The control of multi-joint movements relies on detailed internal representations

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Abstract

This paper addresses the question what level of detail is required in internal representations used in control of multi-joint movements, focusing on contact control tasks. Following Bernstein, we define the central problem to be which strategies are used in the nervous system in order to control the vastly redundant musculoskeletal system. Simplifications based on equilibrium point theories are rejected on the basis that when they are simple they do not lead to adequate behaviour, whereas when they are complex they implicitly introduce the detailed internal representations that they were meant to dispense with. Based on both experimental data and on simulation results, it is argued that timing of muscle activation needs to be precisely tuned to the task at hand and the environmental conditions. It is argued that it is impossible to achieve this without detailed internal representations of the properties of the effector system in relation to the environment. It is attempted to link Bernstein's notion of a hierarchical organization of the nervous system in which tasks are delegated to subsystems as low as possible in the hierarchical structure of the central nervous system, to recent advances in neuroscience.
1. Introduction

Multi-joint movements are not realized by simply stringing together the movements in the joints involved. Due to mechanical coupling and the action of poly-articular muscles, motions in one joint affect those in many others as well. Moreover, a human subject moving on one or two feet in a gravitational field can be considered as a highly unstable interlinked inverted pendulum controlled by a redundant set of actuators which are far from ideal force generators. This enormous complexity of our action system was convincingly discussed already half a century ago by Bernstein (e.g., Bernstein, 1967). Based on his inspiring work and further stimulated by Gibson (e.g., Gibson, 1979) who stressed the guiding role of environmental information on the control of actions, many have tried to identify simplifying principles in the organisation of movement control.

Especially among ecological psychologists the idea of detailed internal representations or motor programs has been disputed over the past decade (see Meijer and Roth, 1988 for discussion of this and related issues in the motor-action controversy). Since, indeed, it appears very unlikely that the central nervous system contains motor programs that deal with all details necessary to realize all variants of any movement observed in various environmental conditions, we sympathise with what has been defined by Turvey as “Round I of theorising on Bernstein’s problem: how to minimize the executive responsibility of the CNS” (Turvey, 1990). We have considerable problems, however, with his “Round II” of theorising where self-organisation is proposed as a general principle underlying the organisation of all types of movement (Turvey, 1990; see also Kelso and Tuller, 1984; Schöner and Kelso, 1988; Schmidt et al., 1991; Kelso and Schöner, 1988). As stated by Schöner and Kelso (1988) patterns are supposed to emerge spontaneously in the interaction between actor and environment “with no ordering influence from the outside and no executive homunculus inside”.

Van Wieringen (1988a, Van Wieringen, 1988b), however, argued that the emergence of skills during learning is difficult to imagine as the result of a free interplay of forces and information in the actor-environment system. Though some representatives of dynamic system theory use a considerably more carefully balanced appraisal of the concept of learning nowadays (Zanone and Kelso, 1992) as compared to earlier studies (“discovering an optimal self-organisation”, Fowler and Turvey, 1978), we believe that many present action theories still fail to explain important aspects of the control of skilled multi-joint movements.
In our contribution to this special issue on "Coordination of multi-joint movements" we will focus on discrete, largely automated, arm and leg tasks in which one has to exert forces on the environment in order to displace objects or one's own body. These "contact control tasks" are quite common in daily life but hardly addressed in theories of motor control. As we will try to substantiate, successful execution of such tasks is possible only if rather detailed internal representations of the properties of the effector-environment system are present in the CNS. On the other hand we support the view that many fascinating phenomena such as multistability and phase transitions as observed in various rhythmic movements are not likely to be prescribed by internal clocks included in motor programs. As convincingly demonstrated in this issue by Beek et al. (1995), non-linear dynamics provides powerful tools to explain these phenomena which can, indeed, be qualified as self-organisation. However, it will be clear from Beek and Peper (see also Zanone and Kelso, 1992) that this expression does not imply that there is no structural mechanism or neuronal medium at the physical or biological basis of these phenomena. In this respect we would support Van Wieringen (1988b) in his recommendation with respect to the "self-organisation or representation" controversy: Let's have both!

2. The need for simplifying strategies

As acknowledged by most movement scientists working in the field of motor control, the work of Nicolai Aleksandrovitch Bernstein (1896–1966) almost 30 years after his death, still provides an excellent introduction into the major issues of motor control (e.g., Bernstein, 1967). Bernstein was far ahead of his time when he addressed the enormous complexity of the musculo-skeletal system and the problems which arise in the interaction between an actor and his environment. The question how the CNS resolves the management problem to produce coherent and functionally effective movements is therefore usually referred to as "Bernstein's problem".

As excellent discussions of Bernstein's problem are available in literature (e.g., Turvey et al., 1982; Sporns and Edelman, 1993), we will restrict ourselves here to an outline of those elements that are central to the main topic of this paper:

*The inverse kinematics problem.* The human skeleton contains 100–150 degrees of freedom. As the goal of most tasks can be defined in terms of a very small number of degrees of freedom (e.g., movement of the hand or an
object or one’s own centre of gravity in work space), an infinite number of movements in the (many) joints involved is available to achieve the goal.

