by the CNS. In this particular case, resistance training was associated with neuromuscular adaptations that allowed the trained muscles to be controlled more effectively within the context of the coordination task. There was positive transfer from the resistance training to the functional task. To understand the principles that govern whether there is positive or negative transfer of performance from resistance training tasks to related functional tasks, it is necessary to consider the nature of the neuromuscular adaptations that occur in response to resistance training.

1.1.1 Neural Adaptations

A candidate mechanism for an improvement in the ability of resistance-trained muscles to be controlled by the CNS is an increase in their force-generating capacity. Dettmers et al.[18] found that neural activity increases in the primary motor cortex and caudal supplementary motor area as individuals exert greater levels of isometric force. If each motor unit within a muscle is capable of producing more force after training, it follows that fewer motoneurons need to be recruited, and a reduced level of cortical activation is required to produce an equivalent kinetic or kinematic outcome. It has been proposed that the potential for interference between functionally proximal areas of the cerebral cortex increases with the degree to which these are activated.[19] According to this hypothesis, increased spread of neural activation increases the potential for the activation of neural elements that interfere with optimal task performance. In the context of movement control, the neural elements that interfere with performance may be any pathways or circuits that lead to the recruitment of motor units that do not contribute effectively to an intended movement. Resistance training may enhance performance in related tasks by reducing the extent of cortical activation and therefore the activation of neural elements that interfere with the optimal execution of movement. Dettmers et al.[18] also found that when individuals increased the force that they exerted in a simple key pressing task to levels above 10% maximal voluntary contraction, muscle activity was observed in a number of stabilising muscles that did not directly contribute to force production in the task. Thus, even in simple, low force tasks there occurs considerable spread of activation throughout the neuromuscular system. The observation of such diffuse neural excitation clearly identifies the potential for the activation of neural elements that interfere with optimal task performance.

It has also been consistently reported that coordination tasks that rely critically on the activation of the finger extensor muscles are performed less effectively than comparable tasks relying to a greater degree on flexor muscles.[20,21] Finger extensor muscles typically display a lower intrinsic capacity for force generation than finger flexors and a greater spread of cortical activation occurs during the recruitment of extensor muscles than flexors.[22,23] Furthermore, cortical activity is greater during thumb extensor activity than flexor activity even when the level of force exerted is matched relative to the maximal voluntary contraction force in each direction.[23] That is, even when thumb flexors exert a greater absolute level of force than thumb extensors, a lower extent of cortical activity is required to produce thumb flexion. These observations provide additional evidence for the hypothesis that an increase in force-generating capacity may enhance muscular coordination by reducing the extent of neural activity within the motor centres of the CNS. It appears that muscles are controlled more effectively by the CNS when lower levels of neural activity are required to produce a given level of muscular force.

It is apparent that adaptations occurring distal to the motoneuron could underlie enhancements in movement control via a reduction in the level of central drive required to produce force. It is also true, however, that adaptations to structures before the neuromuscular junction could act to increase the efficiency of the central command. Changes in synaptic efficacy or in the organisation of neural circuitry within the spinal motoneuron pool or the motor cortex could serve to reduce the level of drive from other cortical or subcortical motor areas that are involved in the control of movement. There is evidence that activity is reduced at a number of supraspinal sites, such as the dorsal pre-motor area, the parietal cortex and the lateral cerebellum, with the acquisition of motor skill.[24-26] It is likely that alterations of synaptic circuitry in the motor cortex underlie some of the reductions in the level of neural activity within associated supraspinal motor centres. Rioult-Pedotti et al.[27,28] found that the synaptic effectiveness of layer II/III horizontal connections within the primary motor cortex was modified when rats learned to perform a difficult reaching movement. Furthermore, there is indirect evidence that the synaptic effectiveness of neural connections between areas within the primary motor cortex can be altered through motor training in humans.[29,30] Thus, motor learning may be associated with physiological adaptations within the primary motor cortex that contribute to more efficient execution of the learned movements.

