Neuroscience and Biobehavioral Reviews 186 (2026) 106671

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

A neuromechanical framework for the development of interlimb coordination

Sina Salehpour [a,1], Samuel Mathieu [a,1], Francesca Sylos-Labini [b,c], Yuri Ivanenko [b], Francesco Lacquaniti [b,c], Arthur H. Dewolf [a,*]

[a] Laboratory of Physiology and Biomechanics of Human Locomotion, IoNs, UCLouvain, Louvain-la-Neuve 1348, Belgium
[b] Laboratory of Neuromotor Physiology, IRCCS Santa Lucia Foundation, Rome 00179, Italy
[c] Department of Systems Medicine and Center of Space Biomedicine, University of Rome Tor Vergata, Rome 00133, Italy

ARTICLE INFO

Keywords:
Neonatal stepping
Early development
Interlimb coordination
Human locomotion

ABSTRACT

Interlimb coordination is a defining property of human locomotion that emerges from the interplay of spinal pattern generation, sensory feedback, and supraspinal modulation across development. Evidence from neonatal, and infant studies shows that left–right and arm–leg couplings are present at birth yet remain highly flexible: neonatal circuits can express alternating or synchronous patterns depending on sensory context, and their coupling strength changes with loading or mechanical constraints. Over the first two years, coordination becomes more reliable and task-specific as supraspinal pathways, intraspinal circuits, and multisensory integration mature in parallel with growth-related biomechanical changes. These processes are accompanied by reductions in variability and stabilization of phase relations. Synthesising humans and non-human animals' evidence, we argue that interlimb coordination should be understood as a multilevel, calibrating system. We further show how neuromechanical models that integrate different levels of control, together with developmental parameterisation, offer principled tests of otherwise intractable hypotheses. Finally, we outline translational opportunities in paediatrics, where conserved arm–leg interactions and model-informed interventions may help identify atypical developmental trajectories and guide early rehabilitation.

1. Introduction

Accurate left-right coordination is essential for the regulation of upright posture and locomotion in human. Studies from diverse species including lamprey, zebrafish, turtle, cat, and rodent (*e.g.* Grillner and El Manira, 2020; Stein and McCullough, 1998) have shown that the spinal cord contains networks of neurons that can produce rhythmic output termed central pattern generators (CPGs, Brown, 1911, 1914; McCrea and Rybak, 2008; Guertin, 2009; Frigon, 2012). These networks can produce a variety of rhythmic outputs independently of rhythmic sensory or supraspinal inputs (Cowley and Schmidt, 1994; Mortin and Stein, 1989; Pearson and Rossignol, 1991; Whelan et al., 2000), supporting the different interlimb coupling required for the generation of multiple distinct gaits. Indeed, Grillner and Zangger (1979) in a cat preparation with all dorsal roots transected, showed that the most frequent type of interlimb coordination was alternation between the two sides, but that cats can change from the alternation used in walk and trot to the gallop pattern in which the hindlimbs are occasionally in synchrony (Miller et al., 1975). Such flexible coupling between rhythm generators on each side of the body relies on bilateral spinal commissural circuits (Cazalets et al., 1995; Kjaerulff and Kiehn, 1996; Lafreniere-Roula and McCrea, 2005), which have more recently been resolved into genetically defined interneuron populations with distinct functional roles in left-right coordination (Gosgnach, 2023; Goulding, 2009; Kiehn, 2016; Maxwell and Soteropoulos, 2020). Within this framework, each side of the spinal cord can be viewed as a semi-autonomous rhythmogenic module, whose interaction is mediated by a distributed network of functionally specialized commissural interneurons. Importantly, this circuit-level organization provides a mechanistic substrate through which different coordination patterns can emerge and be flexibly modulated by sensory and supraspinal signals, in response to task, biomechanical and developmental constraints.