**The inverse dynamics problem.** Although each movement can only be realised by one particular combination of net joint torques as a function of time, there are two problems to be solved by the CNS. First of all, the number of muscles that we are provided with (about 800) is considerably larger than twice the number of degrees of freedom in our joints. As a result, particular net joint torques can be realised by an infinite number of combinations of muscle forces (the indeterminacy problem), and the CNS is faced with the problem of selecting a suitable one. Quite aside from this problem of redundancy, it seems unlikely — if not impossible — that the required net torque patterns as a function of time are organised through neural calculations comparable to what biomechanists do when calculating the net joint torques from segmental inertias, kinematical data, gravity and external forces. As argued by Sporns and Edelman (1993) a 5 degrees of freedom system would already require tens of thousands of multiplications to solve the two pages of Newtonian equations which describe the motions of such a simple system. It is, therefore, generally accepted that computational strategies as used in robotics have no relevance for biological systems.

**The controllability problem.** Apart from the problems mentioned above, Bernstein noted that muscles are not ideal force generators. There cannot exist a fixed relation between the excitation of a muscle and its force because muscle force is dependent on many other factors as well (muscle length and velocity, “history effects” such as potentiation and fatigue, activation and relaxation kinetics). In part these factors are due to the so-called “context conditioned variability” which indicates the fact that even stereotyped movements always differ to some extent in initial conditions (position relative to gravity and to objects in the environment, etc.). This context conditioned variability may give rise to quite different movement kinematics even if we would possess ideal force generators. Such considerations did lead Bernstein to the conclusion that there cannot and does not exist an unequivocal relation between central commands and the kinematics of movements.

Many scientists from various disciplines have searched for strategies by which the CNS might solve Bernstein’s problem. Clearly, Bernstein’s arguments and a number of complicating phenomena identified since that time by, for example, ecological psychologists, can be seen as convincing evidence against the so-called computer metaphor of motor control which
assumes a sequence of perception—cognition—action. In this (still quite widely supported) approach, perception serves as input for cognitive decisions about what motor programs have to be retrieved from memory and then executed. In contrast to some action theorists, however, we do not believe that a rejection of this computer metaphor should necessarily also lead to a rejection of the necessity of detailed internal representations in the brain. As will be substantiated below, contact control tasks require that we adapt the magnitude and timing of the activation of individual muscles so that the appropriate net joint torques as a function of time emerge. It will be shown that the popular equilibrium point models fail to meet these requirements. After showing that internal representations are a prerequisite for accurate execution of contact control tasks, the question is: what then is the nature of these internal representations? Is there direct evidence for the existence of such representations and to what extent are these representations associated with specific anatomical structures? Action theorists such as Turvey and his colleagues (Turvey, 1990; Schmidt et al., 1991) argue that theories which emerged in Round I based on for example connectionists models, synergy formation in relatively autonomous subsystems, etc., still leave too much responsibility to a supervisor and rely too strongly on reference signals, feedback loops, comparators and error-detecting devices. They seem to have considerable problems with associating specific sensory-motor functions to anatomical structures in the CNS (e.g., Reed, 1982; Kelso and Tuller, 1984; Turvey and Kugler, 1984). Latash and Latash (1994) even blame Bernstein for doing so occasionally.

Although we are aware of the difficulties in the interpretation of motor problems associated with lesions in particular brain structures, a second objective of this paper is to provide some neuroscientific evidence for the existence of learned (or in part possibly innate) pattern generating supraspinal centres.

2.1. Equilibrium point models

In the context of the type of discrete movements to be discussed here point attractor dynamics is often seen as an important organising principle (e.g., Kelso and Tuller, 1984; Schmidt et al., 1991; Feldman, 1986; Bizzi et al., 1992). Popular applications are the equilibrium point models (not to be simply equated with point attractors in dynamic system theory). These models are based on the idea that muscles (or muscles in combination with spinal circuits) behave like tunable springs generating length-dependent
forces which lead the arm or leg to a certain equilibrium point. The charm of this hypothesis is that the limb is attracted to the equilibrium point irrespective of disturbances, initial conditions, its own or added inertia, etc. In other words: most of the complicating aspects which constitute Bernstein's problem seem to be dealt with in the equilibrium point control. The hypothesis was first proposed by Feldman and colleagues (see Feldman, 1986 for references). His application has become known as the lambda-model and includes the control of lambda, the threshold of the stretch reflex. A second version of the equilibrium point hypothesis was proposed by Bizzi and colleagues (see Bizzi et al., 1992 for references). In this, so-called alpha-model equilibrium positions are realised through co-activation of antagonists on the basis of the intrinsic force-length characteristics of the muscles themselves that give rise to spring-like behaviour.

Although there is quite some debate with and among representatives of both models, the equilibrium point control hypothesis receives considerable support among motor control theorists and is described in some textbooks (Brooks, 1986). This is not only due to its charms in the light of Bernstein's problem but certainly also to remarkable observations in experimental studies (e.g., Berkinblit et al., 1986; Bizzi et al., 1984; Flanagan et al., 1993; Giszter et al., 1993). Important for the discussion to follow in this contribution is the fact that in recently proposed versions of the equilibrium point hypothesis applicable to multi-joint movements, it is assumed that the CNS generates a series of equilibrium points along a specific trajectory. This trajectory does not necessarily coincide with the required trajectory of the limb's end point but may deviate in order to realise, for example, an external force on the environment in contact control tasks. Since the strengths and weaknesses of the equilibrium point hypothesis have been extensively discussed by others (e.g., target articles of Berkinblit et al., 1986 and Bizzi et al., 1992 and the open peer communication in the same issues), it is assumed in the present paper that the reader is familiar with these details.

3. Bernstein's problem revisited

Our rejection of the idea of spontaneous pattern formation without reference to representations included in a neuronal medium in general and our criticism of the equilibrium point hypothesis in particular is largely
based on identification of phenomena which further complicate Bernstein’s problem.