It is important to recognise that the evidence that resistance training may enhance coordination in come related tasks by reducing the level of cortical activity associated with the activation of trained muscles was drawn largely from experiments that have focused on distal upper limb and hand muscles. Similarly, most of the studies that have demonstrated cortical adaptations following motor training have involved hand muscles. The extent to which this evidence is applicable to more proximal limb muscles, the control of which typically relies to a lesser degree on direct cortico-spinal connections, is not clear.

Milner-Brown et al.[31] provided specific evidence that resistance training induces changes in synaptic effectiveness within the motoneuron pool. They found that resistance training caused an increase in the tendency of motor units to fire synchronously (motor unit short term synchronisation) and, in a cross sectional analysis, that the motor units of resistance-trained individuals fired with greater synchrony than those of untrained individuals. Motor unit short term synchronisation occurs when a number of motoneurons receive input from axonal branches of the same presynaptic neurons, thereby increasing the probability of near-simultaneous discharge in the target motoneurons.[32-34] A change in the level of synchrony observed during a low-force isometric contraction therefore reflects an increase in the number or strength of common presynaptic inputs onto populations of motoneurons. There is also evidence that motor unit short term synchronisation in hand muscles is brought about largely via descending cortical-spinal tract neurons with branched-stem axons.[32,35,36] The implication of these findings is that resistance training may alter the connectivity between cortico-spinal cells and spinal motoneurons.

Although there remain caveats associated with the original Milner-Brown et al.[37] study, Semmler and Nordstrom[38] have provided converging evidence, based upon comparisons between resistance-trained individuals, untrained individuals and skilled musicians. They found that the resistance-trained individuals displayed greater motor unit short term synchronisation than the musicians and untrained people. Taken together, these experiments suggest that resistance training is associated with an increase in motor unit short term synchrony, which is caused by changes in synaptic efficacy within the motoneuron pool. This implies that the number or strength of common connections onto the motoneurons of trained muscles may increase following resistance training.[32-34] Adaptations to basic neural elements such as the synapses between motoneurons and cortico-spinal cells, which play a fundamental role in the execution of voluntary movement, are likely to influence the manner in which trained muscles are recruited during a wide range of tasks.

1.1.2 Principles of Transfer

It is not yet possible to identify a general set of principles that govern the impact of resistance training on the manner in which trained muscles are recruited during related tasks. This is both because there exists insufficient information about the precise nature of the neural adaptations that accompany training, and because few experiments have been conducted to investigate transfer between particular resistance training and functional tasks. For example, there remains uncertainty regarding the basic consequences for movement control of the neural adaptations that underlie changes in muscle activation. On the one hand, if resistance training causes increases in the force-generating capacity of muscle fibres or the strength of the connections between motoneurons and cortico-spinal cells, fewer descending fibres will be activated to execute any given task involving the trained muscles. These effects would be expected to enhance the effectiveness of neuromuscular control in many movement tasks.[20,21]

Alternatively, we have argued that resistance training induces adaptations that lead to an increase in motor unit synchrony. There is evidence that increased synchrony of motor unit recruitment leads to greater fluctuations in force during simple isometric tasks.[39,40] Decreases in the steadiness of contraction may serve to reduce performance in certain tasks. Furthermore, motor unit synchrony is lower in musicians than in untrained individuals.[38] Thus, in contrast to resistance training, the neural adaptations associated with years of practice of skills requiring considerable fine control of force lead to reductions in motor unit synchrony. These findings imply that resistance training induces some specific adaptations that may reduce the effectiveness of neuromuscular control within some movement contexts. However, in contrast to this expectation, resistance training has been found to cause reductions in force variation in elderly individuals and patients with essential tremor.[41-43] The discrepancies that are evident between the expected and observed functional consequences of the neuromuscular adaptations that occur in response to resistance training confirm that a number of neuromuscular adaptations interact to determine the nature of transfer from resistance training to functional movements.

