

Guiding Movements without Redundancy Problems

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Abstract.

Approaches to the problems of multi-muscle and joint redundancy have typically been based on the assumption that control levels of the nervous system directly deal with variables describing the motor output – electromyographic (EMG) signals, forces and kinematics. An alternative approach to these problems can be developed in the framework of the • model based on the empirical solution of another classical problem in the motor control - that of the relationship between posture and movement. This solution implies that control levels guide movement by changing specific neurophysiological parameters and modify their pattern if the resulting action is in error. Specifically, these control parameters interfere with the transmission of afferent signals by spinal and supraspinal neurons to motoneurons. Some parameters reset the spatial coordinates at which a stable posture of the body or its segments can be reached. Other parameters deal with stability of posture and movement. This parametric control strategy releases higher control levels from the burden of solving redundancy problems at the level of output, i.e. mechanical and EMG variables. In response to changes in control parameters, appropriate values of mechanical and EMG variables and their transformations (e.g., from the hand kinematics to joint angles) emerge automatically, following the natural tendency of the neuromuscular system to reach an equilibrium state. This process results from the natural tendency to minimize the overall activity and the interactions between different components (neurons, muscles and joints) of the neuromuscular system in response to resetting of control parameters (the principle of minimal interaction). Based on these ideas, we outline non-computational, dynamical solutions of the problems of multi-muscle and multi-joint redundancy. This approach does not reject the notion of synergies, primitives, or recently proposed classification of multi-joint co-ordinations into a controlled and uncontrolled manifolds. Rather, it suggests that synergies or manifolds, like trajectories and forces, may be an emergent property of the neuromuscular behavior resulting from the response of the system to changes in control parameters in specific environmental conditions.

Introduction.

The number of available degrees of freedom (DFs) of the body is typically greater than that required to reach the motor goal (*DFs- redundancy*). The number of muscles per one DF is much greater than 2 (*multi-muscle redundancy*). The nervous system takes advantage of these redundancies to control actions in a flexible way so that, for example, the same motor goal can be reached differently depending on our intentions, external environmental (e.g. obstacles) or intrinsic (neural) constraints. Despite this flexibility, the central control of actions is unambiguous: each time the body moves, a unique action is produced despite the possibility of using other actions leading to the same goal. It is unclear how these seemingly opposite aspects – flexibility and uniqueness- are combined in the control of actions. Following Bernstein (1967), we refer to these aspects of action production as the “redundancy problem”.

Approaches to redundancy problems have typically been based on the assumption that control levels of the nervous system are directly involved in programming, computation and specification of the motor output (muscle activations, forces, and kinematics). In the most explicit form, this assumption underlies force-control (FC) models of movement production (e.g. Wolpert, Ghahramani & Flanagan 2000). Initially stemming from robotics (Hollerbach 1972), such models have become especially popular following the recent advances in computational neuroscience. FC models have also integrated the notion that, in

movement production, the nervous system relies substantially on motor memory, takes advantage of previous experiences, learning, implicit or explicit knowledge of physical properties of the body and the environment (Lashley, 1951). In the force control formulation, this capacity has become associated with inverse and forward internal models that represent the basic dynamical properties of the system or its components. A number of recent articles have presented arguments in support of the idea that control is based on paired inverse and forward internal models (Bhushan and Shadmehr, 1999, Wolpert and Kawato, 1998; Kawato, 1999; Wolpert and Ghahramani, 2000).

FC models, however, seem cannot be reconciled with some basic physiological principles of movement production (Ostry and Feldman, 2003). A major problem with these models is their inability to explain in a physiologically feasible way how control systems produce movements without provoking resistance of posture-stabilizing mechanisms to deviations from the initial posture. This question is the essence of the posture-movement problem that in most explicit way has been formulated by Von Holst and Mittelstaedt (1950/1970). Specifically, they emphasized that there are neuromuscular mechanisms that generate electromyographic (EMG) activity and forces in order to resist perturbations that tend to deflect the body from an initial posture. But at the same time, the organism can intentionally adopt different postures and maintain them with a certain degree of stability. If each new posture of the system is considered to be a deflection from an initial posture, then the deflection would result in resistance that would tend to return the system to its initial posture. However, everyday experience tells us that the nervous system has no problem in moving the body or its segments away from an initial posture and stabilizing different postures without triggering resistance (Balasubramaniam & Wing, 2002).

A solution to the posture-movement problems could be obtained if posture stabilizing mechanisms (“reflexes”) were suppressed, completely or partially, by a central pattern generator when the transition to a new posture is made. This solution has been rejected by Von Holst and Mittelstaedt 1950/1970) on the basis of empirical evidence showing that any posture of the body is maintained by resisting reactions similar to those seen in the restoration of initial posture in response to perturbations (Von Holst & Mittelstaedt, 1950/73). Von Holst and Mittelstaedt suggested that in order to produce movement, the nervous system influences afferent systems in such a way as to reset the initial postural state. As a result, the initial posture appears to be a deviation from the newly specified posture. This implies that the same postural mechanisms that stabilized the initial posture would act to stabilize the new one. The notions that postural resetting underlies movement production and that such resetting is achieved by means of appropriate central influences on afferent systems are the essence of Von Holst’s refference principle that he considered as a solution to the “posture-movement problem”. Note that while formulating the refference principle, Von Holst was well aware of the existence of central pattern generators of different movements and that active movement production is possible in the absence of proprioceptive feedback to muscles (deafferentation). This knowledge did not discourage him from the formulation of the refference principle that implies that, in intact neuromuscular systems, proprioceptive feedback is fundamental for adequate regulation of posture and movement. We think that this implication is well justified by the results of numerous comparisons of movement production in intact and deafferented organisms, both in humans and animals. In particular, in the absence of vision, deafferented patients, even after years of practice are unable to maintain steady-state positions of the arm, walk or stand without assistance, thus implicating a strong role of proprioceptive feedback in the stability and regulation of any posture (Levin et al, 1995).