Firstly, we like to provide evidence that, especially relatively fast leg movements as occur in jumping, skating, cycling and possibly even walking, have to be controlled using a largely feedforward type of control. Secondly, we will address specific requirements of contact control tasks and provide experimental evidence for different types of organisation for mono- and bi-articular muscles, not consistent with equilibrium point hypothesis and finally we will stress the necessity to adapt one’s timing of muscle activation and reject hypotheses of time-scaling as a general principle.

3.1. Closed loops take too much time

Feldman’s lambda-model as well as many other hypotheses concerning motor control (e.g., Duysens et al., 1993; Gandevia and Burke, 1992; Lundberg et al., 1987; Yang et al., 1991) include feedback loops for the organisation of the undisturbed ongoing movement. Though feedback undoubtedly plays an important role in many reaching and grasping movements, we feel that for fast and moderately fast highly automated leg movements this type of control would simply take too much time. What is often overlooked in estimating time delays in feedback loops is the time lag between the neural stimuli to a muscle and its mechanical response (force, power). This time lag is not only caused by the well-known electromechanical delay but possibly also by the necessity to deform elastic structures in the entire limb and between the limb and the environment.

Fig. 1 presents an example of a comparison of the varying electromyographical activity of one of the quadriceps muscles measured in a static position on a bicycle and the resulting varying force on the pedal. Clearly, if one tries to evaluate the involvement of muscles in the art of cycling one should account for the time lag between muscle activations and pedal force responses. For upper and lower leg muscles this time lag was calculated through an application of cross-correlation techniques and appeared to lie in the order of magnitude of 90–100 ms for this cycling task (Van Ingen Schenau et al., 1995). About the same values were previously found in dynamic and static mono-articular knee movements using a dynamometer (Vos et al., 1991), and can also be deduced from Thomas et al. (1988) and Olney and Winter (1985). This time lag together with the shortest neural delay of the stretch reflex in humans of 30–40 ms gives a total time lag in the lambda-model of 120–140 ms. The actual total time lag might even
prove to be considerably larger since Latash and Gottlieb (1991b) found a change in arm muscle activity not until 100 ms after an unexpected block of the movements. We predict that the lambda-model simulations (e.g., Feldman et al., 1990; Flanagan et al., 1993; Latash and Gottlieb, 1991a,b) would look unacceptable if this time lag would be incorporated. Clearly, in fast leg movements such lags would give rise to considerable instability if the feedback gain differs much from zero (Hogan, 1990). Moreover, one would expect a clear gamma lead with respect to alpha activity which is not observed in general (Bizzi et al., 1992; Loeb et al., 1985). In the light of the long time lag discussed here, we would support Loeb et al. (1985) in their statement that the gamma system and the often observed alpha-gamma coactivation is meant to optimise the sensory information flow from the muscle spindles. This information is used for kinaesthesia, updating internal representations of system properties, motor learning and fast responses to sudden disturbances but not in the organisation of the ongoing movement (see also Rothwell et al., 1982; Sanes and Jennings, 1984; Sittig et al., 1987 and on the other hand Duysens et al., 1993; Gandevia and Burke, 1992 for more discussion).

Fig. 1. Intensity of EMG of the vastus medialis (shaded), representing its neural activation, and simultaneously measured external force exerted by the foot. Note that the force curve is shifted to the right relative to the EMG curve. The magnitude of this shift (determined by a cross correlation technique) is approximately 120 ms.
3.2. The necessity to generate prescribed net joint torques

Many arm and most leg movements in sports, labour and daily life require that the hand or foot exerts a specific force on the environment. Such tasks are usually referred to as contact control tasks. From robotics it is known that such tasks are considerably more complicated than point to point movement tasks. According to Hogan (1990) contemporary robotic devices may break into pathological chattering on contact with an object, a phenomenon referred to as "contact instability". Living organisms, however, have no problem with such tasks at all. During leg movements in standing, walking, lifting, running and jumping, the ground reaction force is not only responsible for the required translational acceleration of the body centre of gravity but its direction, or more precisely its torque relative to the body centre of gravity determines the change in angular momentum of the entire system (Jacobs and Van Ingen Schenau, 1992a) and is thus directly related to the maintenance of equilibrium. Based on this insight it is understandable why the necessity to control the magnitude and direction of this force can be interpreted as an important constraint in such unstable movement tasks (Jacobs and Van Ingen Schenau, 1992a; Doorenbosch et al., 1994; Toussaint et al., 1995).

As originally identified in an analysis of cycling (Van Ingen Schenau et al., 1992a), the control of these external forces relies entirely on the generation of particular combinations of net torques in the joints involved. A simplified example of an arm task, previously used in a discussion

![Diagram](image)

**Fig. 2.** An example of a contact control task with conflicting requirements with respect to joint torque and joint displacement. Imagine that the subject is seated at a table and tries to displace a heavy object to the left. This requires an external force $F$ to be exerted by the hand which can only be realized through a horizontal adduction torque about the shoulder and a **flexing** torque about the elbow. Note, however, that the movement requires an **extension** of the elbow joint.
concerning Bizzi's alpha-model (Van Ingen Schenau et al., 1992b) may illustrate this requirement (Fig. 2). If a subject has to displace an object across a horizontal table to the left, he will have to exert force on that object in the direction indicated. This force can only be realised by a combination of a net flexing torque in the elbow and a net horizontal adduction torque in the shoulder. However, if the object starts to move in the required direction we observe an elbow extension which is opposite to the direction of the required net elbow torque.

