12. DEVELOPMENT AND MOTOR CONTROL: FROM THE FIRST STEP ON

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Abstract

For performing their very first unsupported steps, often considered as a 'milestone' event in locomotor development, toddlers must find a compromise between at least two requirements: (1) the postural stability of the erect posture integrating the direction of gravity and (2) the dynamic control of the body and limbs for forward progression these two aspects. In adults, a series of experimental studies have provided evidence for coordinative laws that lead to a reduction of kinematic degrees of freedom. When the elevation angles of the thigh, shank and foot are plotted one versus the others, they describe a regular gait loop which lies to a plane. The plane orientation and the loop shape reflect the phase relationship between the different segments and therefore the timing of intersegmental coordination. The general pattern of intersegmental coordination and the stabilization of the trunk with respect of vertical are immature at the onset of unsupported walking in toddlers, but they develop in parallel very rapidly in the first few weeks of walking experience. Adult-like cross-correlation function parameters were reached earlier for shank-foot pairs than for thigh-shank indicating disto-proximal maturation of the lower limb segments coordination. We also demonstrated that a dynamic recurrent neural network (DRNN) is able to reproduce lower limb kinematics in toddler locomotion by using multiple raw EMG data. In the context of motor learning the DRNN may be considered as a model of biological learning mechanisms underlying motor adaptation. Using this artificial learning during the very first steps we found that the attractor states reached through learning correspond to biologically interpretable solutions.

Introduction

Human motor repertoire can be divivided into two classes, gross and fine motor behaviour. The first classe involves the skifull use of the whole body including mobility and posture, whereas the second classe involves the use of individual body parts mainly head and hands in goal directed movements. In human, the upright position of the body has permit a full expression of upper limb movement extremities but has it the same time render the postural task more problematic by the restriction of the sustantation base. Standing and balance functions must work in conjunction in order to constantly assume antigravity muscle contraction to hold the body in upright position and to maintain the projection of the centre of gravity in the sustantation base avoiding falling over. With respect to this conservative postural task the displacement of the body is assumed by rhythmic or cyclic motor activity which is mainly organized by a "central pattern generator"(CPG) (Grillner and Zanger 1975) localized in the lumbosacral spine (Deliagina et al. 1983; Dimitrijevic et al. 1998; Yakovenko et al. 2002).

The CPG is also considered as a more general neural network co-ordinating the activity of multiple muscle into postural synergies (Forssberg and Hirschfeld 1994). These authors proposed a CPG with two functionnal levels: the first level selects the robust muscle activation pattern whereas the second

level finely tuned the selected pattern by multisensorial input from visual, vestibular and somatosensory systems. The two levels CPG model is supported by experimental data on postural responses during sitting (Hadders-Algra et al. 1996). They demonstrated that the expression of the first CPG level occurs before the infant is able to sit independently (5–6 month-old) and provide a large repertoire of direction specific responses from which the most appropriate patterns are selected. Ontogenic evolution may occurs within this CPG level by improved trigerring action of afferent and/or supraspinal influences. The activity of the second CPG level emerges at about 9 months of age and is able to finely modulate the amplitude of the postural synergies.

The classical approach to motor development consists in a *follow up* of the emergence of motor and sensory abilities since the very first days of live. It describes the different behavioural states which are numerous and present diverse evolutions including extinction (e.g. the disappearance of the stepping reflex due to body mass increases (Thelen 1984; Schneider et al. 1990), reinforcement or bifurcation.

This *follow up* approach also comprise precise studies of different parameters of movement reflexly or voluntarily elicited. However, this approach is confronted to the redundancy of effective movements, first pointed out by Bernstein (1967). In fact, the human motor system is mechanically complex and can make use of a large number of degrees of freedom. Moreover, this classical approach is faced to the problem of "contex conditionned variability" (Tuller et al. 1982). During development motor systems show remarkable adaptability and flexibility in the presence of changing biomechanical properties of motor organs and when faced with different environmental conditions or tasks. For example, a given innervational state does not have a fixed movement consequence (e.g. the pectoralis major changes its role as a function of the angle of its pull with respect to the axis of the joint). Because of these problems it is difficult to establish the follow up of a precise motor event along a long period of time. What is the relevant event or movement parameter among the large number of movement in a full motor repertoire? How we can be sure that the studying event conserves the same nature along time and that it can be considered as the corresponding primitive of the mature event?

One way to partly avoid these problems is first to define in the adult movements some coordinative principles and to look backward in children toward their point of emergence. The present Chapter tempt to demonstrate the usefulness of this later approach and then to scrutinize the EMG-kinematics relationships

by means of a dynamics recurrent neural network (DRNN).

Emergence of a Coordinative Template in Human Locomotion

Our understanding of the emerging coordinative principles in toddlers may benefit from recent advances in the study of walking kinematics. Mathematical approaches, ranging from neuromodulation of coupled oscillators (Kopell 1995), to synergetics (Thelen and Smith 1994), and topological dynamics (Das and McCollum 1988 ; McCollum et al. 1995), have described gait in either continuous or discrete space,
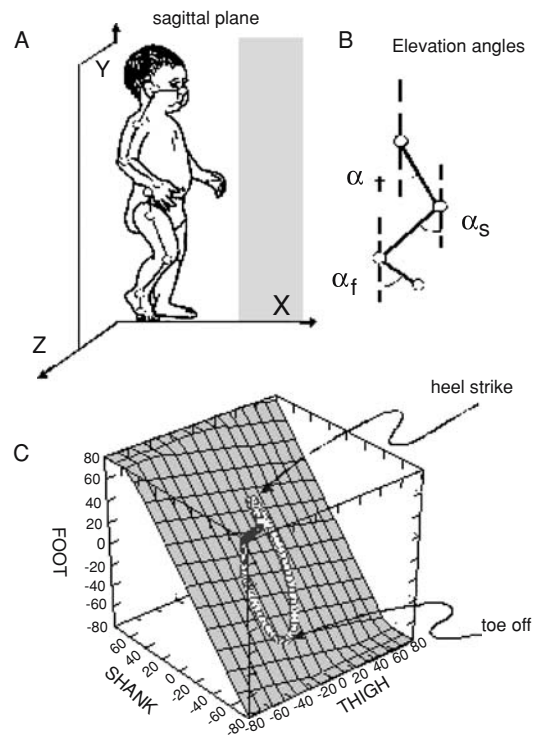

