REVIEW

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Governing coordination: behavioural principles and neural correlates

Abstract The coordination of movement is governed by a coalition of constraints. The expression of these constraints ranges from the concrete—the restricted range of motion offered by the mechanical configuration of our muscles and joints; to the abstract—the difficulty that we experience in combining simple movements into complex rhythms. We seek to illustrate that the various constraints on coordination are complementary and inclusive, and the means by which their expression and interaction are mediated systematically by the integrative action of the central nervous system (CNS). Beyond identifying the general principles at the behavioural level that govern the mutual interplay of constraints, we attempt to demonstrate that these principles have as their foundation specific functional properties of the cortical motor systems. We propose that regions of the brain upstream of the motor cortex may play a significant role in mediating interactions between the functional representations of muscles engaged in sensorimotor coordination tasks. We also argue that activity in these "supramotor" regions may mediate the stabilising role of augmented sensory feedback.

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Constraints on coordination

The coordination of movement is governed by a system of *constraints* of musculoskeletal and neural origin. Some of these constraints are easily discerned, such as the restriction that certain joints function only as simple hinges. Other constraints are less tangible, and find expression in terms of more abstract relations. The act of playing the piano provides a case in point. Each movement element, the depression of a key, is quite easy to perform. Nonetheless, our powers of coordination are challenged when these simple elements must be combined in a temporally precise sequence involving multiple fingers and both hands.

There has been a recent tendency in the literature to treat the various sources of constraint as distinct and exclusive (e.g. Mechsner et al. 2001), rather than acknowledging and understanding their mutual interplay. It is important to recognise that all constraints on coordination—whether perceptual, cognitive or musculoskeletal—are mediated by the integrative action of the central nervous system. In the present paper, we aim to illustrate this point by focussing upon two types of constraint: those associated with cognitive strategies based on perception, and those arising from the neuroanatomical properties of skeletal muscle. When appropriate modes of analysis are employed, it can be shown that the expression of both forms of constraint, and their interaction, can be understood in terms of motor-function related cortical dynamics.

Cognitive intent

The presence of constraints on actions that are mediated by cognitive intent was first reported by Kurt Wachholder in the course of his pioneering studies of human motor control (Wachholder and Altenberger 1926; see Sternad 2001). Wachholder and Altenberger noted that when producing rhythmic flexion and extension movements of the wrist, some individuals accentuated the flexion phase of the movement, whereas other participants accentuated

the extension phase. In contrast, when rhythmic movements of the finger were produced, the flexion phase of the movement cycle was always accentuated. Differences in accentuation became even more pronounced when participants placed a voluntary emphasis upon one or other phase of the movement cycle. Indeed, it was apparent that rhythmic movements could only be performed smoothly and fluently if the voluntary emphasis was consistent with that which was naturally accentuated. If the participants were instructed to place emphasis upon the opposite phase, the resulting movements were characterised by irregularities. Subjectively, the task also became more difficult (Wachholder and Altenberger 1926). Thus, the phase relationship defined by the intrinsic asymmetry of the movement cycle (flexion vs. extension) and the timing of the voluntary accent determined the level of coordination.

The explicit (and dual) nature of cognitive (intentional) constraints was elaborated in experiments conducted by Kelso and colleagues (Kelso et al. 1988; Scholz et al. 1990; see Kelso 1995, chap. 5 for review and discussion). Kelso et al. showed that, on the one hand, individuals can intentionally stabilise bimanual antiphase movements at movement rates at which they would otherwise become unstable and switch to inphase coordination. At the same time, participants found it far easier to switch intentionally from antiphase to inphase coordination patterns, than the other way around. Thus, intentional factors play the joint role of stabilising or destabilising coordination depending on context. That is, intentions influence, and are influenced by the relative stability of patterns of coordination (which is affected, in the present case, by parameters such as movement rate).

A further striking demonstration of the impact of cognitive intent upon the stability of sensorimotor coordination was provided by one of us, using a deceptively simple experimental paradigm (Kelso et al. 1990). Individuals were required to coordinate peak flexion of the index finger either on the beat (synchronisation) or off the beat (syncopation) of an auditory metronome. The latter condition required that a flexion movement be made midway between successive metronome beats. It was noted that all of the participants were capable of maintaining the flexion-on-the-beat pattern as the rate of the metronome was increased. In contrast, in the flex-off-the-beat condition, the coordination pattern became unstable, and broke down, at relatively low movement frequencies. It transpired that only one of the seven participants tested was capable of maintaining the flex-off-the-beat pattern through the entire range of pacing frequencies. This individual had adopted a strategy of performing an *extension* movement in synchrony with the metronome rather than a *flexion* movement between the beats. This latter observation suggested that in some circumstances, an increase in the stability of coordination could be derived from a simple change of cognitive strategy.

