Development of Bipedal and Quadrupedal Locomotion in Humans from a Dynamical Systems Perspective

Üner Tan
(Honorary Member of the Turkish Academy of Sciences, Ankara, Turkey)
Çukurova University, Medical School, Department of Physiology, Adana
Turkey

1. Introduction

Locomotion is the movement of an organism from one place to another, often by the action of appendages such as flagella, limbs, or wings. In some animals, such as fish, locomotion results from a wavelike series of muscle contractions (The American Heritage® Science Dictionary, 2005). Walking is the act of traveling by foot; gait is the manner of walking; running is the act of traveling on foot at a fast pace; crawling is a slow mode of hand-knee or hand-foot locomotion. Quadrupedal locomotion, walking on all four extremities, is the most remarkable trait of the quadruped animals, and has been elegantly elaborated by dynamic selection processes over millions of years. Non-primate mammals usually utilize lateral-sequence quadrupedalism, in which the hindlimb footfall leads the ipsilateral forelimb, whereas the non-human primates utilize a diagonal-sequence quadrupedalism, in which the hindlimb moves with the contralateral forelimb in a diagonal couplet. The neural control for the quadrupedal and bipedal locomotor processes in monkeys may also be applicable to human locomotion (Xiang, 2007).

2. Historical development

The first historical evidence of the gait analysis is from the time of Aristotle (384-322 BC), who presented the first written reference to gait analysis (Baker, 2007). However, he was not able to test his hypothesis by experiment, and his observation-based ideas were later not supported by applying them to scientific experiments. Galileo Galilei (1564-1642) was the first to be able to test hypotheses by experiments, to prove any conjecture.

Giovanni Alfonso Borelli (1608-1679), one of the Galileo's pupils, first experimented to develop a gait analysis (Borelli, 1989). A rather detailed history of gait analysis was presented by Baker (2007).

The first known instance of human quadrupedalism was reported by the great English photographer Eadweard Muybridge (1830-1904), who created movement by displaying individual photographs in rapid succession (Muybridge, 1901). The child with a paralyzed leg due to infantile poliomyelitis was photographed and animated by Muybridge (1887,

1901). Despite the paralyzed leg, the child was able to move using diagonal-sequence quadrupedal locomotion (Fig. 1).
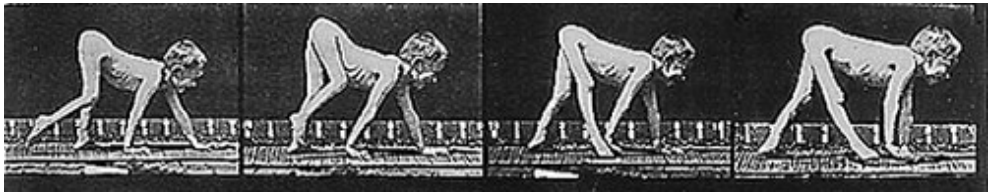

Fig. 1. Child walking on hands and feet, plate 539 from "Animal Locomotion" (Muybridge, 1887).

The first description of human quadrupedalism in adults was that of Childs (1917), a British traveler, during his trip along the historical Baghdad Road, through Havza (Greek: Hafsa) near Samsun (Greek: Samsounta), in the middle region of the Black Sea coast. The man, a beggar most probably belonging to a Greek family, had longer arms than legs, as judged from the slope of the hill, and from the report in Childs's book. He also probably belonged to a consanguineous family, since the Greek population lived in isolation in this region of the Black Sea coast, with many possible interfamilial marriages. Although he could not stand up without assistance, he was a man with rather strong arm and leg muscles, and could easily spring onto his donkey's back. This man is depicted in Fig. 2.

This case was the first adult quadruped man exhibiting Uner Tan Syndrome (UTS) with quadrupedalism, possible mild mental retardation, and dysarthric or no speech (see Tan, 2010a for a review). The arm to leg ratio (calculated from the picture) was rather high, 92%, similar to the arm: leg ratio of 90% in one case with UTS in the Adana 1 family (see Tan, 2006b, c).

Fig. 2. The man with habitual quadrupedal locomotion discovered in Northern Turkey by Childs in 1917 (see Childs, 1917, p. 27).

Children with habitual quadrupedal locomotion were first reported by Hrdlicka (1928): 41 children (59% males, 41% females). The children began to walk on all fours at the age when healthy children begin to crawl on hands and knees. Some of them were later able to stand and begin to walk bipedally, but others continued walking and running on all fours for a long time. Fig. 3 depicts native African children running around on all fours. Their quadrupedal locomotion seems to be their natural gait, with easy and fast running. Fig. 4 depicts children with diagonal-sequence quadrupedal locomotion (right) and moving down or up stairs on all fours (left) (Hrdlicka, 1931, pp. 29 and 109).

Fig. 3. Two native African children scooting around on all fours easily and so swiftly it was even difficult to take their pictures. From Hrdlicka (1931).
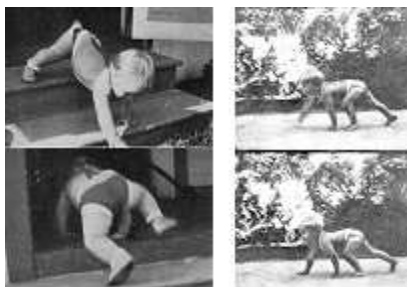

Fig. 4. Children with quadrupedal locomotion: left, a child moving down and up stairs on all fours; right, with diagonal-sequence quadrupedal locomotion (Hrdlicka, 1931).

Interestingly, not a single case with quadrupedalism was reported after the Childs' case (see Childs, 1917) until the discovery of the Turkish quadrupeds, almost 100 years later (Tan, 2005, 2006a). These individuals exhibited a never previously reported novel syndrome, referred to as Uner Tan syndrome (UTS), with the main symptoms of habitual locomotion on all fours, mental retardation, and impaired speech (Tan, 2005; Tan 2006a). Subsequently, nine more families with this syndrome have since been reported in Turkey since the discovery in 2005 (see Tan, 2010a for a review). The clinical and radiological characteristics of these cases are presented in Table 1. The syndrome has sparked a world-wide interest: see, for instance, Garber (2008), Ghika (2008), Caglayan (2008, Thesis), Akpinar (2009), Le Fanu (2009), Held (2009), Kolb (2009, Thesis), Kutty (2010), Bornstein (2010), Pribut (2010), Downey (2010a, b), MacLellan et al. (2011), Arif et al. (2011).

3. Transient quadrupedalism

The most prominent characteristic of the UTS cases was the diagonal-sequence quadrupedalism, which usually started during childhood following a normal hand-knee crawling period at around two years of age. However, a transformation from well-balanced quadrupedalism to ataxic-bipedalism occurred at around 12 years of age in one man, who walks in a bipedal ataxic manner now and has not utilized locomotion on all fours since about 25 years ago. The man was one of six quadrupedal cases in the first discovered family near Iskenderun (Tan, 2005; Tan, 2006a), and the five other cases in the family are consistent quadrupeds.