FIGURE 1. Schematic illustration of the experimental setup. A, Markers placed on the head, right upper and lower limb, for monitoring by the optoelectronic system. The convention of the 3D coordinates is given by the XYZ axes. B, Absolute angles of elevation of the thigh (α_t), shank (α_s) and foot (α_f) with respect to the vertical indicated in the sagittal plane (XY). C, 3D representation of the mature covariation of lower limb elevation angles during two consecutive gait cycles in a 12 year-old child, characterized by a quasi-elliptic loop progressing in the counter-clockwise direction and lying on a plane (grid). (*From Cheron et al 2001, Exp Brain Res. Reprinted by permission*)

and suggested that excess degrees of freedom are constrained by the neural control. As a result, limb dynamics would be confined to an attractor space of lower dimensionality than that of the original parameter space. In adults a series of experimental studies has provided detailed evidence for coordinative laws that lead to a reduction of kinematic degrees of freedom (Borghese et al. 1996; Bianchi et al. 1998a,b; Grasso et al. 1998; 1999; 2000; for a review, see Lacquaniti et al. 1999). The temporal waveform of the elevation angles of the lower limb segments (pelvis, thigh, shank and foot) relative to the vertical is much more stereotypical across trials, speeds, and subjects than the corresponding waveform of either the joint angles (Borghese et al. 1996; Grasso et al. 1998) or the EMG patterns (Grasso et al. 1998, 2000). When the elevation angles of the thigh, shank and foot are plotted one versus the others, they describe a regular gait loop which lies close to a plane (Fig. 1). The plane orientation and the shape of the loop reflect the phase relationship between the different segments and therefore the timing of intersegmental coordination (Bianchi et al. 1998b), on which postural stability with respect to gravity and dynamic equilibrium for forward progression depend. The plane orientation shifts in a predictable way with increasing speed of walking (Bianchi et al. 1998b) and with the walking posture adopted (Grasso et al. 2000). Moreover it reliably correlates with the mechanical energy expenditure (Bianchi et al. 1998a,b). The pattern of a 12-year old child is plotted in Fig. 1C. The walking cycle progresses in the counter-clockwise direction, heel strike and toe-off roughly corresponding to the top and bottom of the loop, respectively.

Developmental Emergence of the Planar Covariation in Toddlers and Children

Recently, we have characterized the developmental emergence of the planar covariation in toddlers and children (Cheron et al. 2001a,b). Figure 2 shows
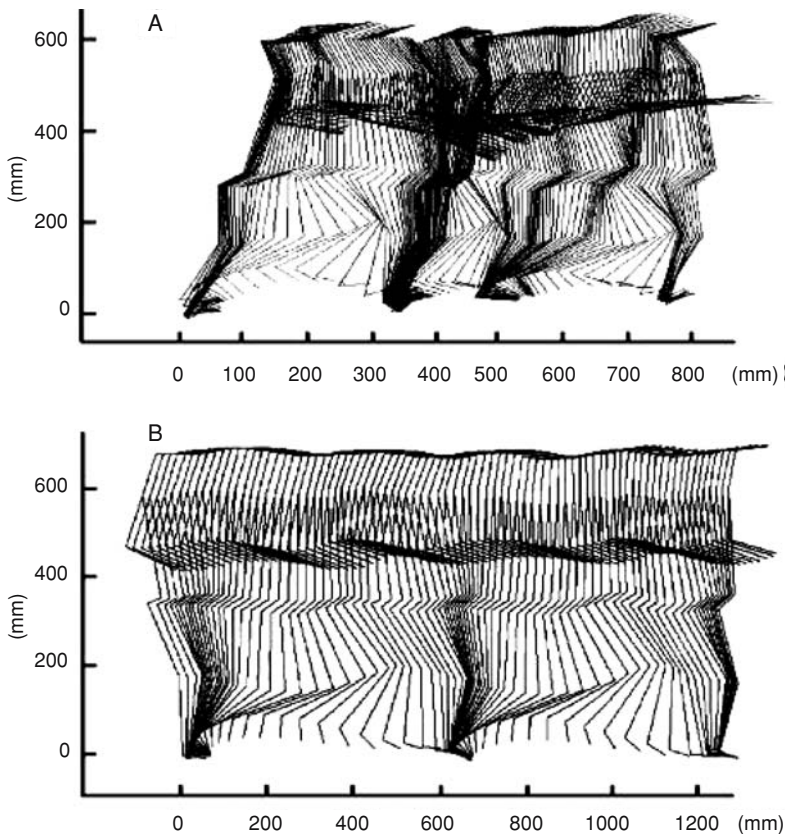