It has now been established that the organisation of neural activity within the cortex is very different for synchronisation and syncopation tasks (Kelso et al. 1998).

Neural correlates of transitions between these patterns of behaviour (i.e. from syncopation to synchronisation), when transduced by multielectrode electroencephalography (EEG) (e.g. Mayville et al. 1999; Wallenstein et al. 1995), are principally expressed as a reduction in power at central and centroparietal sites contralateral to the performing hand, suggesting a decrease in activity in primary sensorimotor cortex. Transitions in the relative phase (with respect to the pacing metronome) of the averaged evoked fields detected by magnetoencephalography (MEG) (e.g. Kelso et al. 1992; Fuchs et al. 2000) occur concomitantly with transitions in behaviour. These phase shifts are exhibited most prominently in sensorimotor areas contralateral to the moving limb. It has also been shown that practice induced enhancements of the performance of the syncopation task are accompanied by changes in the power of the alpha and beta frequency bands of the neuromagnetic signal (Jantzen et al. 2001). Notably several prominent features of the cortical dynamics are preserved, regardless of whether the act of coordination requires a flexion or an extension movement (Kelso et al. 1998).

In summary, the production of rhythmic sensorimotor coordination requires the involvement of an extended network of brain regions. The specific areas involved, and the degree to which they are engaged, depends upon the intended timing relationship between motor and perceptual processes. When there is the intent to produce movement in synchrony with an external stimulus—a behavioural pattern that is highly stable, there occurs activation of contralateral sensorimotor and caudal supplementary motor cortices as well as ipsilateral cerebellum. If, however, syncopated movements are required, there is additional activation of the cerebellar lobes, along with recruitment of the basal ganglia, dorsolateral premotor, anterior supplementary motor, prefrontal, and temporal association cortices (Mayville et al. 2002). When considered in light of the fact that the syncopation pattern is a relatively unstable pattern, these neurophysiological observations suggest that the amount of central control necessary for the maintenance of this mode of coordination may be greater than that required when motor and perceptual events coincide.

Neuromuscular-skeletal factors

A recent series of studies have shown that the neuroanatomical characteristics of the muscles engaged during movement also have a profound influence on the stability of sensorimotor coordination (Carson 1996; cf. Wachholder and Altenberger 1926). Tasks that require synchronisation of a finger flexion movement with an auditory metronome are performed in a more consistent fashion than those that require a finger extension movement to be coordinated with a beat. Furthermore, if the frequency of movement is steadily increased, transitions from an extend-on-the-beat pattern to a flex-on-the-beat pattern are often observed (Carson 1996; Carson and Riek 1998a).

As a result of their phylogenetic origin as anti-gravity muscles, the flexors of the upper limb are stronger than the extensors, requiring a smaller proportion of motor units to be activated in order to produce a given level of force (Vallbo and Wessberg 1993). Unit changes in the firing rate of corticomotoneuronal cells that innervate flexor muscles result in a greater increase of torque than an equivalent change in cells facilitating extensor muscles (Cheney et al. 1991). In non-human primates, the proportion of motoneurons receiving monosynaptic excitation is greater for the flexor muscles of the upper arm than for the extensor muscles (Phillips and Porter 1964). Recent studies employing transcranial magnetic stimulation (TMS) of the motor cortex have provided evidence of a corresponding pattern of organisation in humans. Corticospinal neurones with direct facilitatory projections to motoneurones of elbow flexors are more numerous than neurones that project directly to elbow extensors (Palmer and Ashby 1992). These properties are also reflected in the patterns of brain activity, which occur during functional movement tasks. Cortical activation, registered by functional magnetic resonance imaging (fMRI), is substantially greater during extension than during flexion movements of the fingers, even when the relative activity of the extensor and flexor muscles is equivalent (Yue et al. 2000).