Human gaits usually consist of anti-phase left-right rhythmic limb movement. However, because of well conserved locomotor behaviour

* Corresponding author.
E-mail address: arthur.dewolf@uclouvain.be (A.H. Dewolf).
[1] These authors contributed equally to the work.

https://doi.org/10.1016/j.neubiorev.2026.106671
Received 12 January 2026; Received in revised form 27 March 2026; Accepted 30 March 2026
Available online 31 March 2026

across legged vertebrate species (Catavitello et al., 2018; Dominici et al., 2011), one may expect cross-species similarities in the variety of coordination patterns (Gonçalves et al., 2021). For instance, substantial changes in interlimb coordination can emerge depending on environmental, mechanical, or developmental constraints. Under altered gravitational conditions, skipping, hopping or loping may become the preferred gait, illustrating how different coordination modes can be recruited when the cost landscape changes (Minetti, 1998). A certain level of independence of each hemi-spinal cord can indeed be reflected in the coordination of limb movements on a split-belt treadmill, with the two belts running at different speeds or one belt running in the forward direction and the other one running in the backward direction, or when walking and running while turning (Courtine and Schieppati, 2004; Mesquita et al., 2024). In those cases, the limbs are forced to operate somewhat independently, as demonstrated by asymmetrical left-right stepping (Choi and Bastian, 2007; Dietz et al., 1994; Prokop et al., 1995). Even though each hemi-spinal cord can produce rhythmic movements in each limb separately, activity of both sides must be coordinated during locomotion in humans. Indeed, in any situations, the limbs maintained a reciprocal relationship with the swing phase occurring in one leg at a time. This alternate activity of the left and right flexor-generating centres is likely mediated by crossed inhibition between the sides, activity of the CPGs on one side inhibiting the contralateral ones (Hiraoka et al., 2014; Ting et al., 1998).

Recent evidence further suggests that the interlimb phase relationship may not be strictly controlled on a step-by-step basis. Instead, the nervous system appears to tolerate small deviations from perfect antiphase without actively correcting them, until a threshold (so-called "dead zone") is exceeded (Arai et al., 2024). This dead zone hypothesis implies that the antiphase relationship emerges as a stable coordination default, but is not continuously regulated unless deviations become behaviourally relevant. This also aligns with the notion that interlimb phase might not be explicitly controlled unless the deviation from antiphase surpasses a certain threshold (Arai et al., 2024), consistent with observations that energy efficiency and maneuverability may benefit from allowing small, uncorrected fluctuations.

As mammalian locomotion involves flexibly coordinated neuronal networks controlling forelimb and hindlimb movements (Frigon, 2017a), a finely tuned arm-leg coordination exists in adult locomotion, with flexible neuronal coupling between lower and upper limbs (Dietz et al., 2001; Wannier et al., 2001). The CPGs, housed in the cervical and lumbar spinal cord, generate rhythmic patterns in order to synchronize arm and leg movements, essential for achieving stable and efficient gait. For example, MacLellan et al. (2013) demonstrated that during human quadrupedal crawling on split treadmills, the coupling between upper- and lower-limb CPGs remains strongly constrained toward integer frequency ratios (1:1 or 2:1), supporting the existence of neural connections between the cervical and the lumbosacral spinal cord. Also, rhythmic arm and/or wrist movements can facilitate the soleus H-reflex and even elicit non-voluntary leg oscillations in a gravity-neutral position (Solopova et al., 2017; Sylos-Labini et al., 2014), supporting the functional neural coupling between the upper and lower limbs.