In addition to this case one man (44 years old) from the Adana 1 family (Tan 2006b, c) exhibited consistent quadrupedalism, while the other man (34 years old) from the same

Families	ISK	AD1	ANT	CAN1	CAN2	KA	AFY	AD2	DI 1-2
N	19	3	29	2	2	2	3	5	22
Men	8	2	16	1	1	2	2	4	13
Women	11	1	13	1	1	0	1	1	9
Age	19-35	27-33	12-46	62-65	22	43-44	10-22	12-21	3-30
N (QL)	6	2	7	2	2	2	3	1	7
Men	2	1	5	1	1	2	2	1	4
Women	4	1	2	1	1	0	1	0	3
Age	19-33	27-37	12-46	62-65	22	43-44	10-22	12	7-25
Locus	WDR81	Ch.13q	Vldlr	Vldlr	Vldlr	(?)	(?)	(?)	(?)
Cerebellum	Hypo.	Normal	Hypo.	Hypo.	Hypo.	Hypo.	Hypo.	Hypo.	Hypo.
DTR upp.	Normal	Normal	Normal	Normal	Normal	Normal	Normal	Hypo.	Norm.
DTR low.	Hyperac.	Hyper.	Hyper	Hyper	Hyper.	Hyper.	Hyper.	Hypo.	Hyper.
Mus. Tone	Normal	Normal	Normal	Normal	Normal	Normal	Normal	Norm.	Norm.
Strength	Normal	Normal	Normal	Normal	Normal	Normal	Normal	Norm.	Norm.
Babinski	+(3/5)	Absent	+(3/7)	Absent	Absent	+ (1/2)	+(1/3)	Absent	+(1/7)
Tremor	Mild	Mild	+(1/7)	No	No	No	No	Yes	No
Nystagmus	Yes	Yes	No	No	No	No	No	No	2/3
Early Hyp.	No	No	No	No	No	1/2	Yes	No	Yes
Speech	Dysar.	Dysar.	No	No	No	Dysar.	No	No	No

Families: ISK: Iskenderun, AD1: Adana1, ANT: GaziAntep, CAN1: Canakkale1, CAN2: Canakkale2, KA: Kars, AFY: Afyon, AD2: Adana2, DI 1-2: Diyarbakir 1 and2. Consang.: consanguinity; QL: quadrupedal locomotion; BL: bipedal locomotion; Atax: ataxia; Vest. imp.: vestibular impairment; cereb.cor.: cerebral cortex; DTR: deep tendon reflex, upp.: upper extremity; low: lower extremity; mus.: muscle; hypo.: hypotonia; exp.: expressive; trun.: truncal; bip.: bipedal; habit.: habitual.

Table 1. Families with Uner Tan syndrome hitherto discovered in Turkey

family transformed from childhood quadrupedalism to ataxic bipedalism at about 14 years of age. In childhood this individual propelled himself backwards on his bottom, and then started ambulation on all fours at about two years of age. These persons with adulthood transformation from quadrupedalism to bipedalism were previously reported as consistently bipedal-ataxic cases. Consequently, these results concerning transient quadrupedalism are not consistent with some minor reports accentuating the existence of purely ataxic bipedal cases among siblings of UTS cases. A transformation from balanced quadrupedalism to ataxic bipedalism also occurred during adulthood. For instance, one of the brothers from the Kars family (now 46 years of age) exhibiting UTS, showed a transition from habitual quadrupedalism to ataxic bipedalism about 20 years ago. (seeTan, 2010b).

4. Dynamics

Dynamics in physics deals with the motion and equilibrium of systems under the action of forces, usually from outside the system; it is an interdisciplinary field in contemporary science now, to analyze the behavior *(*Strogatz, 2000, p. 2). The system concept, accentuating the relationships between component parts rather than the parts themselves, opened a powerful new perspective in science. The system thinking is valuable because it can help us to create smart, enduring solutions to scientific questions, and because it offers us a more accurate picture of reality. By definition, a system is a group of interacting and interdependent components that form a complex and unified whole.

Systems can be controlled or uncontrolled. In controlled systems, the information is sensed, and changes are effected in response to the information, a process that can be referred to as *detector, selector, and effector*, respectively (Kuhn, 1974). The detector is the sensing part of the system, and is concerned with communicating information between systems, including environment. The selector is the part of the system that processes information and makes decisions, and the role of the decision-making part of a system is to drive the system towards equilibrium. The effector is responsible for the transactions between systems. Communication and transactions are involved in interactions between systems. From two general approaches, *cross-sectional and developmental approaches,* a system developmental approach was the topic of the present work, dealing with the changes in the system over time. To analyze the development of human quadrupedalism, a *holistic analysis* was performed to examine the system as a complete functional unit, instead of a *reductionist approach,* which looks downward and examines the subsystems separately within the system. Properties of any system are: (i) a system consisting of interrelated and interacting parts exists in an environment; (ii) any system has a preferred state; (iii) the components of a system may in turn be systems themselves. Conceptual systems are utilized in analysis, comprehension, and for improvement purposes. All open and closed systems have a preferred state. For instance, atomic oxygen prefers to be molecular oxygen, a business prefers to be profitable, human beings prefer to be physiologically and emotionally satisfied.

5. Complex systems and self-organization

Complex biological systems, such as families, the human body, the brain, etc., consist of interconnected or interwoven parts (Bar-Yam, 1997, p.1). Complex systems in physics, such as ice crystals, galactic spirals, clouds, or lightning flashes, tend to spontaneously generate new organized forms.

Dynamic complex systems have self-organizing properties, following the principle the sum of the parts is greater than the parts taken independently, contrary to Sir Isaac Newton's argument the motion of the whole is the sum of the motion of all the parts. The dynamic complex systems have the tendency to spontaneously self-organize themselves to produce novel patterns. The process of self-organization is the quintessence of all living systems. The evolution of living beings may also be associated with the principles of self-organization, but Darwinism essentially ignores the process of self-organization (see Waldrop, 1990; Oudeyer, 2006).

The self-organization is closely coupled with "emergence," a fundamental property of complex systems, i.e., a new property or behavior…emergence may be considered the product or by-product of the system… the product of interconnections and the interaction makes it dynamic and unpredictable (Dobrescu & Purcarea, 2011). The emergence of unpredictable outcomes within a complex system such as the human body is closely related to neural networks that are "self-organized critically" (Tetzlaff et al., 2010).

By definition, self-organization occurs through the interaction of its components (endogenously) or by some environmental influence (exogenously). self-organization may be triggered by "strange attractors" , which refers to a kind of steady-state in a dynamical system. One type of attractor is the strange attractor, which may be visible, for instance, in the EEG pattern during rest. Another type of strange attractor may be visible in the EEG

during thinking. Other types of strange attractors may be consciousness and personality. The brain as a dynamic system may have many strange attractors, which may show state transitions, thereby creating novel and unpredictable patterns, such as during the postnatal development of children.

The common factor for UTS to trigger a strange attractor, i.e., the diagonal-sequence quadrupedal locomotion may be their disability or difficulty in achieving bipedal upright locomotion. The extremely rare emergence of human quadrupedalism may be associated with the unpredictability of the strange attractors. Concerning the adaptive motor behavior and intentionality, the dynamical systems tend to control the outcome pattern of the system to find a compromise between *which patterns can possibly be built from the system components to begin with, and the structural constraints of the environmental situation;* a synergetic pattern formation—with possible strange attractors—may be "intentional" with the self-organization phenomena being basic explanations for the adaptive behavior (Tschacher et al., 2003).