It has also been revealed that changes in the posture of the limb, that result in alterations in the lengths and orientations of the muscles engaged in a task, have both predictable and reliable effects on the stability of coordination. In the context of the task described above, the frequency at which the extend-on-the-beat pattern of coordination is compromised is determined by the lengths of the finger extensor muscles and by their moment arms (Carson 1996; Carson and Riek 1998a). It is well known that the capacity of a muscle to generate force is dependent upon its length (e.g. Gordon et al. 1966). The muscle moment arm also determines the muscle activation that is required to generate a given level of joint torque. Chronic changes in the strength of specific muscles, such as those brought about by resistance training, also have a corresponding influence upon the stability of sensorimotor coordination. Specifically, increases in the strength of the muscles that extend the index finger enhance the stability of the extend-between-the-beats pattern of coordination (Carroll et al. 2001). One direct consequence of resistance training is an increase in the gain of the corticospinal pathway (Carroll et al. 2002). Following training, the level of cortical input to the spinal motoneurons that is necessary to generate a particular degree of muscle activation or joint torque is less than that required prior to training. It also appears that factors that decrease the force generating capacity of the peripheral musculature, including muscle fibre damage induced by eccentric contractions, require a corresponding increase in motor cortical excitability, in order to bring about an equivalent movement outcome (Carson et al. 2002).

In summary, chronic changes in muscle strength accruing from resistance training, and acute changes in force generating capacity arising from changes in muscle length and moment arm or from muscle damage, impact in a systematic fashion upon the stability of sensorimotor coordination. That which remains to be clarified is the precise means by which these effects are mediated by altered patterns of neural activity in the higher brain centres.

Distributed activity in motor cortex

It has been proposed that the potential for interference between functionally proximal areas of the cerebral cortex is contingent upon the degree to which these areas are activated (Kinsbourne and Hicks 1978). It is well established that the cortical representations of muscles overlap broadly (e.g. Humphrey 1986; Lemon 1988). In addition, it is clear that movement of any limb segment is mediated by activity that is widely distributed throughout the motor cortex (Schieber 2001). Beta range synchronisation of cortical activity and the electromyogram (EMG), in particular, is widely distributed across multiple motor and premotor areas during finger movements (Chen et al. 2003; Feige et al. 2000; Jantzen et al. 2001). The transsynaptic spread of activity through the motor network is therefore an integral aspect of its function. Yet there also exists within precentral cortex a functional somatotopic organisation (e.g. Graziano et al. 2002), which indicates that basic elements of the movement repertoire, while encapsulated in networks of neuronal connections, are not distributed homogeneously. The observation that both movements and muscles are represented in motor cortex (Kakei et al. 1999) is also consistent with the hypothesis that the specification of referent body configurations (Feldman et al. 1998; Lestienne et al. 2000) provides a basis upon which the activity of multiple muscles may be coordinated. Regardless of the specific movement parameters that are encoded by neurones in precentral cortex, the fact that activity in each spatial location influences many muscles and postures, and the complex connectivity that exists between multiple zones (Luppino and Rizzolatti 2000), point to means by which interference may occur between the cortical representations of the focal muscles recruited in a movement task and brain circuits which do not contribute directly to the required movement (Hufnagel et al. 1990; Schneider et al. 2002).

There is extensive evidence that the distribution of brain activity associated with a functional movement task is determined by the required level of muscle activation. The overall extent of primary motor cortex that is activated increases with the rate of movement (Blinkenberg et al. 1996; Schlaug et al. 1996; Turner et al. 1998). Close relationships also exist between levels of muscle activation, and fMRI measured brain activity recorded both in motor-function related cortical fields, and across the entire brain (Dai et al. 2001). Examination of the relationship between EEG-derived motor activity-related cortical potentials and voluntary muscle activation also reveals that the magnitude of the signal recorded from sensorimotor cortex and SMA is correlated with the intensity of

contraction (Siemionow et al. 2000; Slobounov et al. 2002a). With rising levels of finger flexion force, there is an initial steep increase in motor cortex activity, as measured by relative regional cerebral blood flow (rCBF), reflecting the recruitment of a larger number of small motor units. This is followed by a further less rapid increase in activity as a smaller number of large units are engaged (Dettmers et al. 1995). Following the administration of repetitive transcranial magnetic stimulation (rTMS) that increases the amplitude of motor potentials (MEPs) evoked in a target muscle, there occurs a corresponding increase in the excitability of corticospinal projections to other muscles of the same limb. The spread of EMG activity to other muscles appears to be mediated by intracortical mechanisms, in particular by changes in the excitability of interneurones mediating intracortical inhibition (Lorenzano et al. 2002). Taken together, these findings suggest that 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.

