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DEVELOPMENT OF COORDINATION OF SPONTANEOUS LEG MOVEMENTS.

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A striking feature of the early human motor repertoire consists of spontaneous kicking movements. The first part of this article gives an overview of the origins of locomotor behaviour in vertebrates with special reference to its neural organization. The second part concentrates on experiments on the development of leg movements in human infants. Different attempts have been made to explain the origins of the observed changes in development. Taking this into consideration, we present the setup of our research project and the related hypotheses.

“Without being nursed or even meeting any adult, many lower vertebrates can develop the appropriate locomotor movements and the strategy for how to adapt to the environment. Many mammals can walk and even run minutes after birth. Other mammals, including the cat and rat are immature when born, but even when raised in isolation, they mature and become able to walk and run.” (Grillner, 1981)

Origins of vertebrate locomotor behaviour

One of the greatest problems in controlling complex movements is how to reduce the enormous number of degrees of freedom within the animal or its environment (Bernstein, 1967). The problem is equivalent to trying to solve more unknowns (animal-environment details) than there are equations (desired positions). In tasks that have proven to be important during evolution, like locomotion, there are indications that within the nervous system there exist certain structures that can be held responsible for this required reduction of degrees of freedom. In their classical study, Wiersma & Ikeda (1964) found five interneurons in the abdominal ganglia of the crayfish that could be held responsible for the swimmeret movements that were observed. They called these five neurons ‘command neurons’ which were thought to control the activity of the whole ganglia. In this way, low-dimensional command neurons can be held responsible for high dimensional movements on the output side. Many questions remain about the exact nature of these degrees of freedom reducing ‘one-to-many maps’. An important aspect is the role of feedback.

In the first half of this century, naturalists interested in the Central Nervous System (CNS) formulated two alternative, but not mutually exclusive, hypotheses, about how locomotor movements are generated. The first is that centres within the nervous system are responsible for activating and coordinating the muscles involved in a movement according to a *Central Pattern Generator (CPG)*. This CPG can be regard-

ed as a cluster of neurons with a variable amount of connections that have variable weights. An important feature of the CPG is that the dimension of the output is higher than the dimension of the input and that it can generate output without any sensory feedback. The second hypothesis is that peripheral feedback elicits a cyclical movement by a "reflex chain", i.e., an external signal causes a contraction in a muscle or muscle group; this contraction generates sensory information which serves as a trigger for the next contraction etc. (e.g., Grillner, 1981).

These two hypotheses can be regarded as extreme points on a continuum of motor control: at one side of the continuum, motor control is regarded to be an open-loop process (CPG hypothesis), at the other side, motor control is regarded as a closed-loop process (reflex chain hypothesis). We think there is another continuum on which the reflex chain hypothesis and the CPG concept are extremes, namely a continuum from inflexibility to flexibility. By 'flexibility' we mean that it is possible for a system to change the input/output relation. We regard a CPG as flexible in that it is possible to make or break connections between neurons and to strengthen or weaken synaptic weights. The reflex chain, on the other hand, is in our view less easily adaptable. The simple topology is a constraint on flexibility.

It was Brown (1914) who explicitly attacked the reflex theory. He anaesthetised cats and observed that complex rhythmical movements occur at a depth of narcosis where reflexes are abolished. Brown suggested that rhythmical movements are 'conditioned by the balanced activation of antagonistic and linked efferent cycles (or half centres)', exerting mutual inhibition (e.g., Meijer, 1993). Also von Holst (1973) criticised the reflex chain theory. He observed that excitatory patterns sometimes occurred simultaneously, which challenged the idea of chain-like patterns. It should be noted that this argument is only true if the reflex chain is regarded as a one-dimensional connection.

Von Holst performed experimental tests on deafferented or isolated spinal cords and established their rhythm generating capacities: an indication that a central rhythm generating network located within the spinal cord indeed exists. Other support in favour of the CPG hypothesis comes from experiments by Cohen and Wallén (1980). They were able to show that, under appropriate conditions, the isolated lamprey spinal cord produces patterned activity remarkably similar to what one would expect such activity to be in the intact swimming lamprey. Other experiments in cats also give evidence for a spinal CPG. If the spinal cord is disconnected from the brain, or even the brainstem, then as long as the cat's weight is supported by a sling, the cat can make typical walking movements.

A suggestion made by Grillner (1981) is that the total output pattern of the limb could also result from the *combined* activity of different burst generators. Each unit burst generator (unit CPG) is then assumed to produce the rhythmical activity by itself and to contain all elements required for the bursting. The actual neuronal mechanisms utilized, however, are unknown (Grillner, 1981).