Walking is characterized by anti-phase coordination between the pelvic and scapular girdles, which is considered most flexible and dynamically efficient (Dedieu and Zanone, 2012). Sensory feedback modulates these patterns, adapting coordination based on changes in demands (Wannier et al., 2001) or gait velocity (Donker et al., 2001), illustrating the complex neural and biomechanical systems that maintain effective human locomotion. Arm swing during locomotion results from both passive mechanical dynamics produced in locomotion, trunk rotation and active neural contributions, as shown by studies manipulating pelvis motion or arm mass (Canton and MacLellan, 2018). Passive dynamics arise from the transmission of mechanical energy generated by the swinging lower limbs through the trunk to the upper body, via biomechanical linkages, causing the arms to oscillate as passive masses that help reducing whole-body angular momentum. While this passive energy transfer from the lower limbs helps damping trunk angular momentum, shoulder muscle activity acts eccentrically to modulate swing amplitude and maintain interlimb synchrony even when the mechanical properties of the arms are altered.

According to the discussion above, in humans as in other animals, efficient locomotion requires a continuous interplay between the neural circuits controlling each limb (Fig. 1). However, the intrinsic organization and modulation of mature interlimb coupling remain incompletely understood. Understanding the mechanisms that govern interlimb coordination provides a crucial foundation for studying how these patterns emerge during development and how spinal, sensory, and cortical mechanisms interact to achieve mature, task-specific coordination. In the following, we review how interlimb coordination emerges in humans in perinatal stage, and how multilevel neural mechanisms interact with biomechanics across development.

2. Inborn interactions between limbs

Motor behavior in animals, including humans, begins during the prenatal period Dewolf et al., (2020); Einspieler et al. (2021). Fetal behavior is generally characterized as spontaneous or non-evoked, and appears random and uncoordinated (Hamburger, 1973). However, studies of the rat fetus in vivo have shown spatial and temporal

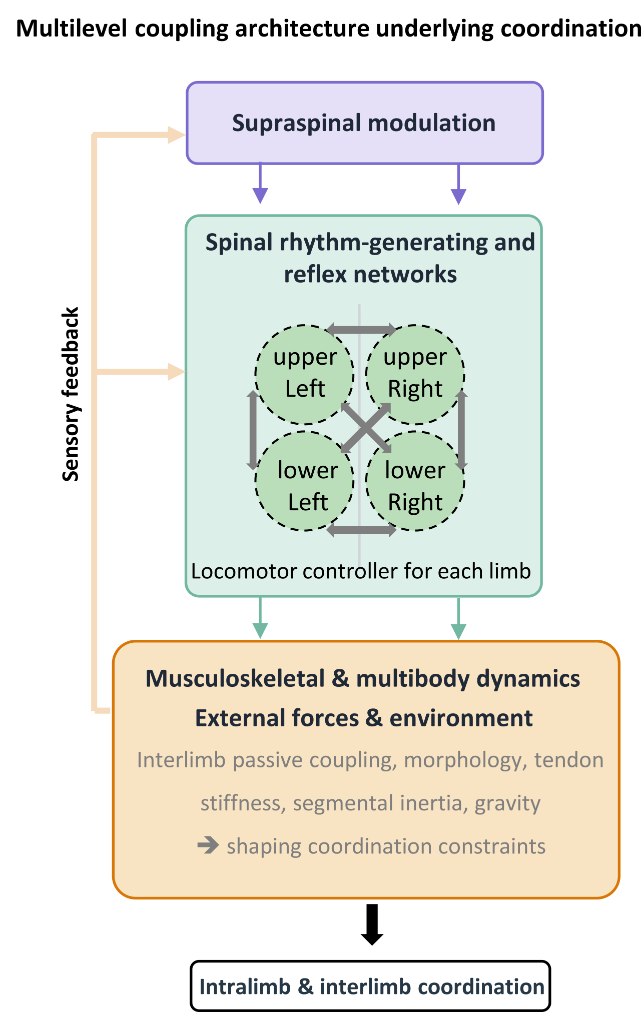

Fig. 1. Multilevel coupling architecture underlying interlimb coordination. Hierarchical control structure. Interlimb coordination emerges from the dynamic interaction between supraspinal modulation, spinal pattern-generating networks, reflex-based sensory feedback, and musculoskeletal and multibody dynamics, each limb being driven by its own locomotor controller.

organization during spontaneous motor activity even within these seemingly random activities (Kleven et al., 2004; Robinson and Smotherman, 1987). In particular, episodes of hindlimb or forelimb coordination are observed in the 20-day-old rat fetus, showing unambiguously that the neural circuitry underlying interlimb coupling is already present before birth (Bekoff and Lau, 1980). Increases in limb coupling occur over the next several days (Kleven et al., 2004; Robinson and Smotherman, 1987), indicating maturation of physiologically relevant network connections during the course of transition from spontaneous-like to voluntary goal-directed movements during development.