The posture and movement problem is especially obvious in FC models that are based on the idea of programming EMG signals and muscle forces (torques) according to the desired trajectory of the effector. Specifically, the programmed generation of forces will produce deviation of system from the initial position. In response, the posture-stabilizing mechanisms will produce resistance tending to bring the system to its initial position. Control levels might attempt to reinforce the programmed action by generating additional EMG and torques that counteract this resistance. However, this strategy would be non-optimal in terms of energy output, since it would require high forces not only for motion but for the maintenance of final posture. The problem is that the force control model has no means to reset the “postural state” in a physiologically feasible way. Moreover, the FC formulation conflicts with a basic physical rule stating that steady states of a dynamical system are determined by intrinsic system parameters that are independent of variables describing its external, output behavior (Glandsdorff & Prigogine, 1971). Applying this rule to biological systems, one can say that transitions from one steady state body posture to another result from

resetting intrinsic system parameters to which external variables (in our case EMG signals, forces and kinematics) do not belong. The output variables emerge in response to this resetting. Focusing on output variables (EMG and forces) FC models were unable to indicate specific neurophysiological parameters responsible for postural resetting. Therefore, the transition between postures remains an unresolved issue in the FC model. This is not an inconsequential failing of the force control formulation. The unopposed shift between postural states is a fundamental characteristic of everyday motor activity. The inability of the force control strategy to re-establish posture at a new location without self-generated resistance is a basic failing of the formulation. Although the force control hypothesis has important applications in robotics (Balasubramaniam & Feldman, 2002), it falls short of explaining a very basic aspect of biological movement production.

The λ model for motor control, a version of the equilibrium-point (EP) hypothesis (Feldman & Levin, 1995) fully respects the “reafference principle”. In addition, the λ model explicitly indicates the parameters that the control systems can reset to produce an unopposed movement to a new posture. In order to explain how this model solves the posture-movement problem, as well as the problems of muscle and joint redundancy, we will first outline the basic features of the model.

Fundamentals of the Equilibrium point hypothesis (the λ model).

The λ model is based on the experimental finding that central changes in length-dimensional parameters - muscle activation thresholds (also called the stretch reflex thresholds) – underlie active motor behaviors (postural resetting, voluntary movement or isometric torque generation; Matthews 1959; Asatryan and Feldman 1965; Feldman 1996; Feldman and Orlovsky 1972). Many, including cortico-spinal descending systems have the capacity to regulate muscle activation thresholds (Feldman & Orlovsky 1972). Deficits in the central regulation of thresholds are associated with dramatic movement problems in neurological patients including those with impairments of cortical areas or deafferented patients (Levin and Dimov 1997; Levin et al. 2000). The basic principles of the equilibrium point (EP) hypothesis are summarized in Figure 1.

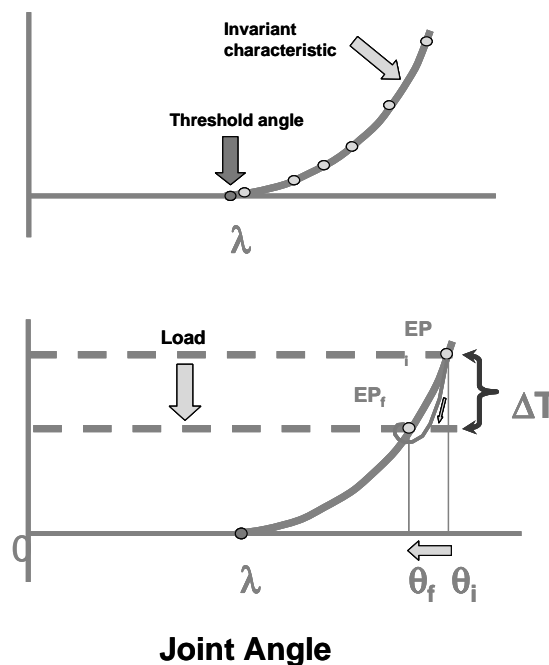


Figure 1. Fundamentals of EP hypothesis. Upper panel. Neural control levels set the threshold muscle angle (λ). Muscle activation and recruitment of its motor units change depending on the difference between the actual and the threshold joint angles. With the threshold constant, the torque-angle relationship is called the invariant characteristic, IC. Given a specific value of the threshold and external load, the system achieve a steady state in which the load is balanced. This state is characterised by the appropriate combination of position and muscle torque. This combination is called the equilibrium point or EP (the point of intersection of the load characteristic and IC). Voluntary movements are produced by setting a new value of the threshold. Lower panel. Involuntary movement. A change in the load (vertical arrow) brakes the balance between the muscle and load torques (ΔT) resulting in motion (green curve) to a new equilibrium point on the same IC (EP_1), if the subject does not intervene, at which the balance is regained.

According to this scheme, motoneurons are recruited in the range where the actual muscle length exceeds its threshold length (λ). In other words, by specifying the activation threshold, control levels “tell” motoneurons, in a feedforward manner, where, in terms of spatial coordinates, they will be recruited and counteract external forces (in particular, those of antagonist muscles). Neither the number nor the frequency of recruited motor units is specified by the control signal. Thus this model illustrates an important notion that the relationship between the central control signals and the motor output is *ambiguous* (Bernstein 1967). For example, during changes in the arm position following unloading (the unloading reflex), control signals remains the same but the motor output (EMG activity, torque, position,) varies depending on the load; in the waiter reflex (waiter holds a steady tray as he unloads dishes from it), the same position is maintained due to a change in the central control signals. Note that by specifying a central control pattern the nervous system limits the set of possible actions whereas the interaction of the neuromuscular system with the environment (the load in this case) reduces this set to a unique action. Having this in mind, one can say that central control signals are *task-specific*, i.e. produce the desired motor output only in specific external conditions. A change in these conditions may necessitate readjustment of control signals to reach the desired goal. Another important point of the model is the notion that nervous system cannot and does not need to program muscle forces, kinematics and EMG patterns. These are characteristics *emerging* from the interaction between all components of the system, including the environment. Yet another important point is that control systems take *advantage of reflexes* (e.g., by changing the stretch reflex threshold) in movement and force or torque production, which is consistent with the contemporary notion that reflexes are broadly adjustable rather than rigid stimulus-response structures. The most important point of the model is that active movements are produced by changing control variables shifting the equilibrium point of the system. This point determines the postural state (steady state) of the system and thus pre-determines the values of output variables (EMG, forces, torques) at which the neuromuscular system might be stabilized. In this sense, posture and movement are controlled by the same mechanisms, thus offering a direct solution of the Von Holst’s posture-movement problem described above. Note that the basic notions described in this section are straightforward consequences of a simple experimental fact that intentional movements result from shifts in the muscle activation thresholds (Asatryan & Feldman 1965).