FIGURE 2. Sagittal stick diagrams at two stages of early walking. A, Very first three steps of an 11 month-old toddler. B, Two steps of the same child aged 20 months. (*From Cheron et al 2001, Exp Brain Res. Reprinted by permission*)
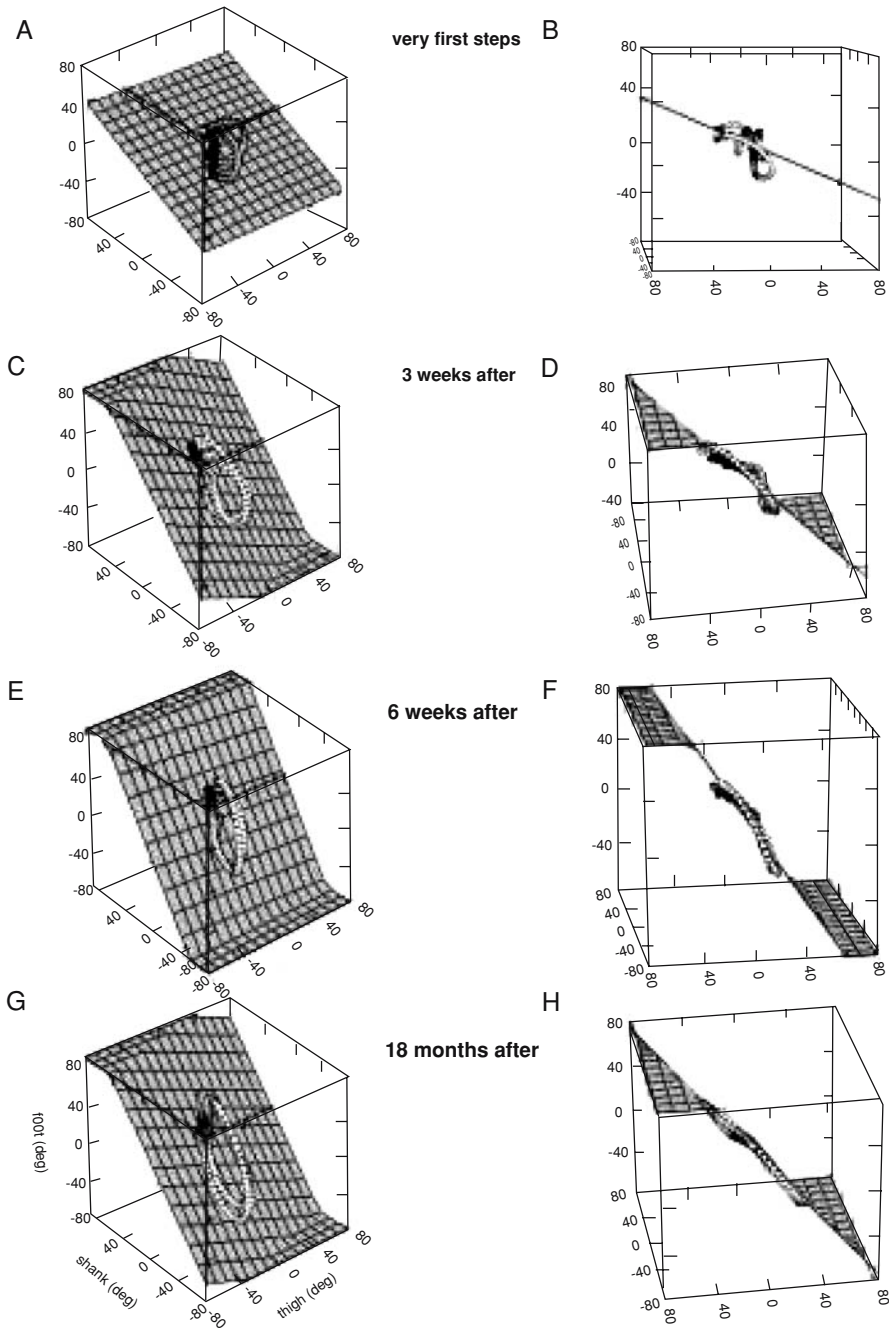
FIGURE 3. Emergence of the planar covariation of elevation angles of the thigh, shank and foot. Covariation of thigh, shank and foot elevation angles during two successive gait cycles performed by the same toddler at the onset of unsupported walking at the age of 14 months (A,B), 3 weeks later (C,D), 6 weeks later (E,F) and 18 months later at the age of 32 months (G,H). Mean value of each angular coordinate has been subtracted. The data with respect to the cubic frame of angular coordinates and the best fitting plane (grids) are represented in two different perspectives (A,C,E,G) and (B,D,F,H). Gait cycle paths progress in time in the counter-clockwise direction, heel strike and toe-off phases corresponding roughly to the top and bottom of the loops, respectively (see also Fig. 1C). (*From Cheron et al 2001, Exp Brain Res. Reprinted by permission*)

the stick diagram of the very first three steps of an 11 month-old toddler (A) and two steps performed by the same toddler at 20 months (B). The first step kinogram is characterized by a more curved trajectory of the foot associated with higher elevation of the thigh, and a larger length of the step as compared with the following steps. The trunk presents a forward sway during the initial part of the swing phase followed by a backward sway initiated well before the onset of the stance phase. This latter movement of the trunk is accompanied by neck hyperextension culminating in the middle of the swing phase. In contrast, at 20 months, during the swing phase, thigh elevation is smaller corresponding to a less marked hip flexion, hip extension occurs at the end of the stance phase and trunk sway is minimal. Head orientation in the sagittal plane is much better stabilized than at 11 month. Figure 3 illustrates the evolution of the inter-segmental coordination in one child, from her very first steps at the age of 14 months (Fig. 3A,B) to the age of 32 months (Fig. 3G, H). During the

very first steps the gait loop in 3D space departs significantly from an elliptic shape (Fig. 3A), and the data are not well fitted by a plane (Fig. 3B). A planar covariation emerges early on during the following weeks of walking experience (Fig. 3C,D), and is stabilized afterwards. Note however that the shape of the gait loop matures much more slowly, with a progressive elongation of the loop along an axis roughly orthogonal to the thigh (Fig. 3E, G). This trend is related to the progressive reduction of the amplitude of thigh movement relative to that of shank and foot.