Human neonates express different types of locomotor-related movements, which can be broadly classified as (i) spontaneous movements, performed in the air, often called *kicking*, and (ii) evoked movements**,** such as *stepping.* Spontaneous kicking movements (Thelen and Fisher, 1982; Yang et al., 1998; Adolph and Robinson, 2013; Barbu-Roth et al., 2014), are produced thousands of times during the first month of life, and have long been considered random. They exhibit in fact structured spatiotemporal features and muscle synergies. Consistent with this idea, Sylos-Labini et al. (2020) demonstrated that during spontaneous movements, neonates recruit a modular organization of neuromuscular activation patterns sharing similarities to those observed during later locomotor behaviors. This suggests that the basic building blocks of coordinated motion are already present at birth, and are progressively refined through sensory feedback, supraspinal influences, and experience. Recent findings by Kanazawa et al. (2023) further emphasize the structured nature of the early motor behaviors. Using musculoskeletal simulations, the authors revealed that even spontaneous movements in neonates exhibit organized sensorimotor interactions between the four limbs, indicating an underlying modular structure in the control of limbs. Such evidence supports the idea that early locomotor-related movements contribute to the self-organization of sensorimotor coordination, which is foundational for later voluntary locomotion.

When held upright with the feet touching a surface, the same neonates are capable of producing evoked, load-dependent stepping movements (Thelen et al., 1982; Forssberg, 1985; Yang et al., 1998; Domellöf et al., 2007; Dominici et al., 2011; Adolph and Robinson, 2013; Ivanenko et al., 2013; Barbu-Roth et al., 2021). Compared to spontaneous movements, neonate stepping often appears more stereotypical. Because the occurrence of stepping has been classically defined as a succession of left-right steps alternation (Sylos-Labini et al., 2017; Yang et al., 1998), the level of flexibility and plasticity of interlimb coupling has not often been investigated. As an example, split-belt treadmill experiments in infants showed that when the two legs experience different mechanical demands, stepping does not remain strictly 1:1 alternating; instead, infants can express asymmetric coordination patterns (*e.g.*, 2:1 step ratios), indicating that interlimb coupling is flexible and can adapt to external constraints rather than obeying a fixed alternation rule (Yang et al., 2005).

In our recent work, we aimed at understanding the nature of the interlimb organization evidenced in the first steps (Dewolf et al., 2022). Previous work showed that, while neonates step, they display episodes of synchronous and alternating left–right coordination (Siekerman et al., 2015; Thelen and Fisher, 1982). To highlight potential interaction between the two limbs with and without sensory feedback from joint movements (Solopova et al., 2019) or mechanical coupling between limbs, we compared the left-right muscle activation during bilateral and unilateral stepping, manually blocking one limb. By comparing the motor response of the stepping and blocked limb of unilateral stepping, we revealed that the blocked limb exhibited highly flexible coordination patterns, alternating between synchronous and alternating muscle activations relative to the stepping limb. Although some synchronous episodes were also present during bilateral stepping (~20% of steps), they became markedly more frequent during unilateral stepping (~50%), indicating that removing mechanical and sensory coupling between the limbs enhances the expression of flexible interlimb patterns. Moreover, in some neonates, we identified episodes of rhythm mismatches between the two limbs, including instances of 2:1 or 0:1 coordination between the two limbs. This may suggest the presence of independent CPGs for left and right limb movements, akin to observations by Grillner and Zangger (1979) in the spinal cords of decerebrated cats and the recordings of fictive locomotion in the isolated spinal cord of rodents (Hägglund et al., 2013). These findings emphasize the adaptability of neonatal locomotor networks, shaped by intrinsic spinal mechanisms and early integration of sensory feedback. These findings underscore the dynamic and sensory-driven nature of a flexible interlimb organization at birth, shaped by independent pattern generators and early feedback mechanisms.

