Biodynamic Basis of Rhythmic Limb Movements in Humans

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Key Words
Biodynamic, limb movements, co-ordination.

Summary
The co-ordination of human rhythmic limb movements has been investigated by two major theories: the neurophysiological theory and the biodynamic theory. This paper focuses on the latter. The biodynamic theory explores limb co-ordination through the application of the physical laws. The physical properties of the muscle such as its length and tension along with the external forces applied to the limb determine interlimb co-ordination. The theory emphasises a self-regulatory mechanism for the limb co-ordination with minimal involvement of the central nervous.

Introduction
Rhythmic movements include those in which different parts of a limb or limbs move in cyclic repetitive fashion.
Examples are walking, running, swimming and typing.
Co-ordination of rhythmic limb movements in humans has been explored by two major theories: the biodynamic theory and the neurophysiological theory. The latter is mainly based on the studies of animal and human locomotion and explains interlimb co-ordination by examining the neural structures inside the central nervous system (Grillner, 1981; Thelen et al, 1987).
In a previous paper, the neurophysiological theory was discussed (Beheshti, 1993a).

The biodynamic theory explains the interlimb co-ordination in humans by exploring the laws of physics and their effect on human limb movements (Kugler and Turvey, 1987; Yates, 1986; Schoner and Kelso, 1988a,b).
According to this theory, the interlimb co-ordination is controlled by the self-regulatory mechanism of the limbs with minimal engagement of the central nervous system (CNS) (Kelso et al, 1980; Kelso and Schulz, 1985; Schoner and Kelso, 1988a, b; Yates, 1982, 1986). The human body is subjected to external forces such as gravity during the generation of movements. The motor system is organised towards counteracting the effect of this force during the movement production.
The effect of mechanical factors in co-ordination is especially important, as humans not only interact with the environment, but they also use these forces to facilitate their movements (Bernstein, 1967).
Bernstein investigated segment forces and total body forces produced by children and adults during locomotion. He reported that the forces produced by the legs during locomotion change with training and experience. That is, for younger children, there was a lot of inefficiency of the limb movements, while adults minimised the energy loss at each step cycle.

The purpose of this article is to provide information about the biodynamic principles involved in normal human rhythmic limb co-ordination such as walking, clapping and foot tapping. The biodynamic theory and experiments based on it are discussed. These experiments avoid investigating non-rhythmic limb movements primarily because they do not follow predictable patterns and require complex methodological procedures. The paper will also examine the biodynamic theory's contributions and shortcomings.

The effect of physical forces on rhythmic limb movement co-ordination has received little attention in physical therapy literature. Yet these forces can effect the kinematic characteristics of the limbs (eg velocity, displacement, acceleration) and as a result have an impact on interlimb and intralimb coordination.
Physical therapists should increase their knowledge of movement mechanics for possible application in training the rhythmic movements of the limbs. The information presented in this article can thus benefit

physical therapists, as it familiarises them with the application of physical laws to normal rhythmic limb movements in humans.

Conceptual Foundation

The biodynamic theory explores the organisation of human rhythmic limb movements through utilisation of physical laws applied to the limb. According to the theory, the length and tension of the muscle, with the effect of external forces on the limb, control the limb movements (Kelso et al, 1980; Schoner and Kelso, 1988a, b; Kugler and Turvey, 1987). The theory is mainly based on the work of Bernstein (1967) and Feldman (1966a, b, 1980). Bernstein (1967) was the first to recognise that the forces acting on the limb from the environment, such as gravitational, inertial, and reactive forces, play important roles in limb movement organisation. By investigating locomotion in children and adults, he provided quantitative evidence indicating that the forces exerted to the limbs during locomotion were different in children as compared to adults. Unlike adults, children who have just begun to walk do not show any constant correspondence between dynamic phases of the gait and the position of the body. Bernstein noted that: “the second, highest stage of co-ordinative freedom corresponds to a degree of co-ordination at which the organism is not only unafraid of reactive phenomena in a system with many degrees of freedom, but is able to structure its movements so as to utilise entirely the reactive phenomena which arise”

Mass-spring System

Another contributor to the biodynamic theory was Feldman (1966a, b, 1980) who introduced the principles of mass-spring system in the field of motor control for the first time. Feldman conceptualised the muscles that make up the limb as springs. A muscle has a certain resting length and can be stretched to different lengths depending on the amount of load applied to it. If such a system is put into motion, it begins to oscillate.