The emergence of the planar covariation rule can be discussed in relation to the neural attractor hypothesis. The idea is that the nervous system settles into preferred activation patterns, whether hard-wired or not (Koppell 1995; Thelen and Smith 1994). Such an activation pattern may depend on interaction with the physical environment, but as neural in nature it can directly control movement. The early emergence of the kinematic coordination suggests that it constitutes a specific response to dynamic functional demands imposed by human gait. The planar loop could result from a dynamical process by which a high-dimensional system compresses the many degrees of freedom involved in the realization of gait down to a low-dimensional system (Thelen and Smith 1994; Schöner et al. 1990).
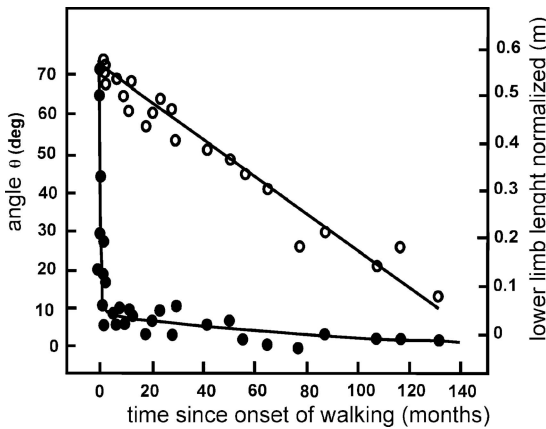

FIGURE 4. Comparison between the age changes of the covariation plane orientation and the corresponding changes of the lower limb length. For each subject and trial the angle θ between the subject's covariation plane and the mean adult plane (closed circles) and the lower limb length normalized to the mean adult value (open circles) are represented as a function of time since the onset of unsupported walking. The adult components of the plane normal are: $u_3\alpha_t = 0.223 \pm 0.092$; $u_3\alpha_s = -0.772 \pm 0.026$ and $u_3\alpha_f = 0.587 \pm 0.042$. A biexponential function and a linear regression are fitted to the angle θ values and the lower limb length respectively (see results section for more details). (*From Cheron et al 2001, Exp Brain Res. Reprinted by permission*)

Contrasting Maturation of Plane Orientation and Anthropometric Parameters

The orientation of the planar covariation represents an important parameter of the inter-segmental coordination, because it reflects the phase relationship between the different segments (Bianchi et al. 1998b). As seen in Fig. 3, the plane orientation in toddlers changes drastically over the first weeks of walking experience. These changes were quantified and compared with the changes in child morphology.

Filled points in Fig. 4A correspond to the angle (θ) between the best-fitting plane in each child and the mean adult plane. The overall time course of changes with age can be described by a biexponential function ($y = a^{-x/t_1} + b^{-x/t_2}$), where x is the time since onset of unsupported walking, t_1 is the fast time constant and t_2 is the slow one. The function fits reasonably well the experimental data (r = 0.89). The first time constant is fast ($t_1 = 0.59$ months after the onset of unsupported locomotion) and the orientation of the plane rapidly converges toward the adult values.
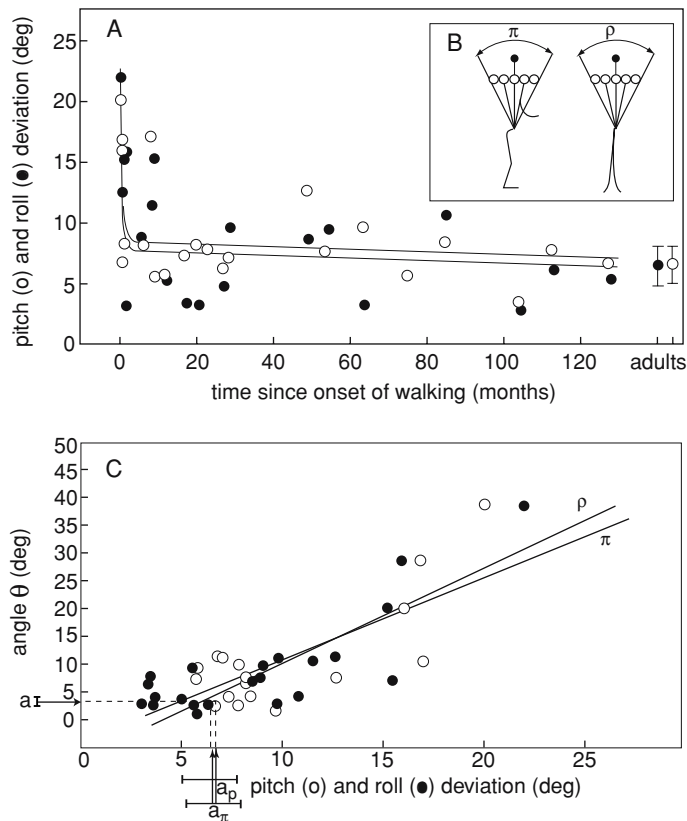
FIGURE 5. Evolution of trunk stability. A, Evolution of pitch (π) and roll (ρ) oscillations of the trunk. Age is from the onset of unsupported walking. B, Schematic definition of pitch (π) and roll (ρ) peak to peak oscillation. C, Relationship between angle θ and pitch (π) and roll (ρ) angles, with correlation coefficients (r) of 0.86 and 0.80 for θ-ρ and θ-π relationships, respectively. Adult means (stripped line) and standard deviations (I) are indexed for angle θ (a), and pitch (a_πp and roll (a_ρ) angles. (*From Cheron et al 2001, Exp.Brain Res. Reprinted by permission*)

We considered the age-related changes of two anthropometric parameters: the length of the lower limb (thigh plus shank length) normalized by the adult mean length (0.863 ± 0.055 m, unfilled points in Fig. 4), and the ratio of the lower limb length over the child stature (ear to malleolus marker distance). In contrast with the biphasic time course of changes of plane orientation, with a first quick phase, the maturation of both the lower limb length and the limb length/stature ratio is monophasic and slow.