Historically, most of the studies on inborn locomotor skills had focused on the lower limbs, while the potential contribution of the upper limbs has been less explored. Curiously, little is known about the coordination of quadrupedal locomotor activity at birth. This bias likely stems from the salient visual and evolutionary significance of stepping as a precursor to upright gait. Nevertheless, evidence for early arm–leg interactions is emerging. Early qualitative observations had suggested some contribution of the arms in primitive locomotor behaviours, such as neonatal swimming (McGraw, 1940, 1939). More recently, sporadic episodes of arm-leg coordination observed during the stepping reflex also provides significant evidence for a neural coupling between the arms and legs during early ontogenesis of locomotion (La Scaleia et al., 2018). In their experimental study, these authors showed that although infrequent, some stepping episodes involved clear alternating arm oscillations. These movements occurred in a diagonal coupling with the legs, resembling the mature adult pattern in which contralateral arm and leg move together (Dietz and Michel, 2009). Together with evidence from prone skateboarding experiments in newborns where coordinated arm–leg propulsive movements emerge (Forma et al., 2019), these findings support the notion that elements of quadrupedal coordination are preserved in human ontogeny, consistent with comparative evidence across species (Zehr and Duysens, 2004). Such innate feature of the human locomotor system is thought to be mediated by propriospinal connections linking cervical and lumbar pattern generators (Juvin et al., 2012), as it is unlikely it can be facilitated by passive biomechanical linkages as in adults (Pontzer et al., 2009).

3. Development of interlimb coordination

During the first years of life, interlimb coordination evolves from the flexible and largely spinally mediated patterns observed in neonates toward the refined, task-specific organization characteristic of mature gait and bimanual control (Fig. 2). This transition does not reflect a replacement of motor patterns, but rather a progressive reweighting of control across neural levels. Indeed, converging evidence suggests that early locomotor behaviour can be viewed as predominantly generated by spinal and brainstem circuits (Blumberg and Adolph, 2023; Zandvoort et al., 2022), whereas supraspinal structures progressively contribute to shaping these outputs, enabling greater adaptability, context-specific modulation, and sensorimotor integration (Ijspeert and Daley, 2023a) (Fig. 1).

It should be remarked that in adult humans and non-human primates the role of corticospinal influences on locomotor patterns and muscle synergies is much greater than in other mammals. For instance, Klishko et al. (Klishko et al., 2024) demonstrated that spinal and intact cats have very similar locomotor muscle activities and synergies, consistent with a minor role of supraspinal signals in default locomotor control. By contrast, humans with a spinal cord lesion have muscle synergies very different from healthy persons (Ivanenko et al., 2003).

As descending corticospinal and reticulospinal pathways mature, they gradually exert top-down modulation over these spinal circuits, enhancing selectivity and task adaptation (Dominici et al., 2010; Koster et al., 2025; Nùñez-Lisboa et al., 2023; Zandvoort et al., 2022).