It is clear that even though the locomotor patterns can be generated autonomously, afferents play a crucial role in modulating the broad features of the motor output (Hasan & Stuart, 1988). Motor patterns generated in the absence of afferent input are

quite labile. A pure open-loop control mechanism for the CPG seems not very likely. Deafferentation experiments in cats reveal an EMG pattern that is more 'fragile': it can easily break down in certain sequences and subsequently become reinstated again (Grillner, 1981). Forssberg, Grillner and Rossignol (1975) showed that the reaction to a perturbation during walking in chronic spinal cats was strongly phase-dependent; identical tactile stimuli applied to the dorsum of the foot gave rise either to a marked flexion or a marked extension response depending entirely on the phase of the step cycle in which the stimulus occurs. This adjustment after a perturbation can be regarded as an indication for a closed loop component in the control of the CPG.

It can be concluded that the emergent picture of the neural control of the basic locomotor synergy is flexible organization of central pattern generators, providing an output pattern that may be modified through a complex organization of feedback systems acting on both motoneurons, premotoneurons and other CPGs (Grillner, 1981). Sensory or descending control systems can be held responsible for inducing the changes in gait (Cohen, 1988). From this point of view, the CPG is suggested to be placed in the middle of the closed loop/open loop continuum.

Development of leg movements in human newborns

It is of course not possible to experimentally isolate the centres of locomotor control in humans as has been done in quadrupeds. The only tools we have to ground our hypotheses on are EMG measurements and kinematic analysis of rhythmical patterns that can be observed.

Features of newborn stepping and infant kicking are highly compatible with the animal-based models for locomotion mentioned above. Like other vertebrates, bilaterally coordinated leg activity is evident long before the achievement of erect locomotion. Newborn infants in the supine position perform highly rhythmical, regularly alternating kicking movements. When infants are held upright, these alternations look remarkably like mature walking and have been called the neonatal 'step reflex'.

Thelen and coworkers (1981) analysed kicking movements in one month old infants and concluded that these movements were a developmental manifestation of a central locomotor program capable of generating spatially and temporally patterned movements of the leg. As cortical structures in the one month-old infants are very poorly developed, especially in the motor areas associated with the legs (Conel, 1941, in Thelen 1981), Thelen argues that it is likely that these human pattern generators are located lower in the CNS. Another important finding supporting this hypothesis is that anencephalic infants can perform patterns of infant stepping that are very similar to normal healthy newborns (Peiper, 1961). Unfortunately, the role of descending control systems cannot easily be evaluated, even when comparisons are made with anencephalic children. Without more evidence from other primates demonstrating evidence of intermediate patterns, it is difficult to know how to place these data in the present phylogenetic context (Cohen, 1988).

The most important observations that can be made in human infants concerning stepping and kicking movements are the following. Stepping movements can be observed immediately after birth. After the age of about two months, these movements can

no longer be elicited. The most widely accepted explanation for this phenomena is that maturing cortical centres inhibit a primitive stepping reflex, just as other neonatal reflexes such as the Moro, tonic neck, palmar and plantar grasp reflexes are suppressed as the motor tract develops (Peiper, 1961; Touwen, 1976).

Unlike erect stepping, newborn supine kicking does not disappear. Spontaneous kicking remains in the infant's repertoire throughout the first 6 months of age. Thelen (1982) concluded that kicking and stepping are the same movements and that the clue to disappearance of stepping and increase of kicking might due to be in the consequences of the infant's posture rather than in some yet unknown central neural processes. There is no agreement among different authors about the observed changes in frequency of the kicking movements. Thelen (1979, 1982) concludes that the frequency gradually increases during the first six months of life and then declines with the onset of crawling and walking. Geerdink (1993) analysed kicking movements in fullterm infants and reported a decreasing frequency of occurrence with age. The above mentioned 'cortical inhibition theory' as an explanation for these observed changes have been shown to provide an impoverished account of the complexities of developmental change (Hopkins, Beek & Kalverboer, 1992). More recently, theorists argue that movement properties emerge from the physical or biodynamical characteristics of the skeletomuscular system (e.g., Lockman & Thelen, 1993). As Thelen (1984) argues, infants undergo dramatic changes in the size, composition and proportions of their bodies, and in the strength and tone of their muscles. If the control parameters are indeed such factors as mass, stiffness and inertia, these must also undergo striking developmental transformations. The relatively lean, poorly muscled leg of the newborn, with its dominant flexor tone and weak extensor development is an entirely different moving creature than the well-muscled, fat leg of the 6 month-old. These changes must be viewed in concert with neurological maturation as essential contributions to movement outcomes. According to this 'biodynamic' approach, new experiments have been carried out to increase our understanding of movement control in infants through the analysis of inter-segmental dynamics (Schneider, 1990, Ullrich, 1991). It was concluded that smooth trajectories of kicking movements in 3-month old fullterm infants resulted not only from the muscle torque which counteracted and complemented gravity, but also from motion-dependent torques generated by movement of the linked segments.