6. Central pattern generators

Central pattern generators (CPG) are embedded within the spinal cord, responsible for creating a locomotor pattern and generating rhythmic locomotor activity, without being controlled by the supraspinal centers (Grillner & Wallen, 1985; Hooper, 2000; Hiebert et al., 2006). The isolated spinal cord in the lamprey (a primitive fish) can spontaneously produce *fictive locomotion* (Cohen & Wallen, 1980; Grillner & Wallen, 1985), as in salamander (Delvolvé et al., 1999) and frog embryos (Soffe & Roberts, 1982). In contrast to lower vertebrates, the existence of CPGs in higher primates is much less convincing (Duysens et al., 1998), and the concept of CPG did not find supporters among system theoreticians.

The progressive maturation of the locomotor networks (CPGs) in the central nervous system, studied by anatomical and electrophysiological techniques, was previously evaluated by Dr. Douglas Stuart, in a detailed review article (Stuart, 2007). Regarding the spinal CPGs operating in human beings, there is only indirect evidence. Locomotor-like movements were recorded in human fetuses at 10 gestational weeks, and neonatal infants often exhibit stepping movements if supported (McGraw, 1945, pp.22-23). However, this first stepping ability subsequently disappeared for many months due to mechanical (Thelen & Fisher, 1982) or neuro-developmental factors (Forrsberg, 1985). On the other hand, the CPGs are not static, previously hard-wired, firmly established systems, but instead they are rather loosely organized neural networks under the influence of the dynamically changing chemical and/or sensory control, resulting with many newly emerged functional circuits (Selverston, 1988, cited by Kelso, 1995, p.243).

In contrast to the theory of stage-like motor and cognitive development, the perspective of behavioral-motor development as a self-organized process seems to be more plausible to explain why and how infants walk within a particular environment (see for review Thelen & Ulrich, 1991). That is, a previously coded neural network, i.e., neural coding, seems to be unlikely, because of the lack of precise point-to-point wiring in the central nervous system with immense overlaps of dendritic and axonal arbors. The   integrative neuroscience emphasizes the "*inside-out*" and "*outside-in*" approaches for the understanding of locomotor control (see Stuart, 2007).

7. Motor development

Needham (1959) reported that over 2000 years ago Aristotle was one of the first people studying embryonic development systematically. He examined embryos of different organisms by opening up birds' eggs, and by studying mammalian and possibly human embryos at different developmental stages. In Aristotle's philosophy, *movement* is a central concept, which means much more than being a merely mechanical process, as emphasized by Tan (2007) in his psychomotor theory.

During embryonic development of the CNS, the large neurons, such as the Purkinje cells in the cerebellar cortex, and the pyramidal cells in the cerebral cortex, are generally produced before the small neurons and the small neurons (interneurons) emerge last during neural development in utero. Also, motor nuclei commence their histogenesis and complete their cell populations before the sensory nuclei (Brown et al., 1997). The thickness of the cerebral cortex steadily increases during in-utero development, and the Broca's area rapidly grows through the first postpartum month, reaching the adult thickness when the child is around four years of age. The pyramidal cells in the cerebral cortex actually start to differentiate by 25 weeks of gestation, but without basal dendrites, with only tortuous apical dendrites. The first synapses in the human cerebral cortex appear at about 23 weeks of gestation (Molliver et al., 1973). The pyramidal cell morphology is completed at about three years of the postpartum development of the human cerebral cortex. The small pyramidal cells mature at the last trimester, during which spines also appear on the dendrites, with a tenfold increase in the dendritic trees during the same time span. Finally, as the neuronal projections approach their final structures, regressive events such as cell death, axonal pruning, and synaptic elimination, occur in the central nervous system (Cowan et al., 1984). Actually, during the embryonic phase of in-utero development, many more neurons are produced than are present in the mature central nervous system. However, while making synaptic connections of their axons, many neurons (about half of them) are eliminated by selective cell death (Oppenheim & Chu-Wang, 1983), which rapidly occurs within a few days. *Programmed cell death is genetically determined but may be influenced by functional changes such as motor activity or inactivity and by the size of the target group of neurons* (Brown et al., 1997, p. 15). The purpose of the programmed cell death may be the elimination of axons incapable of reaching the target, to avoid or clean the connection errors.

With regard to in-utero fetal movements, the first modern concept of the origin of the prenatal movements interestingly originated from Preyer as early as in 1885 (cited by Schröder & Young, 1995). Preyer concluded that the spontaneous fetal movements may start long before the 12th week of gestation, not being associated with peripheral stimuli, suggesting an important function of this spontaneously generated fetal motility in the ontogeny of the organism.

Children were classified according to the development of muscle response synergies, as follows (Woollacott & Sveistrup, 1992; Sveistrup & Woollacott, 1993): pre-sitting in 2-6 months, early pull-to-stand in 7-8 months, pull-to-stand in 9-10 months, independent stance in 10-12 months, independent walking in 12-14 months, and late independent walking in 14-16 months. Postural control may be impaired in children with cerebral palsy, due to an injury to the cerebral cortex resulting from anoxic or hypoxic encephalopathy, intracerebral hemorrhage, and CNS neuropathy resulting from malformation (Olney & Wright, 1994). The stretch reflexes are always exaggerated in children with cerebral palsy. The functional

significance of these hyperactive stretch reflexes is the subject of debate. Accordingly, Nashner et al. (1983) did not find a correlation between stretch reflex abnormalities and functional ability, and questioned the role of the stretch reflexes in postural control. This is expected from the system perspective: many subsystems are dynamically interacting during postural development within the context of the task and environment.

Humans with or without quadrupedalism may share similar CPGs with other quadrupeds, because they are all using the common neuronal control mechanisms for locomotion (Shapiro & Jungers, 1994). Accordingly, Dominici et al. (2011) selected the basic discharge patterns of lumbosacral motoneurons during stepping of neonates, toddlers, preschoolers, and adults. These authors found *two basic patterns of stepping neonates are retained through development… Markedly similar patterns were observed also in the rat, cat, macaque, and guinea fowl, consistent with the hypothesis that, despite substantial phylogenetic distances and morphological differences, locomotion in several animal species is built starting from common primitives, perhaps related to a common ancestral neural network…*(p.997). For animals with diagonal-sequence quadrupedal locomotion, these ancestors may be extended to the first emergence of tetrapods during the Devonian period, about 400 million years ago. In other words, the basic neural networks that emerged about 400 million years ago in the first tetrapods during transition from water to land seem to be conserved in animals with diagonal sequence quadrupedal locomotion from primitive quadrupeds up to the primates including human beings. Stuart (2007) emphasized the need to *"… give equal attention to issues raised concerning the motor control of a variety of animal phyla, classes and species (Stuart, 1985, p.96; Stein, 1999). It has proven to be heuristic value to indicate when common principles of motor control are present across phyla (Pearson, 1993), when evolutionary deviations have occurred (Fetcho, 1992).*

8. Maturation theory

During the first half of last century motor development was approached by longitudinal studies to show the sequence of motor behaviors in infants and young children. This maturation theory was mainly elaborated by Gessel (1928), Shirley (1931), and McGraw (1932, 1943), who searched for rules governing the order of changes during motor maturation. Konner (1991) stated *motor development sequences are largely genetically programmed.* Forssberg (1985) explained the disappearance of the neonatal stepping and its reemergence by the maturation of the supraspinal centers, suggesting that the neural code has been retained in humans since the earlier evolutionary periods. The development of early motor behaviors was also attributed to the maturation of the cortico-spinal pathways (von Hofsten, 1984; Jeannerod, 1988).