To summarize, the λ model suggests a physical rule for movement production given that systems with position-dependent forces have an attractor or equilibrium point. The location of this attractor in spatial coordinates is determined not by forces but by specific parameters of the systems - determinants of the equilibrium state. Since equilibrium postures of the body are not determined by muscle forces, a voluntary movement of the body from one static posture to another can only be accomplished by altering the determinants of the equilibrium state. If the nervous system could alter muscle forces leaving these determinants unchanged, muscles of the body would generate additional forces resisting the deflection from the initial posture and thus preventing the transition to a new posture. In contrast, in response to a change in these determinants, muscle activation and forces would *emerge automatically*, which makes programming or intentional specification of muscle forces unnecessary.

A natural extension of the λ model has been made on the basis of the principle of minimal interaction (Gelfand & Tsetlin, 1971). Activity of each component of the neuromuscular system depends on the difference between the actual and the referent (threshold) value of appropriate physical variable. Intentional movements or isometric torques are produced by shifting the referent values of physical variables. One can say that biological motor actions obey the principle of minimal interaction if the afferent feedback to each

element and the interactions between different elements of the system are specifically organized to drive the neuromuscular system to a state in which the difference between the referent and the physical values of output variables and thus the overall activity in the system becomes minimal, in the limits determined by task constraints. The muscle contraction, stretch reflex and reciprocal inhibition between agonist and antagonist muscles are examples of the processes realizing the principle of minimal interaction. More specifically, in response to activation, muscles shorten thus decreasing the difference between the actual and the referent (threshold length) of the muscle and allowing homonymous and heteronymous proprioceptive feedback to diminish the activity (see Figure 2).

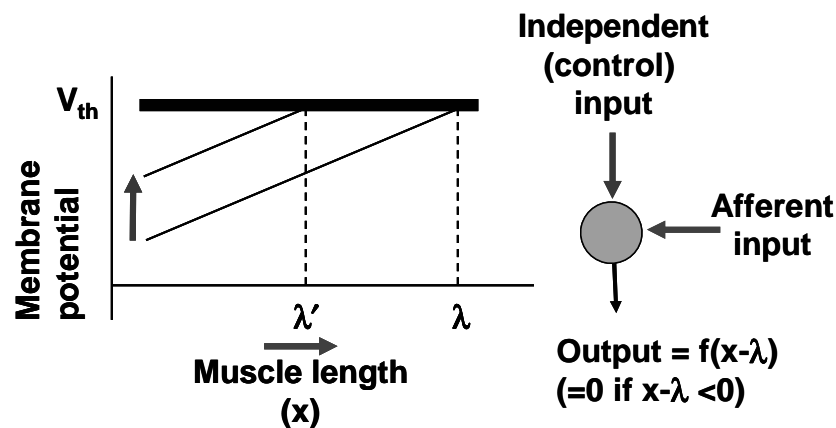


Figure 2. Frame of reference for a single motoneuron. Motoneuron together with length-dependent afferent input and electrical threshold (V_{th}) is a device that transforms independent, i.e. control changes in the membrane potential (red arrows) into length dimensional variable, λ . Left panel. Initially, stretching the muscle quasi-statically results in a gradual increase in the membrane potential of the motoneuron and its recruitment at the threshold length, λ . When an independent control signal is added, the motoneuron is recruited at a shorter muscle length. Thus, the control signal only set the range ($x-\lambda > 0$) of the muscle lengths, x , in which the motoneuron can be active) and counteract to external forces. Right panel. Each neuron has its own FR in which afferent input carries signals on appropriate physical variable, s (which, for a motoneurons, coincides with the muscle length, x). At the level of the membrane of the neuron, an independent control input, is transformed into a threshold value, h (coinciding with 1 for the motoneuron) of the same physical variable. This threshold plays the role of the referent point for the measurement for variables. The output of the neurones is thus frame-dependent.

Although there is a tendency in literature to consider the λ model as analogous to a servo mechanism in which the controller directly specifies a desired position, the analogy is actually misleading. In the model, λ is not the desired position that the system should establish and the difference between the actual muscle length and λ is not the movement error. A more appropriate interpretation of the model is the following. There exists a spatial frame of reference (FR) or a system of coordinates in which motoneurons function. This frame has a referent or origin point - the threshold muscle length. Control systems may shift the referent point to produce muscle activation, force and movement. The neuronal activity in this frame is defined by the distance between the point characterizing the current state of the system and the origin point. A motoneuron that is recruited later in the sequence has a spatial frame embedded in the frames of motoneurons recruited earlier yielding a natural hierarchical structure for movement production. The notion that the activity of all elements of the neuromuscular systems are frame-dependent, that intentional movements are produced by shifting appropriate FRs by changing their referent parameters (origin, scales, orientation, and even geometry), that there is a hierarchical relationship between different FRs, and that all the interaction in the system, both within each FR and between different FRs, obey the principle of minimal interaction seems most useful in our approach to the problem of multi-muscle and multi-DF redundancy as well as to other problems of motor control in general. We will specifically focus on two FRs. One FR

comprises all possible configurations of the body controlled by shifts in the FR origin that represents a particular, referent body configuration specified by the nervous system. The other FR is a FR associated with the environment and controlled by shifts in its origin. Like the FR for motoneurons, each FR is organized based on appropriate afferent inputs to neurons. For example, the FR associated with the environment is supposedly organized predominantly based on vestibular and visual signals.

In the subsequent sections, we will present empirical evidence that appropriate frames are actually used to guide movements in the wake of multi-muscle and multi DF redundancy.

Issues of redundancy.