The equilibrium point hypothesis assumes that muscles behave as springs which means that their force decreases while they are shortening and increases while lengthening. In the example the mono-articular elbow flexors lengthen and the mono-articular extensors shorten, the horizontal adductors shorten and the length change of the biceps will be small due to the combined movement in the shoulder and elbow joint. Now assume that at the instant that the arm passes the position depicted in Fig. 2, the initial activation is such that the net torques do fit the requirements to exert the force on the object in the required direction. Then, if the equilibrium point is static, the spring-like muscle behaviour will cause a decrease in shoulder torque and an increase in elbow torque. This would, however, result in an external force which would no longer point to the left but left-downwards in the plane of the figure. What is necessary is a constant torque in the shoulder combined with a slightly decreasing torque in the elbow. If other forces such as gravity come into play as well, one can easily imagine that at the same required joint and hand displacements one may need completely other combinations of (time-varying) torques. Imagine for example that the arm movement of Fig. 2 is made to throw an object in the gravitational field. In that case the force on the object has to be such that the resultant of this force and the gravitational force on the object provides the acceleration in the resultant direction. These examples show that the required patterns of muscle activation can not be organised on the basis of the required kinematics alone but depend strongly on the mechanical interaction with the environment.

Representatives of equilibrium point models as well as those of many other models take the required direction of the hand or its derivative as the sensory input which guides the generation of muscle activation (Bizzi et al., 1992; Bullock and Grossberg, 1991; Flanagan et al., 1993; McIntyre and Bizzi, 1993; Morasso, 1992). Although the idea of direct control of movement direction finds considerable support in neurophysiological studies in which the firing behaviour of nerve cells in the motor cortex was monitored
(see Georgopoulos et al., 1986; Karst and Hasan, 1990 and their references), the example of Fig. 2 makes clear that this information alone can never be sufficient to guide multi-joint contact control tasks.

In their response to this criticism, Bizzi et al. (1992) propose two possibilities to execute the task of Fig. 2 using equilibrium point control:

1. a virtual trajectory “may be computed” that deviates in such a way from the desired trajectory that it satisfies both force and path requirements of the task.

2. the virtual trajectory may coincide with the desired path, which will result in a deviation between the actual path and the desired one.

Clearly, the first possibility would obliterate the attractive simplicity of equilibrium point control: it would require a detailed internal representation of a complicated virtual trajectory which includes information about all problems mentioned above with respect to Bernstein’s problem. Furthermore, this virtual trajectory would have to depend on the initial state of the limb, which would put it right back into the computational/representational approach. The second solution is largely in agreement with the charms of the equilibrium point hypothesis as a simplifying strategy. The question then arises: are the inevitable deviations consistent with experimental observations? The answer to this question clearly depends on the effective stiffness of the arm. In a study by Shadmehr et al. (1993) hand stiffness measures were published which lead us to the conclusion that for example a force of 60 N in the task of Fig. 2 would cause a deviation from the desired trajectory as large as 10–20 cm. Since we can perform contact control arm tasks such as throwing and sawing with remarkable accuracy, especially after some training, the equilibrium point model alone can not be sufficient to meet all requirements in contact control tasks. The high accuracy by which skilled subjects appear to be able to perform contact control tasks demonstrates that we can learn to let the required net joint torques emerge as a function of time.

Thus, adherents of the equilibrium point hypothesis are faced with the problem that by amending the original hypothesis in order to accommodate arguments such as those presented above, the attractive simplicity of the hypothesis ceases to exist. In a recent study McIntyre and Bizzi (1993) argue that no previous formulation of equilibrium point models can describe the production of fast arm movements and propose a feedforward component in the virtual trajectory command and a feedback loop (not accounting for the entire time lag discussed above). This model, however, is still only based on kinematic information and will thus also fall short in
contact control tasks. Latash and Gottlieb (1991a, Latash and Gottlieb, 1991b) introduced an independent (central) control over antagonists muscles in the lambda model which takes away much of the charm of the point attractor idea and which, again, will not help to generate accurate external forces.

Additional evidence against the equilibrium point hypothesis as a general principle which underlies the organisation of the activation of all muscles can be deduced from studies which show that the organisation of mono- and bi-articular muscles is likely to be based on distinctly different processes. Since this aspect was extensively reviewed recently (Van Ingen Schenau et al., 1994) this point is only shortly addressed here.

In a number of different studies it was found that bi-articular upper arm and upper leg muscles appear almost entirely responsible for the (fine) regulation of the net shoulder and elbow or hip and knee joint torques necessary to control the external force exerted by the hand or the foot and to realise the segmental accelerations (Van Ingen Schenau et al., 1992b; Jacobs and Van Ingen Schenau, 1992b; Gielen and Van Ingen Schenau, 1992; Van Ingen Schenau et al., 1995). Studies of undisturbed forward and backward walking cats as well as posture control experiments in cats revealed results which are largely consistent with these observations (see Van Ingen Schenau et al., 1994 for references).

Remarkably, both in cats and in humans, the activation of mono-articular muscles appears largely associated with kinematic requirements and to a much lesser extent to the required joint torques. This might mean that the organisation of the control of these muscles is, indeed, based on principles as summarised by Karst and Hasan (1990) and applied in the equilibrium point hypothesis. One would, therefore, not necessarily have to reject the idea that virtual trajectories play a role in the organisation of the control of movement.