Developmental Correlation between Trunk Stability and Planar Covariation

Analysis of trunk oscillations showed rapid stabilization in both frontal (ρ) and sagittal (π) planes (Fig. 5B). Initial peak to peak ρ and π oscillations were relatively high (14.0 ± 7.2 deg and 13.6 ± 5.8 deg, respectively, Fig. 5A). Subsequent evolution tended toward adult values (mean ρ and π = 6.4 ± 1.7 deg and 6.6 ± 1.4 deg, respectively). As for the evolution of angle θ, biexponential functions were calculated for ρ and π (r = 0.75 and 0.73, respectively) using the mean value of each angle at time 0. For both angles, the fast time constants (t_1 = 0.36 and 0.34 months after the onset of unsupported locomotion) were roughly comparable to that obtained for θ angle (0.59 months). A significant correlation (r = 0.81) was found between ρ and π trends. Figure 5C shows the existence of a significant correlation between θ and π (r = 0.80) and between θ and ρ (r = 0.86).

In healthy adults, the orientation of the covariation plane has been demonstrated to be directly related to mechanical energy cost (Bianchi et al. 1998b).

Because of the body mass distribution, trunk stability plays a determining role in mechanical energy expenditure (Bianchi et al. 1998a). It could be expected that children would approach a kinematic pattern that minimizes energy expenditure as they approach adulthood. Improvement of the covariation plane in treated patients with Parkinson's disease (Grasso et al. 1999) or hereditary spastic paraparesis (Dan et al. 2000a) also suggests a parallel improvement of the mechanical efficiency. Similarly, the correlation we found between the covariation plane orientation relative to the adult one and trunk oscillations supports the idea that the mechanical efficiency of locomotion is sustained by a highly specific orientation of the covariation plane. The bulk of the current evidence indicates that the planar covariation results from the integration of neural control and biomechanical factors. It may emerge from the coupling of neural oscillators between each other and with limb mechanical oscillators. Muscle contraction intervenes at variable times to re-excite the intrinsic oscillations of the system when energy is lost.

Maturation of stepping patterns has been shown to begin long before the child can walk (Forssberg 1985; Thelen 1985; Thelen and Cooke 1987; Yang et al. 1998) and go on long thereafter (Berger et al. 1984; Brenière and Bril 1998; Cavagna et al. 1983; Cioni et al. 1993; Clark and Phillips 1993; Forssberg 1985, 1999; Lasko-McCarthey et al. 1990; Ledebt et al. 1995; Leonard et al. 1991; Sutherland et al. 1980). This is reflected by the gradual acquisition of gait parameters, some of them as early as in fetal life (De Vries et al. 1984), some as late as late childhood (Hirschfeld and Forssberg 1992). A basic problem in maturational studies is to define the limits of a mature pattern (Forssberg 1985; Dietz 1992; Hadders-Algra et al. 1996). These limits depend on the considered parameters. For example, Bril and Brenière, (1992, 1998) have proposed two phases for walking maturation. The first phase, from 3 to 6 months after the onset of independent walking, is devoted to gait postural requirements (dynamic equilibrium during forward propulsion) and the second one, lasting about 7 years, corresponds to fine tuning of gait. Our results also support the existence of a two phase-process, as demonstrated by the biexponential evolution of the covariation plane orientation and trunk stabilization. The second phase expressed in our data by the slow time constants of the biexponential evolutions represents fine tuning, which matures more gradually than does the first phase. Other authors consider that gait maturation is finalized by the age of 7 to 8 years, through fine tuning of kinematic parameters (Sutherland et al. 1980), muscle activation patterns (Okamoto and Kumamato 1972; Berger et al. 1984; Woollacott and Jensen 1996), ground reaction forces (Gomez Pellico et al. 1995), head control and coordination (Assaiante and Amblard 1993) or anticipatory postural adjustments (Hirchfeld and Forssberg 1992; Ledebt et al. 1998). However, other gait parameters may require an even longer time to reach maturation (Cheron et al 2001a,b).

A Dynamic Recurrent Neural Network for Human Locomotion Studies

The majority of neural networks used for EMG-to-kinematics mapping have been of the feedforward type (Sepulveda et al. 1993; Koike and Kawato 1994). In these networks, information flows, without any feedback connection, from the input neurones to the output neurones. This excludes context and historical information, which are thought to be crucial in motor control (Kelso, 1995). In contrast, recurrent neural networks take these aspects into account and are recognised as universal approximators of dynamical systems (Hornik 1989; Doya 1993). Therefore, they seem particularly relevant to the study of motor control (Draye 2001; Draye et al. 2002).

Figure 6 illustrates the input-output relationships of the DRNN. The central circle represents the whole connectivity of the DRNN. Each EMG signal is sent to all the 20 artificial neurones (hidden unit) which converge to 3 output units acting merely as summation units. Each output neurone provides one specific type of kinematic data (in the illustrated situation: the angular velocity of the thigh, shank and foot).