Although the maturation theory added some valuable information to the basics of motor development, it was far from explaining the dynamics of locomotor development, especially with regard to the behavior in real time and the process of change. In this context, Ulrich (1997) stated *it is not at all clear how genetic codes can be translated into even simple patterned neural organization… behavior is much more than a simple neural pattern* (p.321).

To be able to solve the problems related to development, one must consider the properties of complex systems with many dynamically interacting individual parts. Dynamic systems theory is involved in such an approach, which seeks to understand the behavior of a system, not by taking it as separate parts, but by taking these parts to see under what circumstances

they dynamically cooperate to induce a whole pattern (Thelen, 1996). The most important basic characteristic of dynamic systems theory is that behavioral patterns such as locomotion can emerge spontaneously from the dynamic interaction of multiple subsystems or components; detailed plans or neural codes are not represented *a priori* in the brain, nor are the movement patterns, such as walking and running, from the maturation of fixed CPGs. From the dynamic systems perspective, the developmental emergence of human locomotion is also self-organizing, as in other complex systems. *Multiple subsystems, intrinsic and extrinsic, contribute to behavioral outcomes. for example, neural organization, muscle strength, joint structures and ranges of motion, motivational and arousal levels, the support surface, and the task… the coordination pattern emerges spontaneously, and is self-organized and opportunistic* (Ulrich, 1997, p.324). The classical example of self-organization is Thelen's (1986) discovery showing a-month-old child exerting stepping on a motor-driven treadmill when supported upright. The child's stepping on the treadmill occurred under the influence of multiple subsystems. That is, the sensory receptors first detect the dynamics of the context, and then send the information to the motor neurons through interneurons to activate the muscle synergies, comprising the intrinsic subsystems that contribute to the locomotor behavior. The treadmill belt, the supplemental postural control and weight support provided by the experimenter are extrinsic subsystems.

9. Neuronal group selection theory

In the field of motor control, better understanding of neurophysiology caused a gradual shift from the concept that motor behavior is largely controlled by reflex mechanisms towards the notion that motility is the net result of complex spinal or brainstem activity. It was assumed that motor control of rhythmical movements like locomotion, respiration, sucking, and mastication may be based on CPGs. The activity of the networks, which are usually located in the spinal cord or brainstem, is controlled from supraspinal areas via descending motor pathways. The supraspinal activity itself is organized in large-scale networks in which cortical areas are functionally connected through direct recursive interaction or through intermediary control or subcortical (striatal, cerebellar) structures. Consequently, theoretical frameworks for the processes involved in the development of motor control include two major but current and conflicting theories: neuronal maturationist theories and the dynamic systems theory. There is also a third theory, the neuronal group selection theory, which combines the "nature" part of the neural-maturationist theories with the "nurture" part of the dynamic systems theory (Hadders-Algra, 2000).

It was believed in the mid-1990s that the maturation of the CNS progressively occurred through the genetically predetermined neural patterns, in the cephalocaudal and central-to-distal direction; the locomotor development was regarded as a result of the progressively matured and hence increased cortical control on the spinal reflexes. That is, it was believed that standing and walking result from the cerebral maturation, which is genetically predetermined and not learned by experience. McGraw (1943) considered the locomotor development from a convergent action of "nature" and "nurture". More controversially, Thelen and Ulrich (1991) did not accept the neural-maturationist theories, asking how can the timetable of motor solutions be encoded in the brain or in the genes?

The contemporary ideas about neuronal maturation actually originated from Bernstein (1935), who tried to understand how the CNS solves the problem of locomotor coordination, and

argued that the production of locomotion involves hundreds of muscles and joints, which require specific computational techniques of the nervous system. Kelso et al. (1981) utilized the dynamic systems theory to explain the developmental emergence of locomotion in human beings. These authors suggested that a behavior, such as a locomotor pattern (quadrupedal or bipedal), may result from the combined dynamic effects of, for instance, muscle strength, body weight, postural support, motivation, and brain development, in addition to the environmental initial conditions and task requirements (see also Thelen, 1996; Ulrich, 1997).

Transitions in locomotor behavior, best exemplified in the transition from quadrupedalism to bipedalism in some UTS patients (see above), may occur due to the innate dynamics of the complex systems. Thelen (1996) suggested that the locomotor development as a dynamic system may be considered as a self-organizing process, a series of states of stability, instability, and phase shifts in the attractor landscape, reflecting the probability that a pattern will emerge under particular constraints. In summary, the neural maturationist theories consider the maturational state of the nervous system as the main constraint for developmental progress, whereas in the dynamic systems theory the neural substrate plays a subordinate role (Hadders-Algra, 2000).

The variability in developmental processes, such as motor performance, developmental sequence, or the duration of developmental stages, was emphasized to explain the development by the Neuronal Group Selection Theory (NGST) (Edelman, 1993; Sporns & Edelman, 1993). Neuronal groups are collections of many hundreds or thousands of neurons interconnected by excitatory and/or inhibitory synapses as well as the excitatory and/or inhibitory recurrent feedback circuits. According to the NGST, the functional and structural properties of neuronal groups are determined by evolution. However, the repertoires are variable because of the dynamic epigenetic mechanisms regulating cell division, adhesion, migration, apoptosis, and extension and retraction of neuronal arborizations. Behavior and experience, such as during locomotor development, produce afferent information for the cerebro-spinal locomotor system. This afferent information is used for the neuronal selection induced by changes in the excitatory and inhibitory levels of the synapses and in the intergroup connections within a particular neuronal group. The experiential afferent information induces modifications in the strength of the synaptic connections within and between the neuronal groups resulting in the variable secondary repertoire. The changed connectivity within the secondary repertoire allows for a situation-specific selection of neuronal groups. Thus, the secondary neuronal repertoires and their associated selection mechanisms form the basis of mature variable behavior, which can be adapted to environmental constraints (Hadders-Algra, 2000). The NGST emphasizes the role of the complex information processing originating from an intertwining of information from genes and the environment, which is inconsistent with the "nature-nurture" debate. During motor development in early fetal life, the spontaneous movements (primary variability), i.e., the self-generated motor activity with the consequent self-generated afferent information, may explore all the locomotor possibilities within the neurobiological and anthropometric constraints within the CNS, preserved during evolution.

During postnatal development, all of the intentional motor behaviors are within the frame or in the phase of "primary variability". This developmental phase is characterized by synaptogenesis, which is especially prominent in the cerebral cortex (Huttenlocher et al.,

1982; Rakic et al., (1986). The primary networks developed during this phase are suitable for the selection of the appropriate locomotor circuits, and are indeed associated with ample variations in locomotor activities such as crawling. The neural systems with specific functions can explore all motor possibilities available for the specific intentional motor function. Consequently, the most efficient motor pattern gradually emerges following exploratory and continuous information processing activities within the CNS. The time-sequence for the selection process changes with function, such as the second half year after birth for arm reaching; the postural activity of neck and trunk muscles are direction specific before infants can sit independently at about four to five months of age. Selection of the most efficient postural adjustment in which all direction-specific neck, trunk, and proximal leg muscles are activated, occurs during the third postnatal trimester (Hadders-Algra et al., 1996), which can be accelerated by exercise for balance, facilitating the selection process (Hadders-Algra et al., 1996). The most efficient postural balance selection occurs much later between 12 and 18 months of age.