However, such an organising principle does not constitute an alternative for the necessity of internal representations since the organisation of bi-articular muscles then will have to be based on other, multi-modal, sources of information and on internal representations of the mechanics of the actor–environment system.

3.3. Relative timing is not invariant

During Turvey's Round I and II of theorising about possible simplifying strategies or self organising principles which the CNS might use to master
Bernstein's problem, many have searched for invariants in the muscle activation patterns or in the kinematics and kinetics of arm and leg movements. One of the most popular candidates concerns the supposed invariance in the temporal structure of muscle activation patterns and/or kinematic parameters (Fitch et al., 1982; Kelso and Tuller, 1984; Schmidt, 1988; Shapiro et al., 1981).

In this section we will provide evidence supporting the statement that an invariant relative timing does not exist in general and we will demonstrate that such an invariance would severely limit our dexterity to deal with changing conditions.

In fact, a number of experimental studies have shown that in point to point arm movements it is the path taken by the wrist that is remarkably invariant, even under different positions relative to gravity and when applying additional inertial loads (e.g., Graaf, 1993; Hoy et al., 1985; Soechting, 1989). This, of course means that muscle activation patterns cannot be invariant. More direct evidence has been provided by Marsden et al. (1983) who showed that relative timing is adjusted to changing circumstances. This was also observed in our own analysis of cycling: if cyclists increase their pedalling rate from 50 to 110 revolutions per minute at equal power output one observes that all muscles are activated earlier relative to the crank angle and the burst durations decrease which might still be in line with the concept of invariant relative timing. However, the activation patterns of two muscles (rectus femoris and hamstrings) appear to change significantly (in contrast to those of the other muscles): there is a strong decrease in the amplitude of the rectus femoris while one of the two distinct bursts of activity of the hamstrings at 50 rpm disappears entirely at 110 rpm. These changes appear to account for the increasing inertial forces of the leg segments in order to preserve the propulsive force on the pedal (details will be published elsewhere). Comparable adaptations of especially the bi-articular muscles with increasing velocity or vigour of the task have been reported for cat locomotion (Smith et al., 1977; Walmsley et al., 1978; see Van Ingen Schenau et al., 1994 for more references).

The necessity to adapt one's relative timing becomes self-evident as soon as one realises how sensitive our action system is for even very small changes in timing and how seriously our coordination patterns would deteriorate if even small changes in the properties of our musculoskeletal system due to for example fatigue would not be accompanied by changes in timing. As the effect of slight changes in muscle activation on behaviour is impossible to study experimentally in humans, forward dynamic simulation
studies concerning these questions were undertaken. A mathematical model of the musculoskeletal system was formulated that has the activation of the muscles as its input and the resulting movement as its output (Van Soest and Bobbert, 1993). The skeleton is modelled as a four-segment two-dimensional linkage representing feet, lower legs, upper legs and upper body. Given the position, velocity and the gravitational and muscle forces acting on the skeleton, its acceleration can be calculated. The skeleton is actuated by 6 "muscles", representing the muscle groups contributing to leg extension. These muscles are represented by a Hill-type muscle model. The compound model is applicable to explosive movements such as vertical jumping, for which it is reasonable to assume that muscle activation is controlled in an open loop fashion: due to the short duration of this type of movement, and given the delays in neural feedback loops, there is just no time for feedback-based adaptation of muscle activation during the push-off. First of all, using numerical optimization, the optimal activation pattern, i.e., the activation pattern resulting in maximum jump height, was calculated, and compared against experimental data obtained from well-trained volleyball players. This comparison revealed that (a) kinematics were highly similar, and (b) that a proximodistal sequence was observable in kinematics (i.e., start with hip extension, end with ankle plantarflexion) as well as in muscle activation, both in experiment and in simulation. From this comparison, it was concluded that this model yields a good description of the actual system.

As noted in the preceding, the question how sensitive the movement outcome (in this case: jumping height) is to variations in muscle activation pattern cannot be addressed experimentally. Using the model, however, it is straightforward to address: determine the optimal activation pattern, perturb it, and compare the movements resulting from these activation patterns. An example of such a simulation experiment is shown in Fig. 3, where the optimal push-off movement is compared to the push-off movement resulting when hamstrings activation is switched to its maximal value 100 ms earlier than in the optimal solution. From this figure alone we can conclude that, in this type of task, muscle activation must be extremely precisely controlled in order to produce a well-coordinated movement.

Following up on these results, one might wonder to what extent the required stimulation pattern is a function of (variable) muscle properties. An example of such a question was addressed by Bobbert and Van Soest (1994), who investigated the consequences of muscle strengthening using the model described above. Phrased simply: consider an athlete able to
generate the optimal open loop muscle activation pattern for vertical jumping; suppose he would significantly increase the maximal isometric strength of his muscles through strength training while sticking to the (open loop) activation pattern used previously. What would the effect on jumping height be? The answer to this question may come as a surprise: it was shown that despite the increased strength, jumping height would decrease! The cause of this decrease was shown to be that the "old" muscle activation pattern was "out of tune" with the changed muscle properties. After tuning the muscle activation pattern to the changed effector properties, jumping height increased as expected. In fact it was found that for certain changes in effector properties, even the sequence in which muscles should be "switched on" was not invariant.