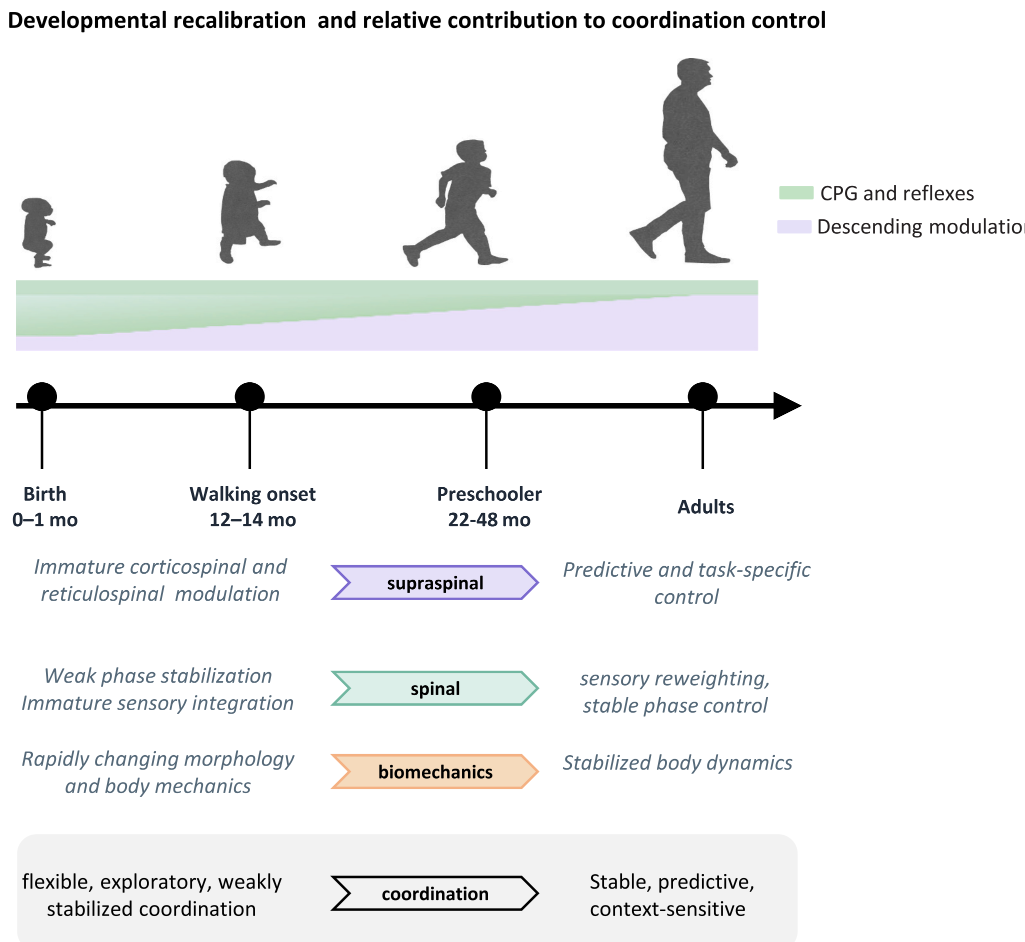

Fig. 2. Developmental recalibration of the relative contribution of supraspinal, spinal, and biomechanical factors to coordination control. Conceptual developmental timeline illustrating how the control of coordination evolves from birth to adulthood.

Concurrently, the biomechanical growth of the body profoundly reshapes the constraints under which the nervous system operates. Changes in limb length, segmental mass distribution, and muscle-tendon stiffness alter the body dynamics (Adolph and Robinson, 2013; Dewolf et al., 2020), imposing the developing system to continuously recalibrate the mapping between sensory inputs and motor outputs. It is through the progressive calibration between descending cortical control, spinal rhythm-generating circuits, and sensory feedback that stable, context-dependent coordination emerges throughout development. Moreover, it has been shown that spinal interneuronal networks are multifunctional in a context-dependent manner, with individual interneurons participating in multiple circuits and adapting their contribution depending on the locomotor task. This multifunctionality is a core property underlying modular locomotor organization (Côté et al., 2018). Consistent with this principle, commissural interneurons, which are specialized spinal neurons whose axons cross the midline, link the left and right locomotor networks and help shaping bilateral coordination. Experimental evidence shows that these neurons can mediate mutual inhibition, which promotes alternating left–right activity, as well as mutual excitation, which can support synchronous or more coupled patterns depending on task demands and network state. This dual organization allows commissural pathways to flexibly regulate interlimb coordination, rather than enforcing a single fixed alternation pattern (Frigon, 2017b).