The establishment of the secondary (sub)cortical repertoires is mainly associated with neural rewiring, which may occur through synapse formation, synapse elimination, increase or decrease in dendrites, their arborizations, and spine number on the dendrites. The long duration of the developmental processes within the brain suggests that long-lasting experiences are needed for the establishment of the secondary neuronal networks, for an efficient motor solution to develop for each specific situation. Children, in general, exhibit non-optimally adapted motor behavior with considerable variation, which negatively correlates with age; small adult values of variation are first reached in adolescence (Forssberg & Nashner, 1982). This may be associated with the late-onset quadrupedalism in some UTS cases, who had never been subjected to any kind of walking exercise, either in infancy or in adolescence or adulthood. Actually, exercise may be beneficial for the selection of the most effective strategy out of the repertoire of adaptive motor strategies, by reducing the amount of secondary variation (Pedotti et al., 1989). The reverse occurs in the absence of exercise, by increasing the motor variation, similar to the UTS cases with no exercise at all. Motor development in light of NGST is summarized below (from Hadders-Algra, 2000):

1. *Primary Variability* (during fetal life and infancy; high variability in motor behavior): the neural system explores, by means of self-generated activity, and consequently, by self-generated afferent information all motor possibilities become available within neurobiological and anthropometric constraints set by evolution.
2. *Selection* (reduced variation, occurring during infancy, at function specific ages): experiential selection of most effective motor patterns and their associated neuronal groups with transient minor reduction in variation of motor behavior.
3. *Secondary or adaptive variability* (from two to three years of age to adolescence): Creation of secondary neural repertoires due to a multitude of experiences, and *Mature situation:* Task constraints: ability to adapt each movement efficiently to task-specific conditions.

The developmental NGST is closely coupled with the concept of the adaptive self-organization. Namely, developmental selection is the differential survival and proliferation of developmental units. This type of internal selection has been proposed as an explanation for diverse examples of self-organization, from the wiring of brains to the formation of pores on leaf surfaces (Frank, 1997).

10. Dynamics of locomotor development in humans

The contemporary views on the development of locomotor skills accentuate the role of the self-organizing processes within the scope of dynamic systems. As mentioned above, the neural networks playing a role in the diagonal-sequence quadrupedal locomotion have existed since about 400 MYA during the Devonian period, having arisen with the first appearance of the ancestral tetrapods. Namely, this type of locomotion is indeed phylogenetically oldest locomotor trait of tetrapods (four-legged animals). Their fossilized 395 million years old bodies were recently discovered across a Polish coast (Niedzwiedzki et al., 2010). From the fossil tracks left by a tetrapod-like animal it was concluded that this animal walked with diagonal strides, reflecting the lumbering locomotor movements like their fishy ancestors living in marine environments (Fig. 5).
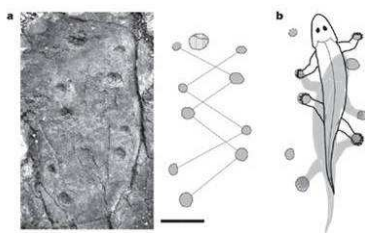

Fig. 5. Trackways. **a:** Muz. PGI 1728.II.16. (Geographical Museum of the Polish Geological Institute). The trackway shows hand and foot shapes in diagonal stride pattern; **b:** a generic Devonian tetrapod fitted to the trackway. Notice the lumbering diagonal sequence quadrupedal locomotion of this tetrapod, similar to its ancestral forms living in water.

Interestingly, the quintessence of this kind of locomotion, did not change during evolution, through salamanders and tuataras (Reilly et al., 2006), till the emergence of non-human primates and even human beings exhibiting diagonal movements between arms and legs even during upright walking (Donker et al., 2001). Fig. 6 illustrates three healthy humans exhibiting diagonal-sequence arm-leg movements during upright-bipedal (above) and requested quadrupedal locomotions (below).

Thus, it may be concluded that the neural generators for diagonal-sequence quadrupedal locomotion may already be present in more or less stable forms in the complex neural systems of primates, including humans. From a systems perspective, it may be argued that the locomotor patterns such as human quadrupedalism may emerge through exploration of available solutions, such as the ancestral neural generators for quadrupedal locomotion and then selection of preferred patterns, such as the ancestral CPGs (Gibson, 1988; Sporns & Edelman, 1993; Thelen & Corbetta, 1994; Turvey & Fitzpatrick, 1993). Following this ontogenetic theory, it may be suggested that the prenatal and postnatal emergence and development of diagonal-sequence quadrupedal locomotion in human beings may be the result of an exploration and subsequent selection process following the principles of the self-organizing dynamic systems (see also Chang et al., 2006).

In the individuals exhibiting UTS, the cases seem to be unable to make the transition from the infantile stage of quadrupedal crawling to upright standing and bipedal walking. Since

they are unable to walk upright due to severe ataxia, their brain then explores the possible solutions during locomotor development, but cannot select the ideal locomotor pattern for upright bipedal walking. Instead, their brain can select only one locomotor pattern for their locomotor activities, which is already present since about 400 MYA. This is the diagonal-sequence quadrupedal locomotion emerged during Devonian period. This walking pattern may also be unstable initially, but becomes stable with practice during childhood, after which they are able to move with great ease, speed, and well-developed balance. On the other hand, the locomotor self-organizing process may take a long time in cases with late childhood emergence of quadrupedal locomotion at about puberty (12-14 years), a period associated with hormonal changes with beneficial effects on the motor system, accelerating the self-organizing processes and resulting in the emergence of a most suitable locomotor pattern to travel around, which in their case is walking on all four extremities (see Tan et al., 2010).

Fig. 6. Diagonal-sequence arm-leg movements (left hand-right foot *vs* right hand-left foot) during walking on two legs (above, bipedal gait) and walking on all four extremities (below, quadrupedal gait) in normal individuals. A1, A2: girl 17 YA; B1, B2: girl 4 YA; C1, C2: boy 14 YA. Photographs are curtesy from Derya Deniz Elalmış (post-doc fellow).

There is another example of the endurance of the adaptive self-organizing processes in the central nervous system through adulthood, namely, two brothers (43 and 44 years of age) with UTS reported by Tan (2010b). One of the brothers exhibited consistent quadrupedalism, but the other exhibited a transition from quadrupedalism to bipedalism despite a mild ataxia, and was able to travel with the aid of a walking stick by early adulthood (20 years of age). Similarly, there was one man in the Iskenderun family (Tan, 2005, 2006a) with a transition from quadrupedalism to late childhood ataxic-bipedalism, and one man in an Adana family with a transition from childhood quadrupedalism to adulthood

ataxic-bipedalism (Tan, 2006b, c). In this context, i.e., transition from quadrupedalism to bipedalism, Nakajima et al. (2004) reported *the animal (Japanese monkey) can also learn to transform its locomotor pattern from quadrupedality to bipedality, and vice versa. This monkey can select a postural strategy appropriate for the execution of both gaits* (p.183).

Interestingly, there were two bright children, with entirely normal brains and cognition, who exhibited facultative quadrupedal locomotion: bipedal walking for everyday activities, but quadrupedal running for speedy actions (Tan & Tan, 2009). Apparently, their adaptive self-organizing brains explored the available solutions for slow and fast locomotion, with subsequent selection of the preferred patterns for traveling around. These outside-in mechanisms (see Stuart, 2007) may involve mesencephalic and subthalamic regions, cerebellum, basal ganglia, and hypothalamus (see Takakusaki et al., 2006); the posterior parietal cortex may plan the travel and the motor cortex may contribute to traveling through fields with obstacles (Drew et al., 2008), allowing the necessary modifications during traveling, and utilizing the adaptive self-organizing processes to explore, select neural groups, and execute the preferred locomotor patterns. For the adaptive self-organization in the brain, dynamic instability, a form of complexity, is typical for the neuronal systems (Friston, 2000a, b, c), allowing the selective consolidation of synaptic connections within the selected neuronal groups (Edelman, 1993).