In conclusion it can be stated that our capacity to adapt the amplitude and temporal structure of muscle activation patterns is an important prerequisite for the execution of accurate multi-joint movements. The same
holds true for our capacity to let the adequate net joint torques emerge as discussed above. As argued in this chapter, these requirements enlarge Bernstein's problem considerably. It appears to us, however, that contemporary knowledge about functions of brain structures, albeit fragmentary, supports the direction of the solution of Bernstein's problem which was indicated by Bernstein himself: development, learning and training as the major means to turn our complex action system into a controllable goal-oriented system.

4. Bernstein's solution revisited

4.1. Bernstein's solution

Though many refer to Bernstein's work as an important source of inspiration to their attempts to solve Bernstein's problem, we feel that not only his problem but also his solution is still largely up-to-date. Therefore, we will place our arguments in favour of the necessity for internal representations in the theoretical framework offered by Bernstein with some extensions based on neurological and neurophysiological observations.

The major elements of Bernstein's solution to Bernstein's problem as we deduced from Bernstein (1967, Bernstein, 1996) can be summarized as:

- the capacity of our CNS to process various aspects in parallel due to the relatively autonomous storeys in our brain building which were stocked during evolution. According to Bernstein, each new storey took control over the phylogenetically older storeys and gave rise to new and richer classes of movements.

- the principle of "sensory corrections" at various levels of this multi-storeyed brain, not only as a means to track the movement to the intended goal (closed loop control) but also, in fast movements, as corrections already included before the actual movement starts (open loop control).

- our capacity to acquire and adapt "solutions" to motor problems during development and through exercise including the capacity of the younger storeys to "teach" the older structures how to couple perception to action.

- our capacity to modulate muscle synergies generated at lower levels and the capacity of especially the neocortex and pyramidal system to take over the control in case of voluntary, non-stereotyped, manipulations which
require for example independent control of the fingers and finely graded external forces.

- the existence of internal representations of "solutions to motor problems" (Gestalt-type of representations) which gave rise to the concept of motor equivalence, generalised motor programs or motor scheme's.

- the argument that learning of motor skills is, in part, guided by the evolutionally determined needs of the organism, not only in animals but also in man (formulated in his later work).

All these elements have received considerable support in the past decades. In fact it is amazing that despite the convincing arguments of Bernstein and his school, the computer metaphor of motor control could still develop since that time.

In the light of the present discussion, we have only two major comments on Bernstein's views. Firstly, according to Bernstein, segmental organisation of the oldest storeys (spinal cord, brainstem and medulla) has become obsolete. He qualifies the spinal cord as a simple impulse transducer and expects that within 100 000 to 200 000 years all descending commands will follow the pyramidal system. This view has not received much empirical support. On the contrary: the spinal cord appears to contain a rich assembly of interneuron circuits, crucial not only for reflex organisation but also used in the organisation of undisturbed movements (see McCrea, 1992, for review and references). Secondly, though we support his argument that human motor behaviour is considerably richer than a collection of conditioned reflexes, we feel that his statement that skill acquisition has nothing to do with "beating" neural connections in the brain cannot hold. Adaptations of synaptic strengths and even neuronal sprouting appear now beyond dispute. Synergies can be formed and tried out by the motor cortex within minutes (Sanes and Donoghue, 1993) and are likely to be taken over by older circuits during skill acquisition (Kennedy, 1990).

Probably as a consequence of this strong anti-Pavlovian position, Bernstein even seems to reject the idea that automated muscle synergies are constructed on the basis of internal representation stored in specific motor centres. Though this view is gratefully referred to by contemporary supporters of equilibrium point principles (e.g., Latash and Latash, 1994), we feel that this position is not really consistent with his view of the CNS as a hierarchically ordered multi-storeyed system with relatively autonomously operating subsystems. As stated above, we do agree entirely that actions can not be based on a type of program stored in memory as a look-up table which contains all details comparable to a program which instructs a digital
computer. Bernstein's solution, however, does not tell us how a high level representation of a "solution of a motor problem" is translated into muscle activation signals at the lowest levels where (according to Bernstein) these signals are constructed.

In his recently discovered book (written in the fifties; Bernstein, 1996), he states that learned skills emerge "only due to vigilant tracking of movements with sensory corrections". In his later work (last chapters in Bernstein, 1967), however, he places more emphasis on the necessity for anticipation ("the honeymoon with cybernetics is over") and our capacity to move without any trigger but here he does not address the problem how such movements are organised either. As outlined below we feel that there is now conclusive evidence for the existence of pattern generators localized in specific neuronal circuits whose architecture and synaptic strengths can be seen as the implementation of the internal representations necessary for accurate and skilled multi-joint movements.

4.2. On localisation and pattern generation

The arguments used above to support the title of this paper were largely based on observations and phenomena that make it extremely unlikely that accurate multi-joint movements can emerge without a detailed internal representation.