We have argued previously that the efficiency with which an action can be generated by the neuromuscular-skeletal system will determine the spatial distribution of activity within the cortex (Carson et al. 1999). In this context, efficiency refers to the level of cortical input to the spinal motoneurons that is necessary to generate a particular degree of muscle activation or joint torque. As noted previously, the flexors of the upper limb are stronger than the extensors, requiring a smaller proportion of motor units to be activated in order to produce a given level of force. The observation that cerebral activity during movements that accentuate extension is greater than in movements in which flexion is accentuated (e.g. Yue et al. 2000) is thus consistent with this proposition. The hypothesis does not imply that the distribution of brain activity is determined solely by the required level of muscle activation. Indeed, a key variable specified by descending systems may be the threshold for activation of different muscle groups acting around a joint (Feldman and Orlovsky 1972). In this vein, there is recent evidence to suggest that the range of central regulation of activation thresholds of agonist and antagonist muscles is reduced following stroke, and in patients with cerebral palsy (Levin 2000; Levin et al. 2000).

The essence of the current proposal is that all other factors (e.g. stretch-reflex thresholds, central or peripheral fatigue) being equal, there will be a monotonic relationship between the distribution of brain activity in the higher motor centres and the level of descending neural drive that is directed to the muscles. Factors which modify the gain of the corticomotoneuronal pathway, such as resistance training or changes in muscle length and moment arm, in so much as they alter the efficiency of motor output, will also impact upon the level of brain activity present during functional movement tasks. We submit that elevations in the extent and amplitude of activity may lead to the recruitment of brain circuits which do not contribute directly to the required movement, and indeed may impede that movement. This is not to suggest however that the interference arises simply from a scrambling of neuronal signals. Rather, the presence of a meaningful functional somatotopic organisation of precentral cortex (e.g. Graziano et al. 2002) suggests that in circumstances in which there is spread of neural activity, for example due to increasing force or velocity demands, the interference will be expressed via the intrusion of muscle activity or postures extraneous to the task at hand (Carson and Riek 2001; Hager-Ross and Schieber 2000). When individuals perform an isometric contraction involving only one finger, the degree to which the other fingers are moved involuntarily is contingent upon the level of applied force (Slobounov et al. 2002b), an effect that is also expressed systematically in EEG derived motor-related cortical potentials (Slobounov et al. 2002a, 2002c). To the extent that the engagement of muscles and postural transitions other than those intended produce patterns of movement that are at variance with those demanded by a coordination task, there will be consequent deficits in the accuracy and/or stability of performance (Carson and Riek 2001; Kelso et al. 1993).

Anterior cingulate cortex mediation of sensorimotor control

One issue that remains unclear at the present time is the degree to which the increased distribution of activity in M1, that accompanies elevations in motor output (e.g. Blinkenberg et al. 1996; Schlaug et al. 1996), is attributable to processes that are local to the motor cortex. It is possible to conceive of circumstances in which increased drive from brain regions upstream of the motor cortex may result in a greater spread of activation, due simply to local connectivity within M1.

In humans, a close association between levels of activity in cingulate cortex, an area thought to be a strategic entry point for limbic influence on the voluntary motor system, and response time has been noted (Dassonville et al. 1998; Naito et al. 2000). On the basis of a negative relationship with reaction time, Winterer et al. (2003) concluded that the degree of activation of anterior cingulate cortex (ACC), expressed in event related fMRI, reflected the amount of effort or volition required by the motor task. In their review of 107 PET activation studies, Paus et al. (1998) were drawn to the qualitatively similar conclusion that ACC activity is closely related to the required level of arousal. During the initial course of sustained muscle contractions, there is an increase in activity in cingulate areas, and in supplementary motor and prefrontal regions. This activity appears to reflect an increase in central drive which compensates for the onset of peripheral fatigue (Liu et al. 2002). Corresponding inferences concerning the role of ACC in mediating the central command for movement during muscular contractions have been made on the basis of PET based measurements of regional cerebral blood flow (Williamson et al. 2003).

The functional connectivity between the caudal ACC and the primary and supplementary motor areas in humans is now clearly established (Koski and Paus 2000). It has also been shown recently that in rat, seizure induced activity in limbic and cortical sites is capable of inducing functional reorganisation of motor maps within primary motor areas (Teskey et al. 2002). Taken together, these findings suggest that the level of input from regions such as anterior cingulate cortex that appear to act as neural mediators of the central command (e.g. Chefer et al. 1997) may also determine the interactions that occur within M1.