The mass-spring system is damped. That is, when the spring is set to move by application of a force, it would eventually return to its resting length or equilibrium position (Polit and Bizzi, 1978; Hollerbach, 1981; Feldman, 1966a, b, 1980; Kugler and Turvey, 1987; Kelso and Holt, 1980). A limb is composed of several muscles with spring-like characteristics and can attain a specified end position from various initial joint angles and in spite of perturbations imposed upon it during its movement trajectory (Feldman, 1966a; Polit and Bizzi, 1978; Kelso and Holt, 1980) Kay et al, 19919 Yaminishi et al, 1980).

In sum, the mass-spring model has been proposed as one of the mechanisms that co-ordinate the movement of the limb(s). The other important mechanism in limb co-ordination is the homoeokinetic factor that will be discussed in the next section.

Homoeokinetic Physics and its Application to Mass-spring Model

Another breakthrough in biodynamic theory was the application of lberall's (1977) concepts of homoeokinetic physics to the mass-spring model (Kegler et al, 1980; Kelso et al, 1980; Kelso et al, 1981; Kugler and Turvey, 1987). According to homoeokinetic physics, biological systems are open systems able to capture, degrade, and dissipate free energy' (Iberall, 1977; Iberall and Soodak, 1986). However, to sustain its movements, the system must receive such energy at the right time and place during the oscillation (Kelso et al, 1981). The amount of energy received in each cycle must be exactly equal to the amount of energy lost in that cycle. Otherwise, the conicity (displacement over time) will increase or eventually stop. Homoeokinetic physics also describes the cyclical movements in biological systems leg limb movements) as ensembles of limit-cycle oscillators (Kelso et al, 1981; Eisenhammer et el, 1991; Haken et al, 1985). A limit-cycle oscillator will return to a stable mode (fixed frequency and amplitude) regardless of the disturbances it may encounter Sikorsky, 1962; Kay et al, 1991). One of the first experimenters who compared the limb movements to non-linear limit cycle oscillators was von Holst (1935). By using the mathematics of coupled oscillators, he predicted interline phase relationships in cockroaches and crayfish. Several other experimenters have confirmed von Holst's endings and observed non-linear limit cycle oscillatory characteristics in ullman limb movements (Kelso et al, 1979, 1981). These findings will be discussed later in this Paper. Human and animal locomotion is also associated and compared with the oscillation of pendulums, the classic objects of study in physics (Kegler and Turvey, 1987). In other words) the locomotion is compared with pendular clocking organisation when animals move at different gaits, this is accomplished through changing the periodicity of the pendular system. Periodicity or cyclicity (clock-like behavior) in a system arises as a consequence of the transfer of energy from a high potential source to a low potential sink. Each cyclic movement has a frequency that is the number of movements occuring in a second. Each gait is associated with a preferred period and while animals tend most frequently to walk in a given gait at the preferred period, they need not do so (Kugler and Turvey, 1987).

In sum, the rhythmic limb movements resemble the mass-spring system. The spatio-temporal organization of the limb movement is 'emergent' from the effector system characteristics (length and tension of the muscles) and the forces applied to the limb. The limbs act as non-linear limit cycle oscillatory mechanisms and their co-ordination, is therefore, a consequence of the dynamic behaviour of the system itself (Kelso et al, 1980; Haken, 1983; Haken et al, 1985) and requires minimal involvement of the central nervous system.

Optimisation of Control

The optimisation of control was first defined by Soviet researchers as reduction of the degrees of freedom of the sensorimotor system (Bernstein, 1967; Gelfand et al, 1971; Gurfinkel et al, 1971; Kots et al, 1971). That is, during the acquisition of a motor skill, different muscle fibres may get involved in the movement production. However, when the skill is learned, only the specific muscle fibres necessary to carry out the task will be involved during the movement production. Bernstein (1967) implied that the central nervous system, when dealing with hundreds of muscles and joints, simplifies the co-ordination process by use of muscle synergies. According to him 'the co-ordination of a movement is the process of mastering redundant degrees of freedom of the moving organ'. A muscle synergy is defined as 'those groups of movements that have similar kinematic characteristics, coinciding muscle groups, and conducting type of afferentation' (Gelfand et al, 1971).