11. Concluding remarks

The first phase in the development of locomotion, primary variability, would occur in normal fetuses and infants, and those with UTS. In both normal and pathological cases, the primary neural repertoire would be set by evolutionary epigenetic mechanisms inherited from the very primitive tetrapods with diagonal-sequence quadrupedal locomotion that lived nearly 400 MYA. The neural system can explore all motor possibilities by means of the self-generated, spontaneous motor activity and consequently occurring self-generated afferent information transmission within the neuronal system. The neural networks for quadrupedal locomotion have apparently been transmitted epigenetically through many species since about 400 MYA, and may be readily available for the next phase of motor development.

The second phase is the neuronal selection process. During infancy, the most effective motor pattern(s) and their associated neuronal group(s) are selected through experience. The normal and UTS cases begin to differentiate in this neuronal selection phase, the former selecting the neuronal groups required for bipedal motor patterns, the latter still selecting and/or improving the neuronal groups required for a better developed and balanced diagonal-sequence quadrupedal locomotion, which was epigenetically inherited during evolution over the last 400 MYA or so. The infants with UTS cannot select the appropriate neural networks for bipedal walking, since some of the neural structures necessary for well-balanced upright walking are damaged in infants with UTS, due to cerebellar hypoplasia, and less prominent cortical gyral simplification.

The third phase, secondary or adaptive variability, starts to bloom at two to three years of age and matures in adolescence. During this phase the secondary neural repertoires are created as a result of a multitude of motor experiences, and each movement is adapted exactly and efficiently to task-specific conditions. In cases with UTS within the same age

range in the secondary or adaptive variability phase, the secondary neural repertoires cannot be created, and instead, they keep the more primitive motor repertoires from the first primary variability phase and the selection phase, exhibiting only the ancestral neuronal groups responsible for the ancestral diagonal-sequence quadrupedal locomotion. The secondary or adaptive variability phase may be utilized by experience only for improving on the previously selected quadrupedal locomotor pattern. This third phase may last much longer in some patients, with a considerable delay in selection of the well-balanced quadrupedal locomotion, which may emerge very late in adolescence in these cases.

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13. References

Akpinar S. (2009). In restless legs syndrome, the neural substrates of the sensorimotor symptoms are also normally involved in upright standing posture and bipedal walking. *Med Hypothesis,* Vol.73, pp.169-176.

Arif, B., Grünewald, A., et al. (2011). An unusual neurological syndrome of crawling gait, dystonia, pyramidal signs, and limited speech. *Mov Dis,* Vol.26, pp.2279-2283.

Baker, R. (2007). The history of gait analysis before the advent of modern computers. *Gait & Posture*, Vol.26, pp.331-342.

Bar-Yam, Y. (1997). *Dynamics of complex systems.* Perseus Books, Reading, Massachusetts, USA.

Bernstein, N. (1935). The problem of interrelation of co-ordination and localization. *Arch Biol,* 38.

Borelli, G. (1989). On the movement of animals. Translated by P Maquet. Berlin: Springer-Verlag

Bornstein, M.H. (2010). *Handbook of Cultural Developmental Science.* Psychology Press, Taylor & Francis Group: New York, London.

Brown, J.K., Omar, T., & O'Regan, M. (1997). Brain development and the development of tone and movement. In *Neurophysiology & Neuropsychology of Motor Development,* Connolly, K.J., & Forssberg, H. (Eds.), Mac Keith Press: London.

Caglayan, S. (2008). Identification of very low density lipoprotein receptor (VLDLR) mutations in cerebellar hypoplasia and quadrupedal locomotion (UNERTAN syndrome) in humans. MsC Thesis, Department of Molecular biology, Bilkent University, Ankara, Turkey.

Chang, C-L., Kubo, M., et al. (2006). Early changes in muscle activation patterns of toddlers during walking. *Inf Beh Dev,* Vol.29, pp.175-188.

Childs, W.J. (1917). *Across Asia Minor on Foot.* William Blackwood and Sons, Edinburgh and London.

Cohen, A.H. (1992). The role of hierarchical control in the evolution of central pattern generators. *Brain Behav Evol,* Vol.40, pp.112-124.

Cohen, A.H., & Wallen, P. (1980). The neural correlates of locomotion in fish. "Fictive swimming" induced in an in-vitro preparation of the lamprey spinal cord. Exp Brain Res. Vol.141, pp.11-18.

Cowan, W.M., Fawcett, J.W., et al. (1984). Regressive events in neurogenesis. *Science,* Vol.225, pp.1258-1265.

Devolvé, I., Branchereau, P. et al. (1999). Fictive rhythmic motor patterns induced by NMDA in an in-vitro brain stem-spinal cord preparation from an adult urodele. J Neurophysiol, Vol.82, pp.1074-1077.

Dobrescu, R., & Purcarea, V.L. (2011). Emergence, self-organization and morphogenesis in biological systems. *J Med Life,* Vol. 4, pp. 82-90.

Dominici, N., Ivanenko, Y.P. et al. (2011). Locomotor primitives in newborn babies and their development. *Science,* Vol.334, pp.997-999.

Donker, S.F., Beek, P.J., et al. (2001). Coordination between arm and leg movements during locomotion. *J Mot Behav,* Vol. 33, pp. 86-102.

Downey G. (2010a). Human, Quadruped: Uner Tan syndrome, part 1. Retrieved from http://blogs.plos.org/neuroanthropology/2010/09/03/human-quadruped-uner tan syndrome-part-1/Downey G. (2010b). 2 legs good, 4 legs better: Uner Tan syndrome, part 2, retrieved from http://blogs.plos.org/neuroanthropology/2010/09/05/2-legs-good-4-legs-better uner tan-syndrome-part-2/

Drew, T., Andujar, J-E., et al. (2008). Cortical mechanisms involved in visuomotor coordination during precision walking. *Brain Res Rev,* Vol.57(1), pp.199-211.

Duysens, J., & Van de Crommert, W.A.A. (1998). Neural control of locomotion; Part 1: the central pattern generators from cats and humans. *Gait and Posture,* Vol.7, pp.131-141.

Edelman, G.M. (1993). Neural Darwinism: selection and reentrant signaling in higher brain function. *Neuron,* Vol.10, pp.115-125.

Fetcho, J.R. (1992). The spinal motor system in early vertebrates and some of its evolutionary changes. *Brain Behav Evol,* Vol.40, pp.82-97.

Forssberg, H. (1985). Ontogeny of human locomotor control in infant stepping, supported locomotion and transition to independent locomotion. *Exp Brain Res,* Vol.57, pp.480-493.

Forssberg, H., & Nashner, L.M. (1982). Ontogenetic development of postural control in man: adaptation to altered support and visual conditions during stance. *J Neurosci,* Vol.2(5), pp.545-552.

Frank, S.A. (1997). Developmental selection and self-organization. *Biosystems,* Vol.40(3), pp.237-243.