Although our solution of the DF redundancy problem has not been elaborated in detail, the main idea is simple and may be illustrated for arm pointing movements. Let us assume that some spinal and supraspinal neurons projecting to motoneurons of skeletal muscles of the body, including the extremities may integrate proprioceptive signals from muscles, joint and skin to receive afferent signals, say, about the coordinates of the tip of the index finger (the endpoint) that is typically used to point to targets. The role of these signals will be similar to those of afferents (muscle spindles) that are sensitive to changes in the muscle length, except that the recruitment and activity of these neurons will depend not on muscle length but from coordinates of the endpoint. Like for motoneurons, control influences on these neurons can be measured by the amount of shifts in the threshold (referent) coordinates of the endpoint. The difference between the actual and the referent coordinates will determine whether or not such neurons are recruited. These referent coordinates may be shifted by control levels in a FR associated with the environment to produce a *referent trajectory*. The neuromuscular system will tend to minimize the discrepancy between the actual and referent coordinates forcing the arm and other body segments to move until the endpoint reaches a final position at which a minimum of activity of the neurons and in the system in general is reached. After this, the system may compare the output with the desired one. In particular, if the final position of the arm endpoint is different from the desired one, control levels may adjust the referent endpoint trajectory until the final endpoint position coincides with the desired one. Again, although the set of possible configurations for each position of the endpoint is redundant, the minimization process initiated by shifts in the referent coordinates of the endpoint will result in a unique pattern of them. This configuration pattern can indeed, vary with repetitions, intentional modifications of the referent pattern, task constraints (including release or restriction in motion of some DFs), and history-dependent changes in the neuromuscular system (e.g. due to fatigue).

Multi-muscle control and the Referent configuration (R) hypothesis.

The configuration of the body may be described geometrically by a set of the current joint angles or coordinates q_i , associated with the n mechanical DFs of the body. These angles comprise an n dimensional vector, Q . It is assumed that the nervous system compares these values with referent angular values r_i that taken together comprises the referent configuration of the body, R . These referent angles r_i resemble the reciprocal commands previously defined in the lambda model. The model has also introduced the notion of coactivation commands (c_i) that determine the extent of the spatial zone in which agonists and antagonists may be active simultaneously (Levin & Dimov, 1997). When $c_i = 0$, then the r_i command is the threshold angle at which the recruitment of muscles in the corresponding DF begins. The ensemble of these threshold angles, a multidimensional vector defines the threshold configuration of the body- R , a collective threshold for all skeletal muscles. One can say that due to the collective threshold, all muscles are involved in a synergy. The threshold nature of the R implies that when configurations coincide ($Q = R$ or $Q - R = 0$), the EMG activity of the all the muscles involved should be zero independent of their biomechanical functions. Such cases are rare (but not impossible, see below) and typically the body moves until the external and muscle forces reach a balance at an "equilibrium body configuration", if stability requirements are met. In

order to produce a voluntary movement, the nervous system modifies R, a change in which elicits an imbalance of forces at the initial body configuration, resulting in motion to a new configuration at which balance and stability are regained.

A slightly different scenario may result when the co-activation command is employed. This command produces changes in muscle activation thresholds to surround the R configuration with a zone of configurations at which agonist and antagonist muscles are active simultaneously. Thereby, the opposing muscle groups produce balanced torques such that the configuration R remains unchanged. In this sense this command is functionally independent of the r command with the following reservation: since the coactivation zone is created around the R configuration and thus travels with it (Levin & Dimov 1997). In the presence of co-activation, the referent configuration no longer represents a purely threshold configuration but may be more generally regarded as the configuration at which the EMG activity of the muscles show minimal activity with the depth of the minimum defined by the magnitude of the co-activation command.

A testable consequence of the referent configuration hypothesis is now presented. In the presence of inertial and reactive forces, changes in R specified by the nervous system cannot be replicated in the actual configuration. However in movements with reversals, the two configurations might approach and match each other although transiently. If such a matching is present, then the global EMG activity of all working muscles should be simultaneously minimal, with the minima's depth being defined by the degree of co-activation present.

This hypothesis has been tested in three different scenarios which are presented here. We will present results from head movements in monkeys, sit to stand movements with reversals and arm-trunk movements with reversals where a global EMG minima was observed at the point of reversal.

1. Head movements in monkeys.

Lestienne et al. (2000) presented targets to monkeys seated in a primate chair with the trunk and abdomen restrained by a seat belt. In a block of 20 trials when the monkey faced the centre of an arc (0°) a fruit was displayed to the left (60°). The monkey turned the head and when the movement approached 60° the fruit was quickly moved to the centre of the arc. Following the target the monkey made a 60° movement to the right. In another block the monkey made an 80° head movements, from an initial head position of 20° to the left to and from a target placed at 60° to the right. Three dimensional coordinates of the monkey's head were recorded along with EMG activity of left and right neck muscles in the large superficial, long and sub-occipital areas linking the skull to the shoulder girdle, vertebral column and the first two vertebrae. The results from the experiment are shown in Figure 3.

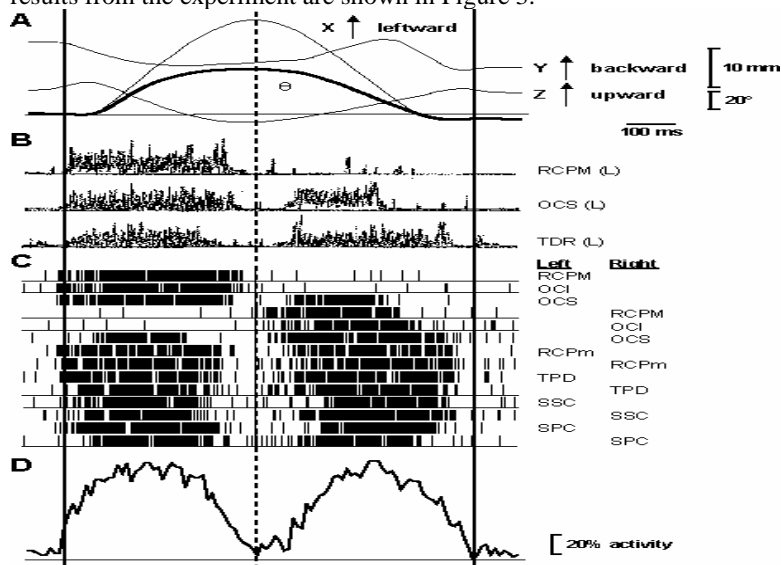


Figure 3. Monkey head movements. Kinematic and EMG patterns of head movements of a monkey during a single movement to and from the left target. B. Typical EMG patterns from three different muscle groups. C. Quantified integral of the EMG activity of seven pairs of neck muscles. D. Ensemble activity of normalised EMG signals of 14 muscles. Reproduced from Lestienne et al (2000) with permission.