Our position would, of course, be much stronger if we would be able to provide more direct evidence about the nature and localisation of such internal representations. As argued by Bernstein (1967) and many others, such evidence is difficult to obtain in the light of our massively interconnected brain subsystems (e.g., Alexander et al., 1992). This makes it not self-evident that specific movement disorders caused for example by well localised lesions in particular brain area's indicate that the affected orders are represented or organised in that area. This can easily be imagined for electronic systems. If, for example, one removes a particular integrated circuit (IC) from an FM-radio and if this would result in the reproduction of a noisy sound, it will be clear that it makes no sense to conclude that particular IC represents a noise-suppressor. This problem, however, should not lead one to the conclusion that no specific functions can be localised in the IC's of our radios. A consultation of the designer of the radio would prove that the opposite is true. Since such type of conversation seems not well possible with our Designer, we are well aware that we have to present our "evidence" in favour of localised functions with some caution.
As reviewed by for example Grillner and Wallen (1985) there is now convincing evidence for the existence of localisable neuronal circuits which can generate complete synergies of muscle actions; at least with respect to innate movements of animals such as the various types of locomotion, scratching and pawshaking. It also has become clear that these so called “central pattern generators” (CPG) have a high degree of modifiability. Both descending as well as peripheral information appears to modulate the output of CPG’s considerably in real time. At a longer timescale, the input–output relation of the CPG’s is known to be modifiable, presumably through changes in the synaptic strengths and/or changes in the topology of the CPG (see also Vaal et al., 1995). Consistent with Bernstein’s multi-storey CNS is the observation that the type of modulation depends on the storey where the descending signal stems from: The younger the storey, the more degrees of freedom can be manipulated independently (Grillner and Wallen, 1985).

Relevant to the motor-action controversy is the observation that sensory information can have considerable influence on not only the motor output of one limb but also on the interlimb coordination (see also Bekoff et al., 1987 and Bekoff, 1992). Of course one can qualify such behaviour as spontaneous self-organisation as suggested by many action theorists but we feel that this spontaneous organisation would not be possible without these (localisable) CPG’s which may be viewed as the embodiment of detailed internal representations, sculpted in the course of evolution (see Beek et al., 1995). As concluded by Bekoff (1992) sensory inputs can even take care of the required changes of the CPG-output during growth. Given the versatility of these spinal CPG’s that are obviously able to solve Bernstein’s problem for these movements, it is difficult to understand why representatives of action theory have such problems to imagine that aspects related to timing and to the necessity to deal with inertial and external loads can be represented at higher level circuitry as well. Why would Nature not use such well working principles in higher level brain circuitry? Clearly, for man who seems not to possess much innate spinal pattern generators the question may arise how such higher level generators might be created during skill acquisition. As will be discussed in the next section, our answer is: by development and learning.

For the present we assume that relatively fast, accurate multi-joint movements as discussed above are indeed organised in pattern generating supra-spinal circuits, albeit that we use the expression “pattern generating circuit” now in a wider sense (including predictors, comparators, etc.) than
a simple autonomously operating generator of muscle activation patterns. The very existence of five different descending tracts makes it likely that different aspects are dealt with by different circuits, however.

Load supporting functions seem to be provided by the vestibulo- and reticulo-spinal tracts (Henatsch and Langer, 1985) whereas there is some evidence that the open loop control necessary for automated fast movements descends via the rubro-spinal tract (Gibson et al., 1985a; Gibson et al., 1985b), both systems receiving parameter settings from cerebellar circuitry. The explanation for the experimentally observed speed-accuracy trade-off in positioning tasks proposed by Galen and de Jong (this issue) fits nicely into this framework. These authors suggest that this finding can be seen as an emerging feature of a system with parallel control of stiffness and net joint torque. Although we would argue that it is unlikely that any of these parameters can be directly controlled by the CNS, due to intrinsic actuator dynamics, we fully support the idea of parallel control of, for example, “movement” and “posture” commands. As recently demonstrated by Gordon et al. (1995) and Ghez et al. (1995), such pattern generating neuronal networks are likely to contain representations of the biomechanical properties of the effector system which can be updated on the basis of proprioceptive and visual information.

4.3. On development and learning of motor control

It is now widely accepted that behaviour, including motor behaviour, is largely moulded by the topology of neural connections and the synaptic strengths, both within and between our brain storeys. These insights underlie the emergence of a new type of theories based on computer simulations of synaptic adaptations in models of interconnected neurons: the connectionist models (see Morasso and Sanguineti, 1992, for an overview and references).

An important point to be addressed concerns the question what principles guide the formation of these architectures during development, learning and training. Most theories are based on the principle of trial and error learning. For example during spontaneous movements of a child, the child perceives which movements are the most successful one’s. Though Bernstein has also supported this view when he stated that successful solutions of motor problems are discovered by “pure luck” during trial and error learning (Bernstein, 1996), he later realized that this type of development and learning would simply take too much time. If, indeed, the optimal
timing sequence and amplitude modulations of all muscles involved in the vertical jump discussed above would have to be discovered by trying out all possible combinations, even the entire time elapsed since the onset of the evolution of living organisms would be too short. This made Bernstein suggest in his later work that the probability to find optimal solutions will be increased through the presence of genetically coded needs of the organism (last chapters of Bernstein, 1967). During the past decades, indeed, considerable evidence has been forwarded against the persistent dogma of some social sciences that (in contrast to other vertebrates) the development of human behaviour starts all the way from scratch. For many aspects of human behaviour, genetic influences appear now beyond dispute. Clearly, such influences may solve a significant part of Bernstein’s problem, since they may explain why even submaximal movements such as walking or bringing a cup of tea to the mouth are so remarkably stereotyped among different subjects. Recently, Sporns and Edelman (1993) successfully applied such increased probabilities as “value systems” in their connectionist models for motor development. Based on our inverse and direct dynamical analyses of the vertical jump discussed above, we strongly support the concept of a value system which guides the CNS to a proximo-distal sequence in the timing of muscles in our extremities. As summarised in Van Ingen Schenau (1989), this sequence is observed not only in jumping but in many other (sprinting, running and throwing) movements which helped our ancestors in hunting and increased their chances to escape from enemies. It seems indeed extremely unlikely that, in contrast to all other species, such an important factor would have to be discovered (or imitated) by each new generation of humans again.