1.2 Groups of Muscles

Evidence that resistance training impacts upon muscular coordination is provided by recent experiments that have focused on the activation of antagonist muscles during maximal contractions.[8-10] The degree to which antagonist muscles are activated during movement is of considerable importance, since the resultant torque about a joint can be increased by a reduction in the activation of muscles that oppose the prime movers. In these experiments, resistance training resulted in a lower level of knee flexor electromyogram (EMG) activity during maximal isometric knee extension tasks. It appears that the participants learned to reduce the level of antagonist muscle activation during the period of resistance training. It is likely that learning of a similar nature occurs when individuals perform more complicated resistance training exercises, that require the precise timing of muscle recruitment and coordination of mono- and biarticular muscles. In this section, we discuss the influence that the physiological changes underlying enhancements in coordination may have upon the control of functional movement tasks.

Carroll and co-workers[17] demonstrated that resistance training causes changes in the neuromuscular system that can have a positive impact on the execution of movements that are somewhat related to the training tasks. Specifically, resistance training enhanced the performance during a difficult sensorimotor coordination task involving the muscles that were engaged during training. However, Barrata et al.[44] reported that the adaptations associated with resistance training had a negative impact upon the performance of a related movement task. The experiment of Barrata et al.[44] involved 2 individuals who were drawn from a larger study involving cross-sectional analyses of hamstring/quadriceps coactivation. The participants performed daily resistance training involving dynamic knee flexions for 2 or 3 weeks. Following the short training period, both participants showed greater knee flexor EMG activity during maximal isometric knee extension. That is, the activity of a muscle group that was recruited as a prime mover during training was increased when it acted as an antagonist following training. This experiment provides direct evidence that resistance training may cause changes in the way that groups of muscles are coordinated that are maladaptive within some movement contexts, since increases in knee flexor activity reduce the net knee extension torque.

Experiments that have demonstrated the specific effects of resistance training upon strength provide indirect evidence that resistance training causes adaptations that can either enhance or interfere with the execution of related movements. For example, Carroll et al.[45] found that individuals who trained 3 times per week showed greater strength increases in a primary resistance training task, which involved hip and knee extension, than those who trained twice per week. In contrast, those who trained twice per week showed a moderate strength increment in novel isometric and isokinetic knee extension tasks, whereas the isometric and isokinetic strength of individuals who trained 3 times per week did not change. This pattern of results suggests that participants who trained more frequently experienced a greater degree of neural adaptation than the individuals who trained twice per week. We have argued that resistance training induces neural adaptations that are associated with learning the optimal pattern of muscle recruitment for the training tasks. Thus, the group that trained more frequently may have shown greater increases in strength on the primary training task than the low frequency group because of a greater improvement in coordination.

However, the optimal pattern of muscle recruitment for the hip and knee extension task is inappropriate for the pure knee extension tasks. More specifically, coactivation of the knee flexors and extensors contributes appropriately to force production in a hip and knee extension task but reduces force in an open-chain knee extension task.[46] The lack of an increase in knee extension strength shown by the high frequency training group can be explained by a greater degree of knee flexor/extensor coactivation in the pure knee extension task. That is, a greater degree of antagonist coactivation after training could have resulted in a lack of change in net torque production, despite increases in the force-generating capacity of the prime movers. The implication of these findings is that the nervous system changes associated with enhancements in coordination on the training tasks may negatively influence the patterns of muscle recruitment during some novel strength tasks. The proposal that negative transfer may occur between some resistance training protocols and certain high force tasks is consistent with the results from Baratta et al.[44] To determine the general principles that govern the nature of transfer between resistance training and other related movements, however, it is necessary to consider the neural mechanisms that may underlie changes in coordination.

1.2.1 Neural Adaptations

The coordination of muscle recruitment during movement requires complex cooperative interactions between a number of spinal and supraspinal centres. The architecture of the neural circuitry at each of these sites influences patterns of muscle activation. For example, considerable divergence exists within the cortico-spinal pathway, such that individual cortico-spinal cells are connected with many motoneurons that project to different muscles.[47-49] Thus, in most cases, output from the primary motor cortex influences the activity of groups of muscles rather than individual muscles. The patterns of muscular coordination that are ultimately exhibited during behaviour are therefore determined by the extent to which cortico-spinal cell fibres diverge within the motoneuron pool, and the efficacy of synapses between particular cortico-spinal cells and the motoneurons that project to the muscles that are engaged in the behaviour. Cortico-spinal cells also make a vast number of indirect connections with motoneurons via oligosynaptic interneuronal pathways.[48,49] The organisation of the interneuronal circuitry that mediates indirect connectivity between cortico-spinal neurons and motoneurons therefore plays an additional role in specifying the particular patterns of muscle activity that are exhibited during movement.