As a result of training, the synergies develop and are organised and controlled by the central nervous system to solve a specific motor problem (Gurfinkel el al, 1971; Kots et al, 1971). These investigators also introduced the concept of 'principles of least interaction' to explain the optimisation of control by the nervous system.

By controlling synergies instead of individual muscles, the central nervous system would have fewer degrees of freedom to control. In biodynamic theory, the word "synergy" has been replaced by co-ordinative structures (Kelso et al 1979; Kelso et al, 1982; Kugler et al, 1980; Haken et al, 1985; Kay et al, 1987), or a single virtual system (Kugler and Turvey, 1987). One degree of freedom is equated with the movement of one or more limbs acting as a single unit.

The unit of action of the motor system was defined by. Greene (1982) as the 'virtual' system. Greene proposed that complex mechanisms were organised into a collection of simpler virtual systems, making its overall operation more manageable. For example, a limb acting as a rigid body could be set in motion by a starting force and would not need further intervention for its subsequent operation. Kugler and Turvey (1986, 1987) redefined the virtual system as an operation that changes the system into a much simpler version of itself while preserving its behavioural components such as its periodicity. An example of a single virtual system is the simultaneous movement of two wrists that is considered one degree of freedom. Therefore, the control of the wrists is much simpler for the system.

Co-ordination of Non-linear Limit Cycle Oscillators

The biodynamic theory views limbs as non-linear limit cycle oscillators and explains their co-ordination through the interaction of their co-ordination through the interaction of their oscillator characteristics. One form of limb co-ordination is entrainment. It is a process in which two or more mutually entrained oscillators function as a single unit. By doing so, the degree of freedom of the movement is minimized resulting in maximum efficiency and minimum energy cost. One form of entrainment happens when the oscillator mechanism of one limb exerts an influence on another limb and changes its frequency to produce a common temporal and fixed phase-relation between them (leg 1:1).

Huygens (as cited in Minorsky, 1962) first reported entrainment in the 17th century, based on his own observation of two clocks which, with similar frequencies, became synchronised when mounted on the same wall.

Entrainment has also been refer'red to in the biodynamic theory as the magnet effect, absolute co-ordination (von Holst, 1935) and synchronisation of the limbs (Kelso et al, 1979, 1980, 1981). Kelso and colleagues (1979) had seated subjects move their fingers from the home keys in front of them to the targets located laterally as fast as possible after receiving an auditory stimulus. Kelso and colleagues reported that the upper extremities showed fixed temporal and phase-linkage relationships during simultaneous movements. Even when the movement distance, direction and accuracy requirements of the tasks changed, the temporal relationship of the limbs remained unchanged. According to Kelso and colleagues (1980, 1981), the synchronisation of the limbs is a self-organising process which causes the upper limbs, a collection of mutually entrained oscillators, to function as a single unit. Kugler and Turvey (1986, 1987) examined the pendular movements of the wrists in humans while the subjects swung weights in a sitting position.

Through use of mathematical techniques and physical laws, they indicated that both wrists moved as a single unit, or a single virtual system, optimising the control process. In other words, entrainment makes the limb movement more efficient by enabling the nervous system to control fewer degrees of freedom (Kelso et al, 1979; Kelso and Scholz, 1985; Kugler and Turvey, 1987; Schoner and Kelso, 1988a, b).

Experiments on the co-ordination of rhythmic limb movements during locomotion also indicate that dynamic properties of the limbs are important factors in the control process. Muzii and colleagues (1984) studied interlimb co-ordination in adult subjects performing simultaneous walking and clapping. The results indicated that a majority of the subjects (78%) exhibited synchronisation of the clap and step cycles. In addition, the data revealed that the step cycle rate affected the rate of the clap cycle in these subjects. This bottom up organisation was explained by the effect of both the large forces produced during the heel strikes phase of locomotion and the neural networks of locomotion.

Synchronisation of the upper and lower extremities has also been reported during non-locomotor tasks. Beheshti (1993b) reported that when seated subjects were asked to perform simultaneous foot tapping and clapping movements at their preferred rates, some of the subjects synchronised the upper and lower extremity movements.