An inspection of Figure 3 shows that the EMG activity of all muscles, irrespective of biomechanical function, showed minima at two phases of head movements. One minimum occurred before the onset of the movement, at static positions corresponding to the resting positions at which forces provided by small tonic activity of the neck muscles and by the passive elastic forces of the head-neck system were sufficient to balance the head gravitational torque. More importantly, an additional EMG minimum or a global minimum lasting 70-100 ms was observed during the movement reversal, followed by activity of neck muscles that guided the head-neck system to its initial configuration, as shown in Figure 4. Despite the biomechanical, anatomical and functional diversity of muscles involved, all showed minimum EMG activity at the point of reversal.

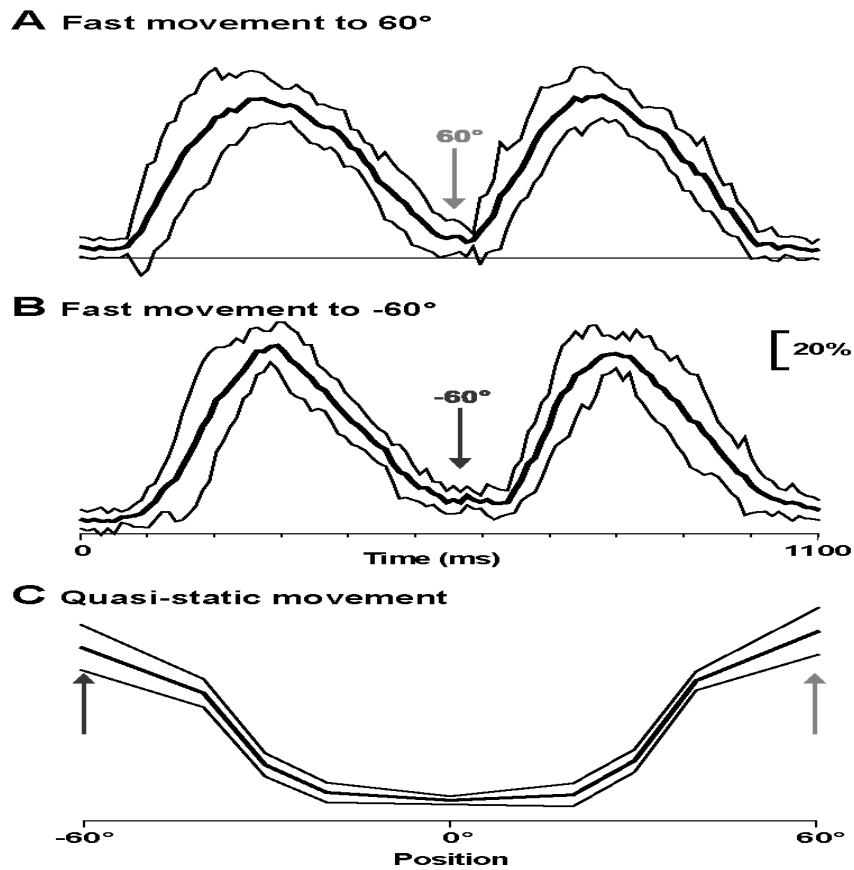


Figure 4. Global EMG minima. Ensemble activity of normalised EMG activity (mean and SD) of 14 muscles during fast movements to the left target (A) and right target (B). During fast movements ensemble activity is minimal at head positions shown by solid arrow in A and open arrow in B, where the activity would be maximal if the appropriate positions were maintained as shown in panel C. Reproduced from Lestienne et al (2000) with permission.

2. Sit-to-stand movements.

Feldman et al (1998) investigated a functionally similar movement task with reversals in human subjects. In response to an auditory signal, six healthy subjects sitting on a stool with their arms resting on their knee, rose from the seat to a semi-standing position and returned to sitting. While lifting their body, subjects stretched their arm pointing (without touching) to a plastic disc target placed in front of them at a height of 100cm. The movement was performed smoothly at a comfortable speed, in each of 10 trials (4-5.5s each, 15s between trials). 3-D coordinates of the right shoulder, hip, knee and ankle were recorded in addition to EMG activity in arm, trunk and leg muscles. The results are summarized in Figure 5.

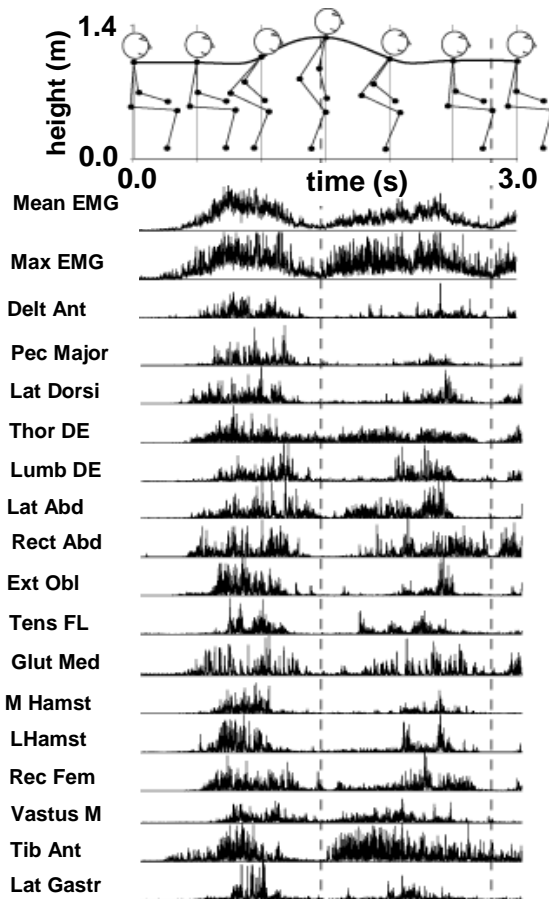


Figure 5. Sit-to-stand movements. An example of normalised EMG signals from arm, trunk and leg muscles and the vertical coordinate of the shoulder during the sit to stand movement with direction reversal. The vertical line shows where the global minimum was observed. The second EMG minimum associated with sitting is shown by the second vertical line. Adapted from Feldman et al (1998) with permission.