It is also possible that increased spread of activity within M1 may result simply from more diffuse input to the motor cortex. Precentral cortex is composed of a mosaic of motor areas, each of which plays a separate role in movement control, and is characterised by specificity of descending projections and cortical afferents (Rizzolatti et al. 1998). There are for example numerous prominent projections from different parts of anterior cingulate cortex into the classic motor zones. On the basis of functional imaging derived observations that this region does not make a uniform contribution to brain functions, it has been proposed that the ACC may be further subdivided into "affect" and "cognition" components (Devinsky et al. 1995). With respect to the former division, the finding that neural activity in the ACC is modulated in parallel with the state of arousal is consistent with the presence of inputs to this region from limbic areas, and with the extensive afferent projections to the ACC from thalamic nuclei (Paus 2001). The cognitive division appears to be involved with response selection occurring in the context of voluntary movement control. In this regard, it has been proposed that cognitive/motor related activity with an initial focus in other cortical regions (e.g. prefrontal cortex) is modulated in the ACC and "funnelled" to the motor system (Paus et al. 1993). Evidently, the degree to which any such funnelling occurs is also likely to determine the extent of activity in the motor areas that receive projections from the anterior cingulate cortex.

At the present time, it is not possible to determine the extent to which the spread of activity in M1 is contingent upon the distribution, as opposed to the level of input which it receives from other centres that constitute elements of the motor system. Nonetheless, it is clear that regions of the brain upstream of the motor cortex, such as anterior cingulate cortex, have the potential to play a significant role in mediating interactions between the functional representations of muscles engaged in sensori-motor coordination tasks.

Cross-modal integration

Although the potent effects of cross-modality cues on behaviour are well known (e.g. Stein and Meredith 1993), it is only recently that the neural mechanisms underlying these effects have been explored. Neuroimaging and evoked potential studies have revealed that many areas of cortex are characterised by multisensory processing (e.g. Paulesu et al. 1995; Sams et al. 1991). Although the neurones in these areas are dedicated to many different functions, at every site at which sensory inputs converge, there exists the opportunity for cross-modal integration (Stein 1998). Of particular interest in the present context is the fact that when inputs from various sensory modalities are present simultaneously, the efficacy of the combined stimuli is greater than that predicted by summing their individual influences (e.g. Stein, Wallace and Stanford 1999). This phenomenon, which is referred to as *response amplification*, appears to represent a general principle of multisensory processing. It is particularly potent when the cross-modality stimuli are derived from the same events, and are thus closely linked in space and time.

We recently conducted an experiment which illustrated the functional significance of response amplification in the context of a sensorimotor coordination task (Kelso et al. 2001). A group of participants produced rhythmic flexion and extension movements of the index finger, in time with the beat of an auditory metronome. The movements were made in either a flex-on-the-the-beat or an extend-on-the-beat pattern of coordination. When the participants produced the extend-on-the-beat pattern, there was a tendency to switch to flex-on-the-beat as the frequency of the pacing metronome was increased. In other conditions, we also required that the participants make contact with a physical stop, the location of which was either coincident with or counterphase to the auditory stimulus. Two effects were observed. When the haptic contact was coincident with the beat, both patterns of coordination (flex-on-the-beat and extend-on-the-beat) were stabilised. That is, few or no transitions were observed with increases in rate for either flexion or extension conditions. In contrast, when the haptic contact was counterphase to the metronome, coordination was actually destabilised, with transitions occurring from flex-on-the-beat to extend-on-the-beat and vice versa. Individuals were drawn to patterns of coordination in which sound and active, intentional touch coincide in time, regardless of whether flexion or extension movements were accentuated. The results also provide an empirical demonstration that the balance between the expression of neuromuscular-skeletal constraints and those based on cognitive intent can be altered by changes in task context (Carson, in press)—in this case through the provision of augmented feedback in another modality.

It is well known that the latency of a manual response to the onset of a stimulus in one modality (e.g. a visual stimulus) is decreased in the presence of a simultaneous stimulus (e.g. an auditory stimulus) in another modality (Hershenson 1962; Todd 1912). The general finding that reaction times in bimodal stimulus trials are markedly shorter than in unimodal trials has been termed *intersensory facilitation*. While most investigations have focussed upon visual-auditory interactions, the phenomenon can also be observed in simultaneous combinations involving tactile stimuli (Forster et al. 2002). Recent studies focussing upon event-related brain potentials have promoted the view that audiovisual (Schröger and Wid-

man 1998) and auditory-somatosensory (Foxe et al. 2000) facilitation occurs primarily in sensory areas. It has also been noted however that rCBF changes in anterior cingulate cortex are greater during visual-tactile cross-modal matching than during intramodal matching (Banati et al. 2000). The necessary conclusion that cross-modal integration is mediated by, and exerts an influence upon, multiple brain areas, is further supported by the observation that more forceful responses are produced following presentation of bimodal stimuli than in response to stimuli presented in a single modality (Giray and Ulrich 1993).