Successful learning was ascertained on the basis of the comparison between the DRNN output and the actual output (provided by experimental data). Figure 7 illustrates the superimposition of these data (Fig. 7B,C,D) when the training has reached an error value of 0.001. The learning performance was examined on-line by inspection of the error curve (Fig. 7A). The learning process was carried out for 5000 iterations. This procedure was recently used and proved useful for the study of the very first step in toddlers. In this case the learning is also possible but with respect to the adult, the percentage of success learning decrease significantly and the number of iteration needed for reaching an error value of 0.001 increase. These difficulties for the artificial learning of the very first step may be explained by the presence of a larger amount of co-activation EMG pattern in toddlers (Fig. 8A) in comparison to the highly reciprocal activation patterns recorded in adult (Fig. 8B).
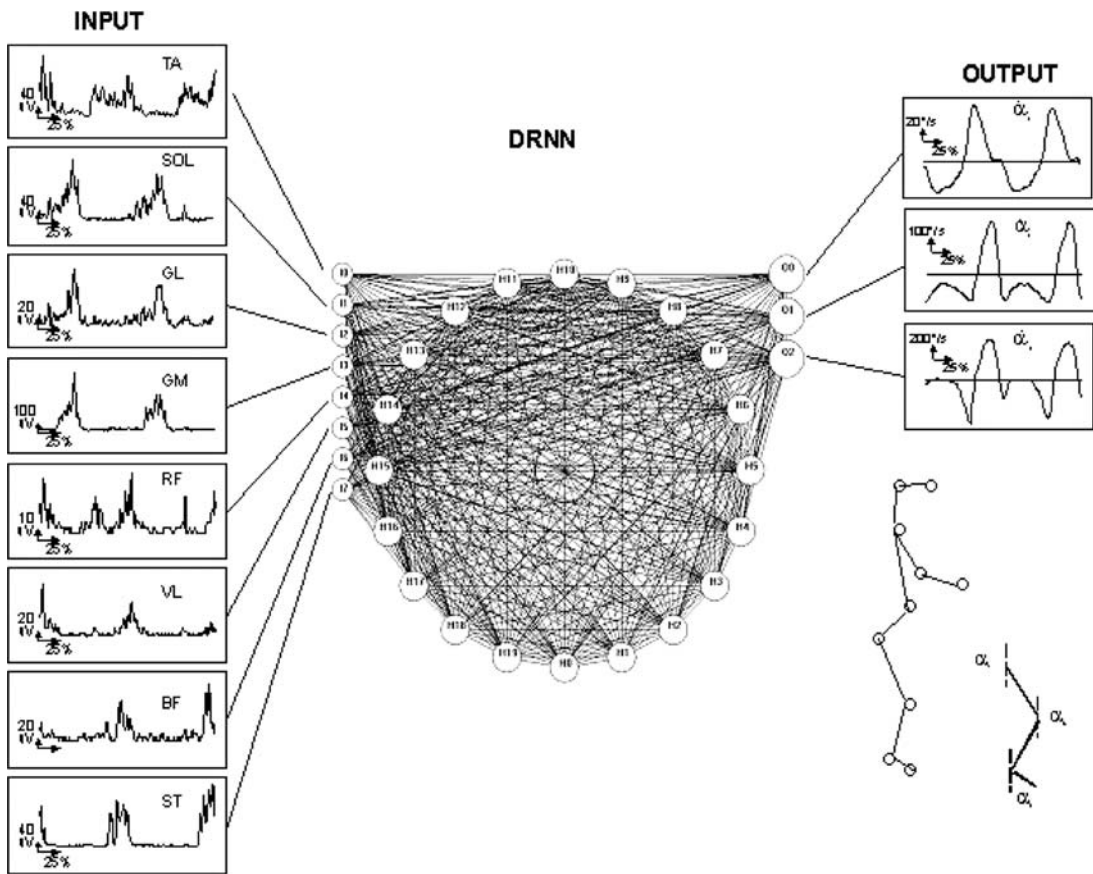
FIGURE 6. Input-output relationships of the DRNN. The central box symbolises the DRNN. Each EMG signal is sent to all 20 artificial neurones (hidden unit) which converge to 3 output units acting merely as summation units. Each output neurone provides one specific type of kinematic data represented by the absolute angles of elevation of the thigh (α_T), shank (α_S) and foot (α_F) with respect to the vertical as indicated in the stick diagram of the insert. The open circles represent the placement of the passive markers.

Biological Plausibility and Developmental Issue of DRNN Approach

In spite of the problems encountered in the EMG to kinematics mapping in toddler we have tested after the learning phase the physiological plausibility of the DRNN identification. The basic idea was to compare the angular directional change induced by artificial EMG potentiation of a single muscle with the physiological knowledge of the pulling direction of the muscle (Cheron et al. 2003). This knowledge is easily accessible for mono-articular muscles, but is less straightforward for the pluri-articular muscles. In the latter, the muscle force can be involved in a force regulation process for which the directional action is not directly defined by the pulling direction of the muscle. Moreover, dynamical coupling between the three joint segments can be implicated in the evoked movement. The implications of such complex dynamical simulations of biomechanics and muscle coordination in human walking have been recently revisited by Zajac et al. (2003). For example, Figure 9 illustrates the effect of SOL and TA artificial potentiation applied throughout the walking sequence on the sagittal lower limb kinogram over 2 steps performed by an adult. Whereas the former results in digitigrade gait (explained by the pulling action of SOL) with increased knee flexion (explained by a coupling action) more marked during the swing phase, the latter results in increased ankle dorsiflexion (walking on the heel explained by the pulling
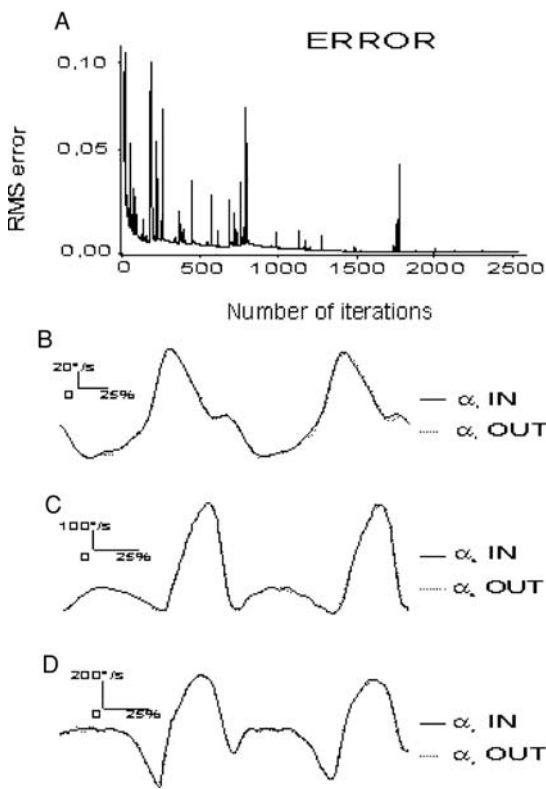
FIGURE 7. Assessment of successful learning. A, Error curve of one learning trial reaching an error value of 0.001 after 5000 iterations. B, C and D, superimposition of experimental (continuous line) and DRNN (dotted line) output signals when training reaches an error value of 0.001.