Global minima of EMG activity associated with the reversal phase were observed in not only the postural stabilizers and prime movers (trunk and leg muscles) but also in the shoulder muscles, anterior deltoid and pectoralis major. A closer look at Figure 5 shows that, although in some muscles, the global minimum occurred during the brief silent period between sequential bursts, the activity of many other muscles terminated substantially before and resumed comparatively long after the transitional global minimum. The finding of the global minima at the transition phase is thus consistent with the hypothesis that changes in the referent body configuration may underlie sitting to standing movements of the body. We believe that these findings add to the richness of the concept of synergy or manifold as presented by Scholz et al (1999) for a similar task and as described in Schöner (this volume).

3. Trunk assisted pointing movements with reversals.

Trunk assisted pointing movements (as illustrated in Figure 6) may be considered the superposition of two synergies; a transport synergy (for arm movement) and compensatory synergy (for changes in shoulder and elbow joint angles). The superposition of the two synergies ensures an invariant trajectory when active trunk flexion is involved in reaching for a target (Pigeon et al, 2000).

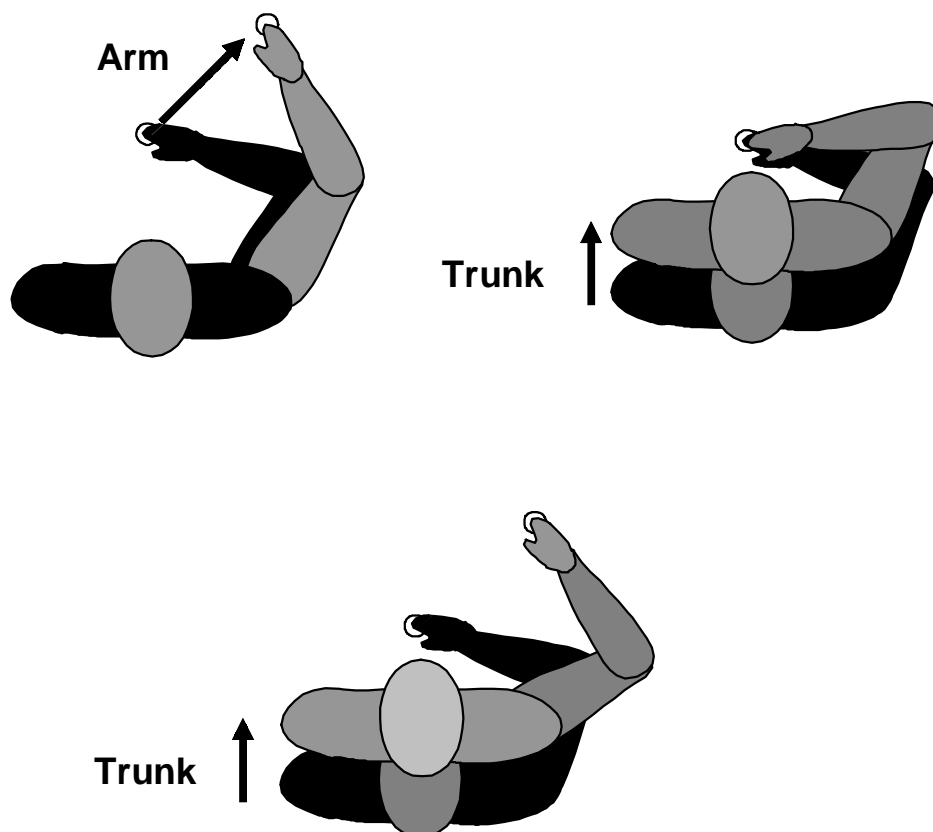


Figure 6. Superposition of synergies. A. Transport synergy for pointing or reaching movement where only the arm moves. B. Compensatory synergy as shown by changes in elbow and shoulder joint angles when bending the trunk forward while maintaining arm posture. C. Superposition of synergies shown in A & B, when the arm moves towards a target ipsilaterally in conjunction with trunk motion where the arm trajectory remains invariant despite additional degrees of freedom as demonstrated by Pigeon et al (2000). Figure adapted from Pigeon et al (2000) with permission.

Balasubramaniam & Feldman (2001) presented targets in both the ipsilateral and contralateral directions from six seated subjects who had to point to the targets (within reaching distance) with redundant use of the trunk (bending the trunk simultaneously) and reverse the trajectory on reaching the target, akin to the lower panel in Figure 6. The targets were placed within reach in the subject's workspace. 3-D positions of the sternum, shoulder, elbow, wrist and endpoint trajectories along with EMG activity in all major arm and trunk muscles were recorded. As shown in Figure 7, at the point of reversal all the muscles of the arm, trunk synergy showed a global minimum irrespective of their biomechanical function, once again confirming the predictions of the referent configuration hypothesis. One can say that when producing global EMG minima, the neuromuscular system strengthens the role of passive muscle properties and external forces, including gravity, in movement production. For example, during horizontal head movements in monkeys, the EMG minimization at the lateral positions allows the head movement to be reversed by the passive forces accumulated in previously stretched antagonist muscles. In sit-to-stand movements, EMG minimization allows the body to use gravitational forces to assist in returning to sitting. These explanations of the occurrence of global EMG minima in terms of mechanics are not alternative to the R hypothesis: they are an integral part of it. At the same time, taken separately, these explanations do not go far enough to answer the question of how the neuromuscular system is controlled to take advantage of the body and environmental forces and thus mechanically optimise the movement. The R hypothesis directly addresses this issue: the mechanical optimisation is not intentionally programmed but emerges each time when the actual and referent configurations match each other.