Remarkably, this position seems to lead us rather closely to recent studies of dynamical systems theorists who describe the intrinsic dynamics of an organism as to “reflect contributions from ancestry and prior experience” (Zanone and Kelso, 1992). The pattern generation process based on such intrinsic dynamics is, in fact, based on detailed internal representations largely specified in the course of evolution in various storeys of our brain and modulated by environmental information as so nicely demonstrated by Bekoff et al. (1987) and Bekoff (1992) who presented her experiments with chickens as “evidence for the continuity of pattern generating circuitry throughout development”. Zanone and Kelso (1992) qualify the learning process “as a specific modification of the intrinsic dynamics” which becomes memorised. We do feel, however, that progress in neuroscience, sports and rehabilitation relies heavily on the extent to
which we manage to develop theories about "where" and "how" this memorisation might take place. In the light of the many controversies among neurologists and neurophysiologists, these questions appear difficult to address (closely associated with the problem of localisation discussed above). Even the function of the cerebellum, so often referred to as an important system in motor learning, appears subject to much debate (see target article of Bloedel, 1992 and open peer communications in the same issue).

Despite these problems and controversies, we feel that there is some evidence that during the learning of new skills, phylogenetically younger storeys of our brain teach the older structures (such as the brainstem and the cerebellum) in realising pattern generating circuits coupling perception to action. The combination of the work of Sanes and Donoghue (1993), Kennedy (1990) and Stein (1986, Stein, 1992) provides some idea how this might work. Sanes and Donoghue (1993) showed that in the primary motor cortex, synergies can be formed, tried out and reorganised within minutes. This is realised through synaptic rearrangement and/or unmasking or activation of existing synapses. It seems likely that this is associated with our capacity to consciously follow instructions or to imitate our coach or therapist during the early phase of learning a new skill which is usually referred to as the cognitive phase in psychological text books on motor learning (e.g., Schmidt, 1988). Kennedy (1990) provided evidence (for primates) that an important aspect of learning is that cortico-spinal control gradually switches over to rubro-spinal control, especially with respect to timing, velocity and force of the movement. This might point at the red nucleus as one of the pattern generating candidates. Interestingly, the output of the red nucleus also controls the coupling of various sources of unspecified (visual, proprioceptive, cutaneous) information to the output of Purkinje cells in the cerebellum via their rubro-olivary projections and the olivary control of the climbing fibres of these Purkinje cells which seem to learn the Purkinje cells to automatically react on specific combinations of sensory information necessary in, for example, feed forward control (Stein, 1986; Stein, 1992). The massive inputs of the red nucleus neurons involved in the rubro-olivary projections from various area's in the cerebral hemispheres might point at a type of supervised learning where the younger neocortex "teaches" the older parts of our brain to generate patterns, triggered and modulated by sensory inputs. Clearly, this explanation is little more than a possible framework indicating how skill acquisition might work since it includes many aspects which are far from proven. Moreover, many
other (e.g., reticular, vestibular) nuclei and associated descending tracts are likely to be involved as well. However, this framework is largely consistent with the cognitive, associative and automised phases of learning observed in practice and described in textbooks of motor learning. Moreover, it is known that motor cortex activity (in particular the activity of the supplementary motor area) does, indeed, decrease as the learning process proceeds (Aizawa et al., 1991; Lang et al., 1992).

Since the cerebellum also receives visual information via subcortical pathways (Johansson and Magnusson, 1991; Stein, 1986), this framework may also help to understand remarkable phenomena observed by ecological psychologists related to fast atomised responses on visual stimuli (time-to-contact phenomenon, equilibrium control in rooms with moving walls, remarkable fast responses to unexpected changes in the visual flow field). Stein (1986) also showed that neurons in the lateral cerebellum may fire up to 400 ms in anticipation of the start of a tracking movement. These observations may give rise to the idea that we can learn to use sensory information in order to account for the context conditioned variability in feed forward control and to automatically initiate changes in anticipatory muscle activations as for example described above for cycling as a function of changing the pedalling rate. Most likely, the cerebellum does not generate such muscle activation patterns itself but merely provides parameters which initiate or modulate pattern generating parallel working control systems for feedforward control for such relatively fast movements.

In sum: we believe that Bernstein's problem is largely solved according to Bernstein's solution for as far as he suggested that relatively autonomous subsystems account for all the complicating problems. Contemporary knowledge about synaptic rearrangement guided by genetically prescribed probabilities and further shaped, adapted and modulated during development, learning and training shows that we do not need any explicit knowledge of all these complicating factors but that this detailed knowledge is implicitly incorporated in the topology of neural connections and the synaptic strengths between neurons throughout our CNS.

5. Conclusion

In conclusion we feel to have provided convincing arguments that accurate multi-joint movements must rely on detailed internal representations, in order to account for all complicating aspects referred to as
Bernstein’s problem. This “knowledge”, embodied in the architecture and synaptic strengths of our massively parallel brain subsystems is acquired on the basis of previous experiences during the evolution of our ancestors and further shaped during development, learning and training. We feel that Turvey’s Round II of theorising is not an attractive alternative for Bernstein’s solution, at least not for the type of movements discussed. In fact we would rather support Aristotle (384–322 BC) when he stated more than 2000 years ago with respect to the control of skilled movements:

“as in a common wealth; when order is once established in it, there is no need for a separate monarch to preside over each separate task”. De motu animalium, p. 703.

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