Friston, K.J. (2000a). The labile brain. I. Neurobal transients and nonlinear coupling. *Philos Trans R Soc Lond B Biol Sci,* Vol.355(1394), pp.215-236.

Friston, K.J. (2000b). The labile brain. II. Transients, complexity and selection. *Philos Trans R Soc Lond B Biol Sci,* Vol.355(1394), pp.237-252.

Friston, K.J. (2000c). The labile brain. III. Transients and spatio-temporal receptive fields. *Philos Trans R Soc Lond B Biol Sci,* Vol.355(1394), pp.153-265.

Garber, K.B. (2008). Editor's corner: VLDL receptor stands tall. *Am J Hum Gen,* Vol.82, p.807.

Gessel, A. (1928). *Infancy and human growth.* New York: Macmillan.

Ghika, J. (2008). Paleoneurology: neurodegenerative diseases are age-related diseases of 38 specific brain regions recently developed by homo sapiens. *Med Hypotheses,* Vol.71, pp.788-801.

Gibson, E.J. (1988). Exploratory behavior in the development of perceiving, acting, and the acquiring of knowledge. *Ann Rev Psychol,* Vol.39, pp.1-41.

Grillner, S., & Wallen, P. (1985). Central pattern generators for locomotion, with special reference to vertebrates. *Ann Rev Neurosci,* Vol. 8, pp. 233-261.

Hadders-Algra, M. (2000). The neuronal group selection theory: promising principles for understanding and treating developmental motor disorders. *Dev Med Child Neurol,* Vol.42(10), pp.707-715.

Hadders-Algra, M., Brogren, E., & Forssberg, H. (1996). Ontogeny of postural adjustments during sitting in infancy: variation, selection and modulation. *J Physiol,* Vol.493, pp.273-288.

Held L.I. (2009). *Quirks of Human Anatomy*; Cambridge University Press: Cambridge.

Hiebert, A., Jonckheere, E., et al. (2006). Visualization of a stationary CPG-revealing spinal wave. *Stud Health Technol Inform,* Vol. 119, pp. 198-200.

Hooper, S.L. (2000). Central pattern generators. *Curr Biol,* Vol. 10, R176.

Hrdlicka, A. (1928). Children running on all fours. *Am J Physical Anthrop,* Vol. 11, pp. 149-185.

Hrdlicka, A. (1931). *Children who run on all fours.* Whittlesey House, McGraw-Hill Book Company, Inc.: New York.

Huttenlocher, P.R., de Courten, C., et al. (1982). Synaptogenesis in human visual cortex-evidence for synapse elimination during normal development. *Neurosci Lett,* Vol.33(3), pp.247-252.

Jeannerod, M. (1988). *The neural and behavioral organization of goal-directed movements.* Oxford: Clarendon Press.

Kelso, J.A.S. (1995). *Dynamic patterns.* A Bradford Book, the MIT Press, England.

Kelso, J.A., Holt, K.G. et al. (1981). Patterns of human interlimb coordination emerge from the properties of non-linear, limit cycle oscillatory processes: theory and data. *J Mot Behav,* Vol.13(4), pp.226-261.

Kolb, L. (2009). Copy nember variant analysis of patients with malformations of cortical development. MD thesis, Yale University, Medical School.

Konner, M. (1991). Universals behavioral development in relation to brain myelination. In: Gibson, K.R. & Petersen, A.C. (Eds.), *Brain maturation and cognitive development: comparative and cross-cultural perspectives.* New York: Aldine de Gruyter, pp.181-223.

Kuhn, A. (1974). *The logic of social sciences.* San Francisco: Jossey-Bass.

Kutty, A.V.P. (2010). *Adam's gene and the mitochondrial eve.* Xlibris Corporation, USA.

Le Fanu J. (2009). *Why us? How science rediscovered the mystery of ourselves.* Panthoen Books, New York. P.320.

MacLellan, M.J., Ivanenko, Y.P., et al. (2011). Features of hand-foot crawling behavior in human adults. *J Neurophysiol October 5,* doi: 10.11.1152/jn.00693.2011

McGraw, M.B. (1932). From reflex to muscular control in the assumption of an erect posture and ambulation in the human infant. *Child Dev,* Vol.3, pp.291-197.

McGraw, M.B. (1943). *The neuromuscular maturation of the human infant.* (Reprinted 1990 as Classics in Developmental Medicine No.4, London: Mac Keith Press).

McGraw, M.B. (1945). *The neuromuscular maturation of the human infant.* New York: Hafner Publishing Company.

Molliver, M.E., Kostovic, I., & Van der Loos, H. (1973). The development of synapses in the cerebral cortex of the human fetus. *Brain Res,* Vol.50, pp.403-407.

Muybridge, E. (1887). *Animal locomotion.* Dover, New York, NY.

Muybridge, E. (1901). *The human figure in motion.* London : Chapman & Hall., Ltd.

Nakajima, K., Mori, F. et al. (2004). Biomechanical constraints in hindlimb joints during the quadrupedal versus bipedal locomotion of M. *fuscata. Prog Brain Res*, Vol.143, pp.183-190.

Nashner, L., Shumway-Cook, A., & Marin, O. (1983). Stance posture control in selected groups of children with cerebral palsy: deficits in sensory organization and muscular coordination. *Exp Brain Res,* Vol.49, pp.393-409.

Needham, J. (1959). *A History of Embryology*. New York: Abelard-Schuman.

Niedzwiedzki, G., Szrek, P., et al. (2010). Tetrapod trackways from the early Middle Devonian period of Poland. *Nature,* Vol. 463, pp. 43-48.

Olney, S.J., & Wright, M.J. (1994). Cerebral palsy. In: Campbell, S. (Ed.), *Physical Therapy for Children,* Philadelphia: W.B. Saunders, pp.489-523.

Oppenheim, R.W., & Chu-Wang, I.W. (1983). Aspect of naturally occurring motorneuron death in the chick spinal cord during embryonic development. In: Burnstock, G., and Vrobova, G. (Eds.), *Somatic and Automatic Nerve-Muscle Interactions.* New York: Elsevier, pp.57-107.

Ouedeyer, P-Y. (2006). Self-organization: complex dynamical systems in the evolution of speech. In: *Self-organization in the evolution of speech.* P-Y. Oudeyer (Ed.). Oxford studies in the evolution of language 6. Oxford University press.

Pearson, K.G. (1993). Common principles of motor control in vertebrates and invertebrates. *Ann Rev Neurosci,* Vol.16, pp.265-297.

Pedotti, A., Crenna, P., et al. (1989). Postural synergies in axial movements: short and long-term adaptation. *Exp Brain Res,* Vol.74(1), pp.3-10.

Pribut, S.M. (2010) Quadrupedal Human Gait. http://www.drpribut.com/blog/index.php/2010/07/quadripedal-human-gait/

Rakic, P., Bourgeois, J.P., et al. (1986). Concurrent overproduction of synapses in diverse regions of the primate cerebral cortex. *Science,* Vol.232(4747), pp.232-235.

Reilly, S.M., McElroy, E.J., et al. (2006). Tuataras and salamanders show that walking and running are ancient features of tetrapod locomotion. Proc R Soc B, Vol.273, pp.1563-1568.

Shapiro, L.J., & Jungers, W.L. (1994). Electromyography of back muscles during quadrupedal and bipedal walking in primates. Am J Phys Anthropol, Vol.93, pp.491-504.