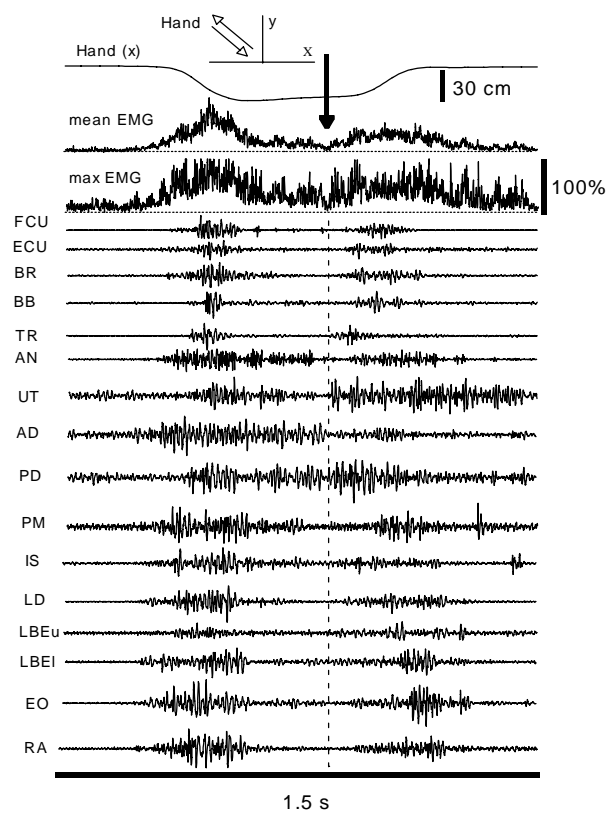


Figure 7. Arm-trunk coordination in reaching. The vertical arrow and dashed line show the occurrence of a global EMG minimum in the activity of 16 muscles of the arm and trunk; diagonal arrow show the direction of the hand movement (x is frontal and y is sagittal direction). EMG of muscles (from top to bottom): flexor and extensor carpi ulnaris, brachioradialis, biceps brachii, triceps, anconeus, anterior and posterior deltoids; pectoralis major, infraspinatus, latissimus dorsi, low back extensors (upper part), low back extensors (lower part), external oblique, rectus abdominus.

Testing the solution of the multi-joint redundancy problem.

Like the solution of the problem of muscle redundancy, the solution of the problem of DF-redundancy leads to some testable predictions. We describe two predictions that have been tested in pointing movements involving the trunk.

1. Hand trajectories remain invariant despite changes in the number of DFs involved.

As described above, pointing movements might result from control signals influencing neurons that receive afferent inputs related to the position of the arm endpoint in space and projecting either indirectly, via interneurons, or directly to motoneurons of all skeletal muscles. These control signals represent the referent coordinates of the endpoint. The neurones are activated depending on the difference between the actual and the referent coordinates. According to the principle of the minimal interaction, the system is driven, both locally and globally, to a state at which the difference becomes minimal, in the limits determined by intrinsic (neural) and extrinsic (e.g. gravity) constraints. Thus, control levels produce a referent trajectory of the endpoint whereas the actual endpoint trajectory emerges following the laws of mechanics and the principle of the minimal interaction tending to diminish the difference between the actual and the referent trajectory. This does not mean that the system will eventually establish the position coinciding with the referent one. Rather, the system will arrive at a position that is distant from the referent position so that the difference between these positions will provide the activation of neurons and motoneurons that is necessary to generate muscle forces counteracting the gravitational and load torques acting upon the arm in this position. The difference between the actual and the referent positions might be substantial in the cases when the movement is blocked (isometric torque exertion): since the actual position remains the same, the changes in the referent position will directly influence its distance from the former, resulting in isometric EMG and torque generation.

Guided by the minimisation principle, the system has the capacity not only to bring it to a steady (equilibrium) state but also to resist intermittent mechanical perturbations and thus rapidly return the endpoint trajectory to that obtained in the absence of perturbations. Such kind of dynamical stability has been demonstrated by Won and Hogan (1995). The principle of minimal interaction provides system's stability in a more broad sense: up to specific limits (that are exemplified below), the actual movement trajectory may remain the same regardless of changes in the number of DFs involved in the motor task, whether these changes are produced voluntarily, by the subject, or involuntarily, by imposing or releasing some DFs from mechanical constraints.

This prediction has been confirmed in several studies of pointing movements involving the trunk. In cases of movements to targets placed within the arm's reach, the endpoint trajectory remained invariant when subjects intentionally involved the trunk or when the trunk was recruited but its motion was mechanically blocked (Adamovich et al, 2001). In pointing to targets placed beyond the arm's reach, the trunk contributed to the movement extent and therefore mechanically preventing the trunk motion made reaching the target impossible. However, even in this case, the hand trajectory remained invariant until the hand approached the limits of the movement extent available for the arm alone (Rossi et al. 2002). In all cases, in response to the trunk arrest, the trajectory was maintained due to appropriate short-latency (about 50 ms) changes in the arm joint angles as shown in Figure 8.

It is also interesting to note that trunk-assisted reaching involves different segments that move in parallel when central commands related to functional components of the task are generated sequentially, akin to those in speech production. It is normally observed that commands underlying speech production are generated sequentially but the motor responses overlap, resulting in an acoustic effect called co-articulation (Fowler & Saltzman, 1993). This sequential control structure is similar to the problem of "serial order in behaviour" as discussed by Lashley (1951). He noticed that components of different behaviours including locomotion, prehension and language are generated sequentially and such generation cannot result from

moment-to-moment responses to a serially ordered environment. Serial order is a manifestation of a control principle that guides the behaviour of the organism, much the same way we propose that movements maybe guided without redundancy.