Muscular coordination is also achieved via networks of local connections between neurons that reside at a number of sites in the CNS. Considerable information exists regarding the synaptic circuitry in the spinal cord that contributes to muscular coordination. For example, the phenomenon of reciprocal inhibition, which is the inhibition of antagonist muscles during activation of the ipsilateral agonist, is known to be at least partly mediated by disynaptic inhibitory interneuronal pathways in the spinal cord.[50] However, there is recent evidence that similar inhibitory connections exist between the cortical areas that ultimately project to pairs of antagonist muscles.[51] Furthermore, the existence of horizontal connections between motor cortical zones that primarily represent antagonist muscles has been confirmed anatomically in the cat.[52] Subcortical neural elements such as the cerebellum and basal ganglia also appear to play an important role in the coordination of synergist and antagonist muscles.[53,54] For example, there is evidence that circuitry within the globus pallidus may facilitate the activity of prime mover and synergist muscles and inhibit the activity of antagonist muscles via cortico-putamino-pallidal-thalamo-cortical pathways.[55] The basal ganglia have also been implicated in the control of timing processes,[56] and may therefore play a role in the temporal coordination of muscles during complicated movements that require precise timing of muscle activation.

Future research may enable us to determine precisely which of the many neural elements that play a role in generating coordinated movement undergo adaptation during resistance training and thereby lead to changes in coordination. For example, there is emerging evidence that plasticity within the motor cortex plays an important role in motor learning.[57-61] A number of recent reports indicate that long term potentiation (LTP) of synapses within the motor cortex may be an important mechanism of cortical adaptation that underlies motor learning.[27,28,62] In this regard, Rioult-Pedotti et al.[27,28] found that cortical adaptation and motor learning are attenuated when *N*-methyl-*D*-aspartate (NMDA) receptors, that are known to mediate LTP, are blocked. They also found that artificial LTP is more difficult to induce in motor cortical sections following learning, and that long term depression (LTD) is exacerbated. Since there is a limit to the extent of LTP that can occur before the effect becomes saturated,[63] the observation that learning reduces the capacity for subsequent LTP suggests that skill learning involves a LTP-like mechanism. Although LTP is a strong candidate to underlie cortical plasticity, the importance of other mechanisms of synaptic adaptation, such as LTD, should not be discounted. There is considerable evidence that LTD is the principle mechanism of synaptic plasticity in the cerebellum.[54] Regardless of the mechanism, it is apparent that motor learning arises, at least partly, from modifications in the strength of connections between neurons within supraspinal motor centres. Thus, resistance training that induces motor learning may cause changes in connectivity between the motor areas that are involved in controlling the resistance training exercises.

If improvements in coordination following resistance training arise as a consequence of changes in connectivity between the elements of the nervous system that control the trained muscles, what are the likely consequences for movements that are related to the movements performed during training? At a simple level, it could be argued that changes in synaptic efficacy within the neural pathways associated with producing particular movements are likely to affect muscle activation whenever these pathways are activated. Thus, if particular circuits involved in coordinating resistance training movements are modified with training, alterations could be expected to the patterns of muscle activation exhibited during other movements that recruit some of the same circuits. However, this expectation does not account for the possibility that additional circuits could be activated to counterbalance the effect of the adaptations and thereby maintain an equivalent functional outcome. It also does not account for the ability of the CNS to facilitate or inhibit particular neural pathways in a task-specific manner.