action of TA) and knee hyperextension (coupling action) more marked during the stance phase. We have also investigated the physiological plausibility of the DRNN for the very first step data by the application of a selective burst increase of the GAS (Fig. 10A) or the TA (Fig. 10B) muscle occurring during the stance phase. In both cases the resulting changes were in accordance with the physiological action of these muscles.

Toward an Integrative Tool for the Sensorimotor Coordination Dynamics

Our approach demonstrated that by using multiple raw EMG data, the DRNN is able to reproduce in adult (Cheron et al. 2003) and toddler a major parameter of lower limb kinematics in human locomotion.

This dynamic mapping provides a new tool for understanding the development of the functional relationships between multiple EMG profiles and the resulting movement. In the context of motor learning the DRNN may be considered as a model of biological learning mechanisms underlying motor adaptation (Cheron et al. 1996). According to Conditt et al. (1997), adaptation to change in human movement dynamics is achieved by neuronal modules. These modules realise learning through dynamic mapping between kinematic states (positions or velocities) and the forces associated with these states. The brain is thus capable of forming and memorizing remarkably accurate internal representations of body segment dynamics (Conditt and Mussa-Ivaldi 1999). This establishes a functional relation between force and motion, which is generally complex and non-linear (Zajac and Winters 1990). Using artificial learning of the mapping between multiple EMG patterns and velocities of lower limb segments we found that the attractor states reached through learning correspond to biologically interpretable solutions. The evolution of these states could be followed during development. This neural network is also able to decipher some motor strategies using interaction torque in multijoint movements (unpublished data). For some authors, EMG patterns are a good reflection of the motor programme used by the CNS for controlling movement (Gottlieb 1993). However, for others, EMG and kinematic patterns are emergent, non-programmable properties of the system and the control signals are positional in nature (Feldman et al. 1998; Gribble et al. 1998; McIntyre and Bizzi 1993). In this controversial context the present method is not intended to propose a model for motor control based on feedforward related EMG signal for predicting kinematics. On the contrary, we propose to use the identification between EMG signals and kinematics for deciphering the complex relatonships between multiple muscular activation and the resulting movements. This dynamic identification is particularly relevant because it represents the solution for the reduction of the number of degrees of freedom and provides an idea of the controlled operation selected by the nervous system (Sporns and Edelman 1993). Moreover, they motivated behaviorally based network modelling taking into account in their architectures neurobiological principles (Draye et al. 1997, 2002) and general theory of brain function such as the theory of neuronal group selection (Edelman 1989; Reeke and Sporns 1993; Sporns et al. 2000). According to this theory, the first basic step in development is the activation of several primary neuronal groups, which are genetically determined and not definitely wired. Then, in cases of the most successful
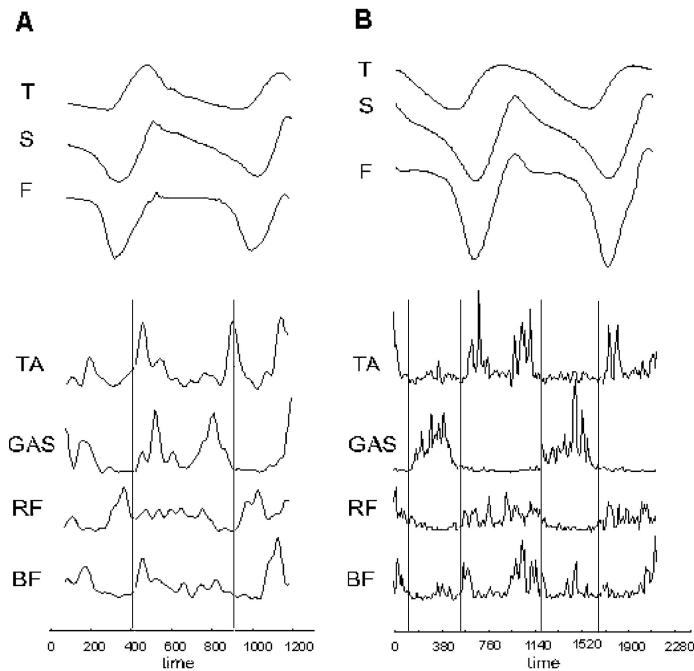
FIGURE 8. Comparison of gait activation patterns and related kinematics in a toddler (A) and an adult (B). Elevation angles of the thigh (T), shank (S) and foot (F) are illustrated in both upper parts. The related activation pattern (rectified EMG) of the tibialis anterior (TA), gastrocnemius (GAS), rectus femoris (RF) and biceps femoris (BF) are illustrated in both lower part. Note that the well characterized reciprocal EMG patterns between TA and GAS and between GAS and RF in the adult (B) are not present in the toddler (A).
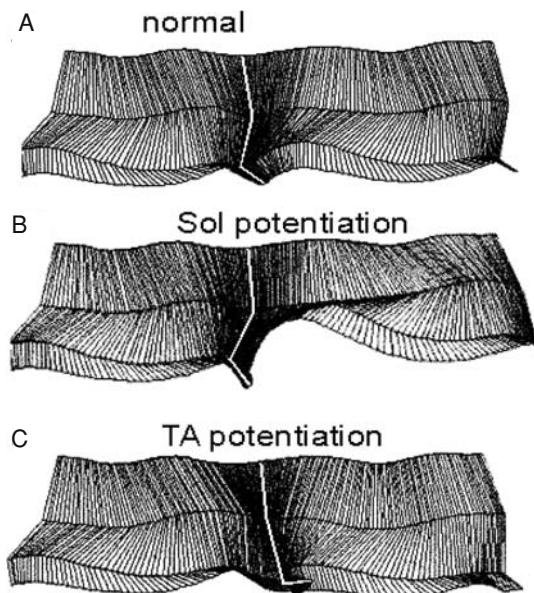