Early infancy is characterized by high variability and intermittent coupling between limbs movements (Disselhorst-Klug et al., 2012; Kanemaru et al., 2012; Piek, 2002; Sylos-Labini et al., 2022). Although this variability might appear as motor "noise," it represents a key feature of the developmental process (Hadders-Algra, 2010). Indeed, variability is not simply error or imperfection but rather reflects a healthy adaptability of the motor system, a concept already emphasized by Bernstein as "repetition without repetition", highlighting the continuous exploration of alternative movement solutions during skill acquisition (Bernstein, 1967). More recent frameworks have formalized this idea as 'optimal movement variability', whereby variability facilitates exploration of the solution space and enables transitions between coordination states (Stergiou et al., 2006; Stergiou and Decker, 2011). From a behavioral standpoint, this variability may be seen as transient shifts between different coordination patterns, reflecting the system's search for dynamically stable attractors (Thelen and Smith, 1994; Zanone and Kelso, 1997). In line with this view, developmental studies show that variability plays a central role in motor learning, allowing infants to explore multiple movement solutions before stabilizing efficient patterns, the specific solutions differing considerably among individuals (Ossmy and Adolph, 2020). Importantly, the ability to flexibly alternate between synchronous and alternate leg movements emerges early in infancy and reflects the intrinsic adaptability of the spinal locomotor networks. Musselman and Yang (2008) showed that most infants exhibit either a preferred alternate or synchronous pattern of interlimb coordination, suggesting flexible left–right coupling. Surprisingly, a short-term practice of the non-spontaneously adopted coordination type (alternating or synchronous) was sufficient to induce a change in preferred interlimb coupling. This change of coordination indicates that the underlying spinal circuits are not hardwired but instead highly malleable through experience and sensory feedback. Such findings point to the existence of shared commissural spinal interneurons, crossing the midline and coordinating left–right activity, capable of expressing both mutually inhibitory interactions, promoting alternation, and excitatory interactions, supporting more synchronous or coupled patterns depending on task demands and network state (Butt et al., 2002; Dewolf et al., 2022; Frigon, 2017b; Hiraoka, 2021). As highlighted in recent work, these commissural pathways encompass distinct interneuronal populations that differentially contribute to left–right coordination, enabling flexible transitions between coordination modes rather than enforcing a single fixed pattern. This organization allows smooth transitions between alternate and synchronous coordination even at a very young age. Consistent with this view, longitudinal analyses show a progressive reduction in both cycle-to-cycle variability and left–right phase variability during the first months of life (Yang et al., 2015). This reduction likely reflects the combined influence of neural maturation and experience-dependent processes. On the one hand, the maturation of spinal and sensory pathways contributes to increased stability and coordination of motor outputs. On the other hand, behavioural studies emphasize the role of exploration and learning, whereby variability supports the search for effective movement solutions before more stable coordination patterns emerge (Hinnekens et al., 2024; Ossmy and Adolph, 2020). Thus, early interlimb coupling may become increasingly stabilized through the interaction between developing neural circuitry and the progressive selection of efficient motor strategies.

Such results support the idea that human interlimb coordination is shaped by both the intrinsic organization of the spinal pattern generators and by the experience-dependent reweighting of their connections. Several studies reported correlated spontaneous limb movements even in the first months of life (Dolinskaya et al., 2021; Kanazawa et al., 2023). A progressive increase in contralateral muscle activity correlations during this period likely reflects the strengthening of spinal circuits, including intersegmental and commissural connections (Brumley et al., 2012; Sylos-Labini et al., 2020), setting the stage for later crawling, and bipedal walking. Such behavioural evidence parallels the gradual decrease in kinematic variability and the emergence of consistent phase relationships across limbs, marking the behavioural signature of sensorimotor maturation. Importantly, however, developmental change in interlimb coordination does not follow a single uniform pathway. Recent work emphasizes that infants exhibit individual, experience-dependant strategies in the emergence of coordinated locomotion, with substantial variability in how and when stable coordination patterns are achieved (Ossmy and Adolph, 2020). This perspective highlights that variability is not merely noise or immaturity but may reflect adaptative exploration shaped by each infant's unique motor history (e.g. the accumulation of prior postural, locomotor and environmental experiences that that interact with neural maturation and biomechanical growth to shape coordination).