The movement synchronisation of the limbs also occurred when subjects performed the task following a metronome set at 1-4 Hz. In contrast to the results of the study by Muzii and colleagues (1984), Beheshti found that both clap and foot tap cycles influenced the rate of the other cycle. Beheshti attributed the phase-linkage of the upper and lower extremities partly to mechanical factors. During clapping and foot tapping movements, some forces are generated by the limb movements.

The co-ordination among the limbs results from the interaction of the oscillatory characteristics

of the upper and lower extremities.
Another form of entrainment, relative co-ordination or harmonic phase-linkage, occurs when one oscillator adapts a frequency equal to an integer ratio of frequency of another oscillator to which it is coupled (eg 1:2, 1:3 phase relationship). Relative co-ordination may occur when two oscillators move at their preferred rate (von Holst, 1935; Muzii et al, 1984) or at two different frequencies (Kelso et al, 1981; Kugler and Turvey, 1987; de Guzman and Kelso, 1991; Schoner and Kelso, 1988a, b; Klapp, 1979; Beheshti, 199b). In one experiment, subjects were asked to move one finger at their preferred rate and to move the other finger at a different frequency (Kelso et el, 1981). The finger moving at the slower frequency exactly coincided with the appropriate subharmonic oscillation at the faster frequency (eg 1:2, 2:3).
Re-entrainment is another characteristic of non-linear limit cycle oscillators. Re-entrainment is defined as regaining a previously established co-ordination among limbs (eg absolute or relative) after movement of one or more limbs is perturbed (Kelso et al, 1981, 1983; Kay et al, 1991; Yaminishi et al, 1980). Examining bi-lateral finger movements (Haken et al, 1985; Kay et al, 1991) and bi-lateral hand movements (Yaminishi et al, 1980), the authors reported that unexpected momentary perturbation to one hand did not disrupt the phasing relation between the hands. The perturbed hand returned to its previous frequency almost immediately.
In addition, the amplitude and peak velocity of the finger movements also remained stable under pertubation (Kay et al, 1991).
In some, during the rhythmic limb movements, the limbs function as non-linear limit cycle oscillators. Some of the characteristics of these oscillators include entrainment and re-entrainment. During the entrainment, one limb exerts an influence on another limb and dominates its frequency. Even when the movement of one limb is perturbed momentarily, the interlimb movements return to their previous co-ordination after the perturbation is removed.

Conclusions

This paper has focused on the biodynamic theory of limb movements in humans. The theory has provided information about normal rhythmic limb movements in humans through investigation of the physical laws and their role in the movement organisation of the limbs.
In addition, it has contributed to the understanding of the role of the muscle/joint system in dynamic control of the limb.
The theory nevertheless has its shortcomings. The majority of the experiments have investigated the rhythmic movements only of the upper extremities. In addition, the studies have mainly dealt with simple stereotyped limb movements in the laboratory setting.
The tasks studied have involved few degrees of freedom and have not included real life situations. Additionally, the theory has not investigated limb movements in individuals with limb movement disorders.
Most evidence suggests that human limb movements are co-ordinated by both neural and mechanical factors (Berkinblit and Feldman, 1987); Feldman, 1980). The mechanism that regulates the length/tension properties of the muscle is in fact a part of the CNS, which sets up the resting length of the muscles. The mechanical properties of the muscle will then move the muscle to its new equilibrium points at times without a need for feedback. The results of studies investigating rhythmic limb movement co-ordination suggest that further research in this area should incorporate both neurophysiological and biodynàmic levels of analysis.
Physical therapists can benefit from the information provided by the biodynamic theory to train their patients in rhythmic limb movements such as gait training. Tne findings of the studies discussed earlier strongly suggest that the movements of upper and lower extremities interact. Locomotion studies in humans suggest a bottom-up organisation in the majority of subjects.
At present, however, the pattern of influence among limb movements is not predictable enough to provide hard evidence to develop

specific strategies for new exercise regimens. In addition, few studies have investigated the interlimb co-ordination in humans with neurophysiological or biodynamic impairment. One way this latter limitation may be reduced is to expand the experiments to include pathological cases.

A major methodological problem facing such studies will be forming control and experimental groups. If the research were to continue in this direction, the applicability of biodynamic theory in clinical conditions could increase. In the meantime, physical therapists should not remain indifferent or ignorant of the biodynamic theory and its usefulness to their practice.

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