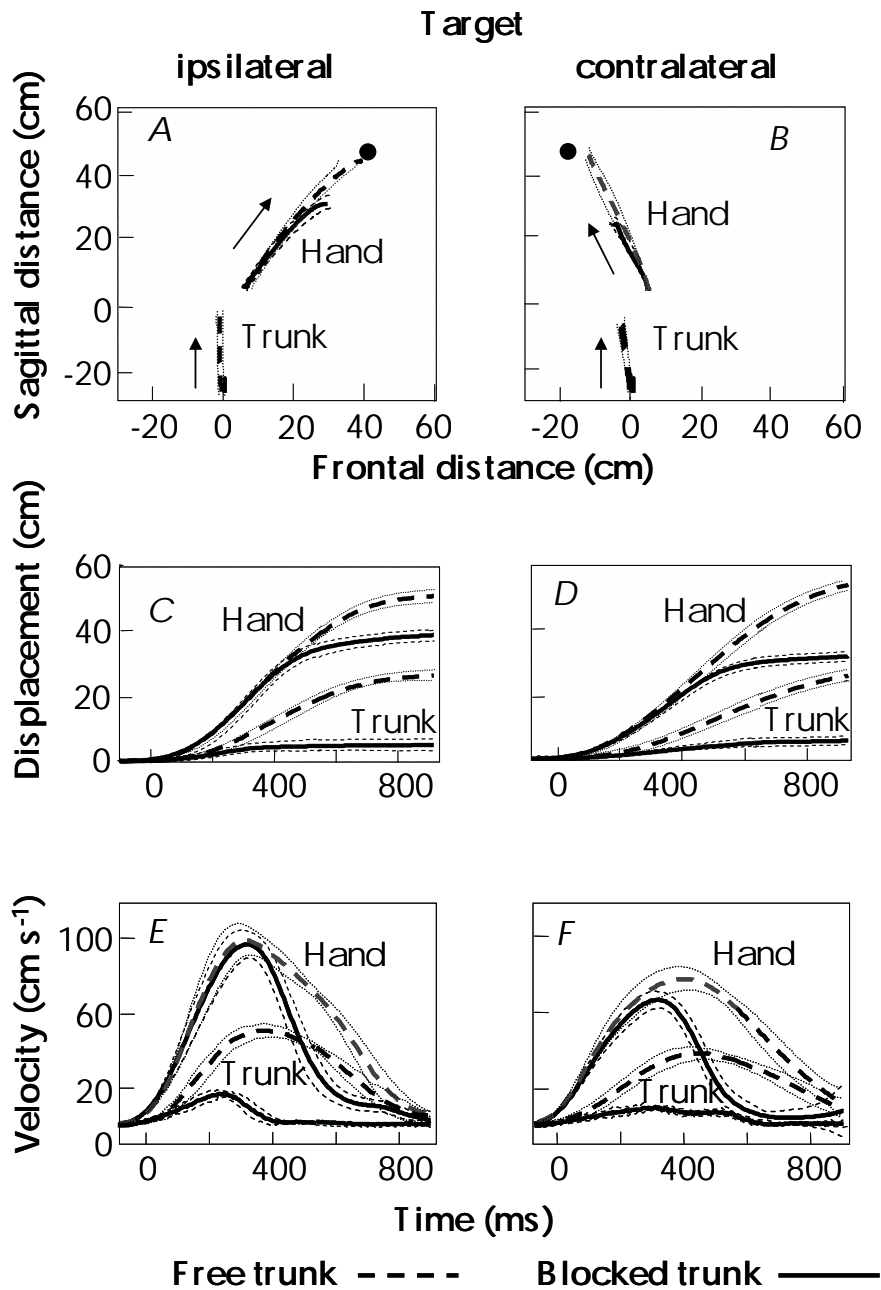


Figure 8. Sequential activation of synergies. Typical kinematic effects of trunk arrest in movements to targets located beyond the reach of the arm. Mean traces with SD for conditions when trunk motion is not obstructed (thick dashed lines) or blocked (thin dashed lines); arrows in A and B show movement directional and filled circles show targets. In free trunk movements subjects leaned the trunk forward about 23 cm and these displacements were reduced by about 3 cm when trunk movement was mechanically blocked. Despite differences in the trunk motion, the endpoint trajectories (A, B), displacements along them (C, D) and velocity profiles (E, F) initially followed the paths in trials in which the trunk was free to move. Adapted from Rossi et al. (2002) with permission.

2. Hand trajectory invariance may be provided in different FRs, depending on task demand.

Another consequence of the solution of DF-redundancy problem is related to the concept of FR. When we discussed the production of pointing movements we implicitly assumed that, since the targets were placed on a table, the referent coordinates of the endpoint were specified by the nervous system in a FR associated with the environment (experimental room) and, respectively, the invariance of the endpoint trajectory was observed in this FR. The invariance was maintained by substantial changes in the arm interjoint coordination in response to the trunk arrest. However, one can produce pointing to a target on the body (e.g. to the nose) so that the target will move with the trunk. To reach the target, the referent coordinates of the arm endpoint should be shifted in a FR associated with the trunk. One can predict that, the trajectory of pointing to such target will remain the same whether or not the motion of the trunk was prevented. Trajectory invariance, however, will be observed not in a FR associated with the environment but in a FR associated with the trunk. In addition, in contrast to pointing to targets in the environment, no change in the inter-joint coordination will be necessary to keep the trajectory invariant despite the trunk arrest. The ability to produce pointing movements in two different FRs with substantially different behaviours at the joint levels has been confirmed in a recent study (Ghafari et al. 2002). This study also shows that the transformation of the motor performance from one FR to another does not require learning, suggesting that FRs are pre-existing structures and it remains for the nervous system to choose an appropriate (“leading”) FR to control movement.

Synergies (primitives, controlled and uncontrolled manifolds) as emergent characteristics of motor behavior.

In the previous section describing the control of pointing movements, we emphasised the capacity of control levels to select task-specific FRs with the origin representing the referent coordinates of the endpoint. When one of the FRs is chosen as leading, it subordinates the FR comprised of all-possible body configurations by controlling its origin – the referent body configuration. The configurational FR, in turn, subordinates local FRs associated with single muscles and eventually motor units. Our solution of the DF-redundancy problem implies that control levels may guide the motor performance by shifting the origin of the leading FR whereas appropriate referent body configurations and eventually individual values of muscle thresholds emerge automatically. Moreover, while control levels may reproduce the same referent trajectories at the leading level, the emerging referent body configurations and, as a consequence, actual body configurations may change with the task conditions (like was the case in response to trunk arrests). By analysing these movements in terms of kinematics one can find appropriate functional subdivisions of DFs (synergies, primitives or manifolds), as for example was found for pointing movements involving the trunk or pistol shooting (Scholz et al, 1999, 2000, 2001) and Schöner (this volume). One can consider these subdivisions as a property emerging following the tendency of the system to minimise the activity and interactions in the system including the environment.

Using the λ model, we have shown that movements may be guided without redundancy in a non-computational, dynamical manner. Previous attempts to solve the redundancy problems such as force control models have been unsuccessful as they have always been formulated in terms of output variables (EMG, forces, and kinematics) with which the control functions of the nervous system are not directly associated. We believe that the referent configuration which is grounded in physiology may be very important in guiding multiple muscle systems without redundancy in the production of movements. Control in such systems is achieved by taking advantage of a position dependent attractor, which dictates the organization of moving parts into synergies (or manifolds as the case may be) and makes coordination

possible. Coordination dynamics is the study of the formation and evolution of such an attractor (Kelso, 1995). The stable states of these systems are controlled by system parameters and not forces.

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