The precise role played by cross-modal integration in rhythmic sensorimotor coordination is likely to be complex. When syncopation is required (e.g. extending between the beats of a metronome), the accented phase of the movement cycle (extension) must be performed counterphase to the sensory stimulus. In bimodal versions of this task (e.g. Kelso et al. 2001), the phase of the movement that is not the focus of emphasis (flexion) is contiguous with the primary sensory stimulus (the metronome), whereas the accented phase of the movement cycle (extension) is associated with the secondary sensory (tactile) stimulus. In such circumstances there exists the potential for response competition. It has long been assumed that when alternative behavioural responses must be coordinated with multiple sources of sensory information, specific attentional control mechanisms must be engaged (e.g. Awh and Gehring 1999). Several lines of evidence now indicate that the anterior cingulate cortex plays a critical role in this regard.

Recent studies employing recordings of event-related brain potentials (e.g. Gehring and Fencsik 2001) and fMRI (e.g. Dreher and Grafman 2003) have indicated that the ACC is engaged in circumstances in which it is necessary to resolve conflicts between alternative stimulus-response associations. The ACC assumes a particular role in detecting the presence of response competition, and thus the conditions under which performance errors are likely to occur (Carter et al. 1998). It has been established that engagement of the ACC is specific to the detection of conflicts in response execution, rather than stimulus identification (van Veen et al. 2001). The additional observation that the functional consequences of focal damage to the ACC depend on the nature of the required motor response (e.g. manual or vocal) (Turken and Swick 1999) lends further weight to the proposal that the region plays a critical role in response selection.

On the basis of the foregoing analysis it is possible to speculate as to the role of the ACC in relation to the stabilising role of augmented sensory feedback, and in mediating the differential stability of syncopation and synchronisation tasks. When response conflict arises in the context of rhythmic sensorimotor coordination, for example when the accented phase of the movement must be performed counterphase to a sensory stimulus, additional engagement of the ACC may be required. In contrast, when the accented phase of a rhythmic movement is made in-phase with a sensory (e.g. auditory) stimulus, or when augmented sensory feedback in another modality (e.g. touch) is provided, a reduced role for the ACC is to be anticipated. If, as has been proposed, there is close correspondence between the level and distribution of activity in anterior cingulate cortex and the classic motor zones, this association may represent the neural basis of the increases in the stability of sensorimotor coordination that are observed in the presence of coincident multi-sensory cues. To the best of our knowledge this hypothesis has not yet been examined directly.

General summary

The extensive intrinsic connections that exist within the cortical motor network give rise to distributed interactions that form the basis of natural movements. We have argued that the focality of motor output during sensorimotor coordination is governed in part by the level and distribution of activity in brain regions such as anterior cingulate cortex that mediate affective and cognitive influence on voluntary movement control. We have proposed that factors, such as chronic (e.g. Carroll et al. 2001) and acute (e.g. Carson and Riek 1998a) alterations in muscle strength, that alter the efficiency with which movement is generated by the motor system, engender corresponding changes in the pattern of input to the classic motor zones from these brain regions. To the extent that such changes alter the interactions between the cortical representations of the focal muscles recruited in a movement task and brain circuits which do not contribute directly to the required movement they may also impact upon the stability of sensorimotor coordination.

When augmented feedback is provided, and input from the various sensory modalities occurs synchronously with the accent of a voluntary movement, the stability of coordination is enhanced. In contrast, in circumstances in which multisensory cues do not coincide, and it is necessary to resolve conflicts between alternative stimulus-response associations, deficits in coordination emerge. We have argued that the anterior cingulate cortex may also play a significant role in this regard, by mediating the influence of cross-modal sensory integration upon motor output.

We have raised the possibility that the functional contributions of different brain areas are altered profoundly during sensorimotor coordination, by relatively subtle variations in the characteristics of the task. In addition to demonstrating that the various constraints on coordination are complementary and inclusive, we have sought to clarify the means by which their expression and interaction may be mediated by the integrative action of the central nervous system.

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