The considerable scope for flexibility in the mechanisms employed by the CNS to generate muscle activation is illustrated clearly by the nature of the interactions that occur between neural circuits within the spinal cord during the control of voluntary movement.[48,49] Interneurons in the spinal cord receive input from afferent fibres, descending fibres and the fibres of other interneurons, and ultimately influence the activity of motoneurons. The interaction of these various inputs onto interneuronal circuitry determines which motor units are recruited during movement. For example, afferent input alters the excitability of spinal interneurons that also receive input from descending fibres, and can thus modify the specific populations of motoneurons affected by the descending neural commands. However, spinal interneuronal activity and the synaptic effectiveness of connections between afferent fibres and motoneurons and interneurons (i.e. via presynaptic inhibition) are also greatly influenced by descending output from supraspinal motor centres. Thus, the activation of motoneurons via both corticospinal cells and spinal reflex pathways is partly determined by the manner in which supraspinal and segmental elements interact to set the excitability states of interneuronal circuits. An important consequence of this arrangement is that the same corticospinal output can activate different populations of motoneurons depending on the state of circuitry within the spinal cord. The flexibility of this circuitry suggests that, in many cases, the CNS may be capable of selectively modulating the excitability of particular circuits that may have experienced adaptation during motor learning. For example, the impact of adaptations to spinal chord circuitry that would ordinarily serve to reduce performance in a related task may be countered by the modulation of descending input from supra-spinal centres, thereby avoiding negative transfer.

1.2.2 Principles of Transfer

The experiments cited in the previous sections have shown that resistance training can induce adaptations that have the potential either to enhance or interfere with the performance of related tasks. It is important to note that performance decrements have only been demonstrated for high force tasks that are relatively novel to the participants. It remains to be determined whether the neural adaptations that underlie refinements in coordination have a significant effect on patterns of muscle recruitment during tasks that have dissimilar force requirements from the resistance training exercises. The impact of neural adaptation on the coordination of well-learned movements and tasks that are practised concurrently with resistance training is also yet to be established. Martin and Morris[63] have speculated that considerable potential for interference exists when the same neural elements are required for different types of learning. However, the CNS has a high capacity for flexibility in the generation of muscle activation patterns. It seems likely that, with appropriate training, there exists the potential for a large number of related movements to be executed with high efficiency; even if conflicting patterns of coordination are required for optimal performance of these tasks.

However, as a general principle, negative transfer may occur when a pattern of muscle recruitment associated with optimal performance on a resistance training task would serve to retard performance if it was expressed during a transfer task. An example would be if the training task required strong coactivation of a particular set of muscles, and the transfer task required strong activation of some of the muscles in the set, but inhibition of other muscles in the set. This situation occurs when the training task involves simultaneous knee and hip extension and the transfer task requires isolated knee extension, since coactivation of knee flexors and extensors is necessary for optimal performance on the training task, but reduces performance on the transfer task. In this case, it is anticipated that an overflow of activation may occur from the muscles that are strongly activated in the transfer task (e.g. quadriceps muscles) to muscles that would best be inhibited (e.g. hamstring muscles). The mechanism of this overflow would be via the neural pathways responsible for facilitating cocontraction in the training task, since these pathways are likely to be reinforced during training. In contrast, positive transfer may occur if the process of learning the optimal patterns of muscle activity for the resistance training exercises strengthens excitatory neural connections between muscles that act as functional synergists in the context of the transfer task. Positive transfer is also expected if learning reinforces inhibitory circuits between muscles that, if activated together, would degrade performance.

2. Conclusion

The evidence presented in this article indicates that resistance training induces adaptations that can influence the manner in which trained muscles are recruited by the CNS during related functional tasks. Adaptations at a number of sites in the neuromuscular system are likely to contribute to changes in movement execution and control. There is direct evidence that resistance training causes changes in synaptic efficacy within the motoneuron pool,[31,38] and evidence from a number of sources that adaptations in various supraspinal motor centres underlie motor learning. Furthermore, the physiological adaptations associated with resistance training may interact to produce either positive or negative transfer of performance to functional tasks. Yet, the precise nature of many of the neuromuscular responses to resistance training and the principles that govern the transfer between resistance training and other movements are still to be determined.

Research that seeks to identify these principles has the potential to enhance our basic understanding of the neural basis of movement control and learning, as well as provide important information to assist the design of resistance training programmes in practical settings such as rehabilitation and athletic training. The challenge for future researchers is to determine the precise nature of the neuromuscular adaptations that accompany resistance training, and to identify patterns of interaction among these adaptations for various classes of movement.

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