FIGURE 9. Kinematics simulation after artificial EMG potentation in the DRNN. (A–C) Sagittal stick diagrams of the lower limb kinematics obtained in an adult after DRNN learning of normal locomotion (A) and after artificial EMG potentiation of SOL (B) and TA (C) muscles. (*Reprinted by permission from Cheron et al 2003, J Neurosc. Meth.*)
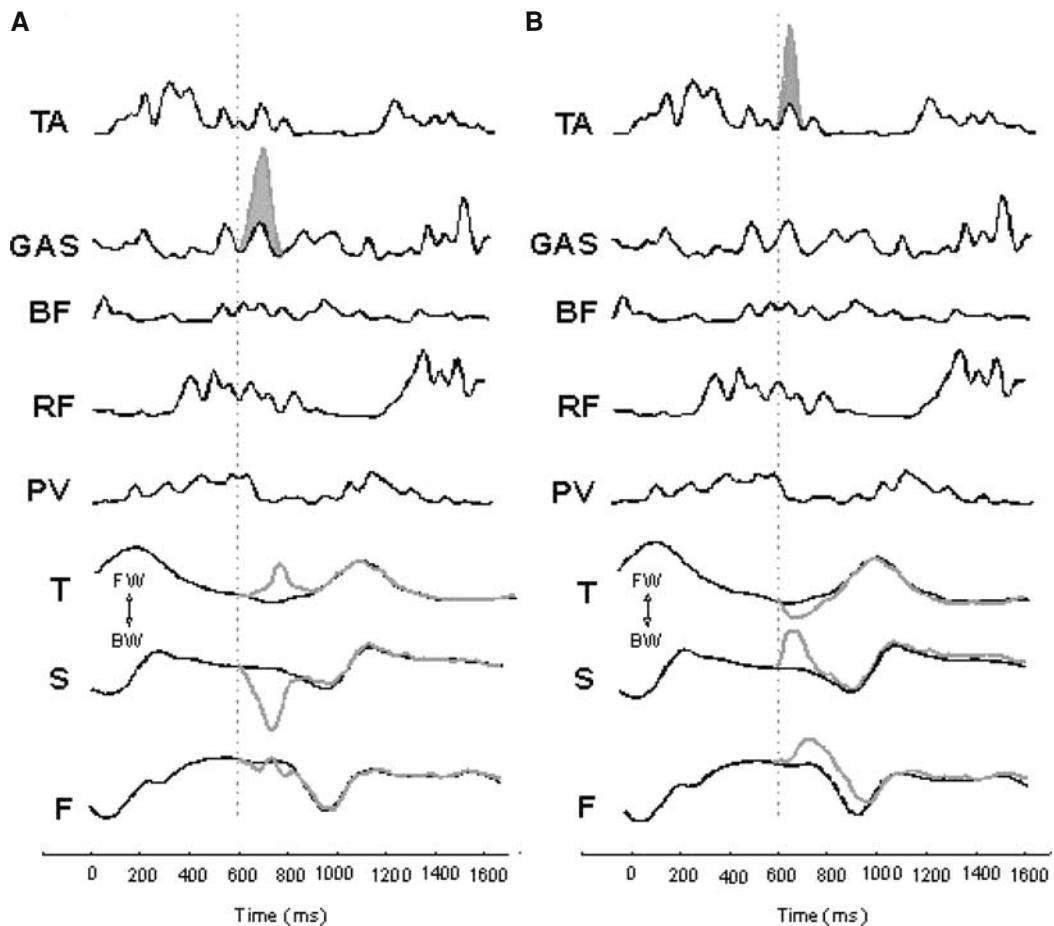
FIGURE 10. Biological plausibility of DRNN for the very first steps of a toddler. Multiple EMG patterns recorded during the very first step of a toddler and used for the DRNN learning (A,B). Artificial potentiation of GAS burst (A) and TA burst (B) resulting in ankle extension (A) (similar as those illustrated for an adult in Fig. 9B) and ankle flexion (B) (similar as those illustrated for an adult in Fig. 9C), respectively.

motor outputs, experientially driven selection occurs on these primary neural groups by synaptic reinforcement. The simulation obtained by the DRNN approach makes possible insights into how coordinated behavior is controlled by neuronal activity accessible in human on the basis of EMG recordings.

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