Schröder, H., & Young, M. (1995). Classics revisited: Wilhelm (William) Th. Preyer: Specielle Physiologie des Embryo. pp.644 (Grieben, Leipzig). *Placenta,* Vol.16(1), pp.105-108.

Shirley, M.M. (1931). The first two years: a study of 25 babies. *Postural and locomotor development*. Vol.1. Minneapolis: University of Minnesota Press.

Shumway-Cook, A., & Woollacott, M.H. (1985). Dynamics of postural control in the child with Down syndrome. *Phys Ther,* Vol.65, pp.1315-1322.

Soffe, S.R., & Roberts, A. (1982). Tonic and phasic synaptic input to spinal cord motoneurons during fictive locomotion in frog embryos. *J Neurophysiol,* Vol.48(6), pp.1279-1288.

Sporns, O., & Edelman, G.M. (1993). Solving Bernstein's problem: a proposal for the development of coordinated movement by selection. *Child Dev,* Vol.64(4), pp.960-981.

Stein, P.S.G. (1999). Central pattern generators and interphyletic awareness. *Prog Brain Res,* Vol.123, pp.259-271.

Strogatz, S.H. (2000). *Nonlinear dynamics and chaos.* Perseus Books Publishing, LLC.

Stuart, D.G. (1985). Summary and challenges for future work. In: Stein, P.S.G. (Ed.). Short course syllabus—motor control: from movement trajectories to neural mechanisms. Bethesda, MD: Society for Neuroscience. P.95-105.

Stuart, D.G. (2007). Reflections on integrative and comparative movement neuroscience. *Integ Comp Biol,* Vol.47, pp.482-504.

Surhone, L.M., Tennoe, M.T., et al. (2010). *Uner Tan Syndrome.* VDM Publishing House, U.S.A.

Sveistrup, H., & Woollacott, M.H. (1993). Systems contributing to the emergence and maturation of stability in postnatal development. In: Savelsbergh, G.J.P. (Ed.), *The Development of Coordination in Infancy.* Amsterdam: Elsevier, pp.319-336.

Takakusaki, K., Saitoh, K, et al. (2006). Neurobiological basis of state-dependent control of motor behaviors. *Sleep Biol Rhyth,* Vol.4, pp.87-104.

Tan, U. (2005). Unertan syndrome; quadrupedality, primitive language, and severe mental retardation; a new theory on the evolution of human mind. *NeuroQuantology,* Vol. 4, pp. 250-255.

Tan, U. (2006a). A new syndrome with quadrupedal gait, primitive speech, and severe mental retardation as a live model for human evolution. *Int J Neurosci,* Vol.116, pp.361-369.

Tan, U. (2006b). Evidence for "UnerTan syndrome" and the evolution of the human mind. *Int J Neurosci,* Vol.116, pp.763-774.

Tan, U. (2006c). Evidence for "Uner Tan syndrome" as a human model for reverse evolution. *Int J Neurosci,* Vol.116, pp.1539-1547.

Tan U. (2007). The psychomotor theory of human mind. *Int J Neurosci*, Vol.117, pp.1109-1148.

Tan, U. (2010a). Uner Tan syndrome: history, clinical evaluations, genetics, and the dynamics of human quadrupedalism. *The Open Neurol J,* Vol.4, pp.78-89.

Tan, U. (2010b). Two new cases of Uner Tan syndrome: one man with transition from quadrupedalism to bipedalism; one man with consistent quadrupedalism. *Webmed Central NEUROLOGY,* Vol. 1(9): WMC00645.

Tan U, Tan M. (2009). A new variant of Unertan syndrome: running on all fours in two upright-walking children. *Int J Neurosci,* Vol. 119, pp.909-918.

Tan, M., Karaca, S., & Tan, U. (2010). A new case of Uner Tan syndrome – with late childhood quadrupedalism. *Mov Dis,* Vol.25(5), pp. 652-653.

Tetzlaff, C., Okujeni, S., et al. (2010). Self-organized critically in developing neural networks. *PLoS comp biol,* Vol. 6(12), e1001013. The American Heritage of Science® Dictionary Copyright © 2005. Houghton Mifflin Company.

Thelen, E. (1986). Treadmill-elicited stepping in seven-month-old infants. *Child Dev,* Vol.57, pp.1498-1506.

Thelen, E. (1996). The improvising infant learning about learning to move. In: Merrens, M.R., & Brannigan, G.G. (Eds.), The developmental psychologists: research adventures across the life span. New York: McGraw Hill, pp.21-35.

Thelen, E., & Fisher, D.M. (1982). Newborn stepping: an explanation for a "disappearing reflex." *Dev Psychol,* Vol.18, pp.760-775.

Thelen, E., & Corbetta, D. (1994). Exploration and selection in the early acquisition of skill. *Int Rev Neurobiol,* Vol.37, pp.75-102.

Thelen, E., & Ulrich, B.D. (1991). Hidden skills. *Monograph of the Society for Research in Child Development*. Vol.56, pp.1-98.

Tschacher, W., Dauwalder, J.-P., & Haken, H. (2003). *Self-organizing systems show apparent intentionality. Dynamic systems approach to cognition: concepts and empirical paradigms based on self-organization.* Tschacher, W. (Ed.), World Scientific Publishing Company Inc. Singapore, p.183.

Turvey, M.T., Fitzpatrick, P. (1993). Commentary: development of perception-action systems and general principles of pattern formation. Child Dev, Vol.64(4), pp.1175-1190.

Ulrich, B.D. (1997). Dynamic systems theory and skill development in infants and children. In: *Neurophysiology & Neuropsychology of motor development*. Connolly, K.J., & Forssberg, H. (Eds.), Mac Keith Press: London, p.321.

Xiang, Y., John, P., et al. (2007). Dynamics of quadrupedal locomotion of monkeys: implications for central control. *Exp Brain Res*, Vol.177, pp.551-572.

Von Hofsten, C. (1984). Developmental changes in the organization of prereaching movements. *Dev Psychol,* Vol.20, pp.378-388.

Waldrop, M. (1990). Spontaneous order, evolution, and life. *Science,* Vol.247, pp.1543-1545.

Woollacott, M., & Sveistrup, H. (1992). Changes in the sequencing and timing of muscle response coordination associated with developmental transitions in balance abilities. *Hum Mov Sci,* Vol.11, pp.23-30.
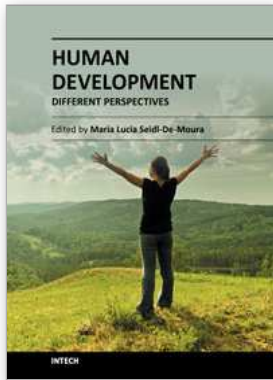
Human Development - Different Perspectives

Edited by Dr. Maria Lucia Seidl-De-Moura

Human development has different meanings depending on the area we focus on. To the psychologists it is the ontogenetic process of individual development. It considers systematic psychological changes that occur in human beings over the course of their life span. To sociologists and economists, among others, the main consideration is the macro-level of countries or regions and their development conditions related to human needs. Our book has two parts. The first one is entitled "Development in the ontogenesis" and it consists of three chapters whilst the second is "Human development: contextual factors", also including 3 chapters. Together, the two parts give the readers a panoramic view of very complex subjects and complement each other. Researchers of ontogenetic development cannot ignore that contextual factors are the basis of this process. On the other hand, social scientists worried about the macro variables need to remember that they are dealing with people, who are affected one way or another by those variables and whose development is the product of biology and culture.

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