Another striking feature in the development of kicking movements is the fact that the phase relation between the movements of the joints (inter and intra-limb) become less rigid (Thelen, 1985; Geerdink, 1993). Thelen (1985) argues that maturation involves a fundamental shift in the timing relationship between antagonist pairs from an in-phase activation to a predictable phase lag, with the acquisition of finer and more complex patterns of coordination. To explain these developmental changes, we suggest that the hypothetical CPG's are more influenced by external sources of information with increasing age emanating from higher centres and proprioceptive information. It is likely that *if* a CPG is more influenced by variable external information, this is reflected in more variable output. Thus with age, the CPG becomes less independent (see Figure 1).

Forsberg (1985) made comparable suggestions in the context of locomotion at

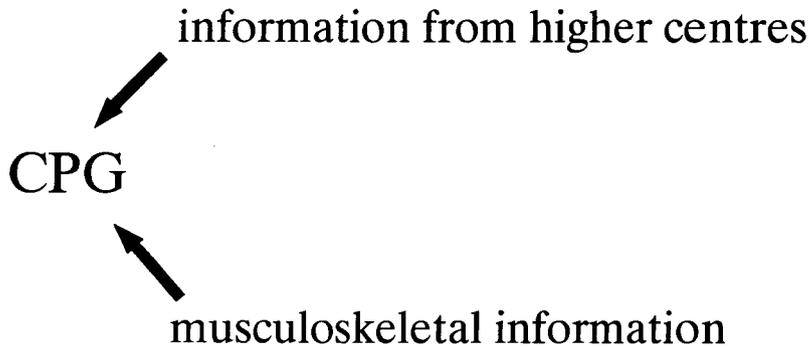


FIGURE 1 The central pattern generator influenced by external information.

later ages. He described the development of human bipedal locomotion from the first day of life until the first steps without external support about one year later. The main result was that infant stepping, supported locomotion and the first period of independent locomotion, lacked several of the functions that are specific to human plantigrade gait. Forssberg assumed a hierarchical system for human locomotor control similar to that of quadrupeds, but with additional neural mechanisms that transform the original pattern. An innate central pattern generator, initially programmed for non-plantigrade gait, creates the basic infant stepping rhythm. Descending locomotor driving systems establish control during the first year and give the child the ability to control the locomotor activity. Forssberg concluded that man has a unique system which influences the central pattern generator and transforms the activity to the specific human plantigrade gait (Forssberg, 1985).

From hypothesis to research questions

The purpose of our research is to come to a better understanding of changes in the coordination of leg movements that can be observed in infants during the first year after birth. The two questions we address are:

- 1) Assuming that a spinal CPG exists, what is the role of proprioceptive information in the development of this CPG?
- 2) What is the effect of changing physical characteristics of the musculoskeletal system on the development of spontaneous kicking movements?

The ultimate goal of this project is to formulate a simplest possible model of these components that yield a satisfactory description of the observable development.

In order to investigate the role of proprioceptive information, kinematic and electromyographic, data will be gathered during experimental manipulations in a longitudinal study with measurements at 6, 12, 18 and 24 wks of age. In order to evaluate the effect of changes in the external (gravitational) force field, two manipulations will be combined. On the one hand, the infant will be placed in the supine and upright positions; on the other hand, masses will be attached to the legs. To investigate the role of kinematic constraints on the activation of ipsi- and contralateral leg muscles, the movements of one leg will be restricted. During all manipulations head position and behavioural state will be monitored.

As an 'experiment in nature', the same manipulations will be carried out on

infants with perinatal brain damage. In these subjects, it is likely that the supraspinal component develops abnormally. As it is expected that the spinal circuitry and the musculoskeletal system are unaffected in the first instance, it is hypothesised that the spontaneous kicking movements will not be much different from the movements of the fullterm at the youngest age. With age, the differences are hypothesised to become larger.

Besides gaining insight into fundamental principles concerning the development of leg coordination, the relevance of this study can be sought in two directions. In the first place, the results may be of diagnostic value in medical settings. In particular the data concerning the brain damaged children may have consequences for deriving intervention programmes. In the second place, our results may be useful in the field of robotics. Modelling a biological system that is able to make adaptations to perturbations is a typical problem in this field.

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