As infants approach mid-infancy (≈6–10 months), crawling introduces clear diagonal limb coupling, engaging both cervical and lumbar CPGs (Adolph et al., 2011; MacLellan et al., 2013). Quadrupedal coordination displays different interlimb sequences whose variability gradually declines with practice (Patrick et al., 2012). Beyond crawling, infants also engage cruising (stepping sideways while holding onto support) which constitutes a distinct pre-walking locomotor mode with its own coordination demands and balance constraints (Ossmy and Adolph, 2020). Indeed, evidence suggests that cruising and crawling may rely on partially different coordination strategies, further underscoring that pre-walking development involves multiple locomotor pathways rather than a single linear progression toward independent walking. Concomitantly, reaching and manipulation reveal emerging asymmetry and functional differentiation between the two arms, as one arm increasingly stabilizes while the other manipulates (Fagard, 1998). These behaviours mirror the progressive specialization of cortical and callosal pathways that reduce interhemispheric interference and enable role-differentiated bimanual control (Johnston et al., 2013). Around walking onset (≈12–14 months), electromyographic analyses reveal an increase in the number of motor primitives and reduced stride-to-stride variability, indicating a reorganization of locomotor control into more structured, adult-like modules (Dewolf et al., 2020; Dominici et al., 2011; Sylos-Labini et al., 2022). Reciprocal arm swing emerges gradually with experience and balance improvement (Ledebt, 2000; Meyns et al., 2013; Van de Walle et al., 2018). By the end of the second year, interlimb coordination becomes more temporally stable, context-sensitive, and functionally adaptive.

This developmental trajectory likely results from the gradual integration of multiple interacting factors: growth-related biomechanical changes, experience-dependent learning, and the progressive interplay between spinal, sensory, and cortical levels of control. In line with dynamic systems approaches to locomotor development, recent findings further suggest that changes in coordination reflect the continuous coupling between perception, action and environmental constraints, with infants flexibly reorganizing their coordination patterns according to task demands and prior experience (Ossmy and Adolph, 2020). Recent longitudinal evidence further shows that this transition toward mature coordination is accompanied by a progressive functional symmetrisation of neuromotor modules. Lin et al. (Lin et al., 2025) demonstrated that, as infants shift from supported to independent walking, the covariation of left-right joint angles gradually reorganize into bilaterally symmetric kinematics. Importantly, their analysis revealed that this symmetrisation depends on age-related changes in limb biomechanics. This result provides compelling evidence that interlimb coordination does not emerge solely from neural maturation, but from the co-development of neural and mechanical properties. Furthermore, the CPG itself modulates sensory pathways, meaning the interaction is bidirectional: sensory input shapes locomotion, and locomotor state gates sensory processing. During development, sensory feedback becomes increasingly refined, contributing to the stabilization of locomotor patterns, the improvement of coordination, and adaptation to body growth (Côté et al., 2018; Picton et al., 2025). Current views describe the locomotor CPG as a distributed and modular network in the spinal cord, built from different interneuron groups that work together rather than a single "rhythm center." Rhythm is produced when descending drive activates these circuits, and excitatory and inhibitory connections shape the timing and coordination of flexor–extensor and left–right alternation, allowing the same network to be flexibly modulated across tasks and speeds (Gosgnach, 2025; Picton et al., 2025).

Such multilevel calibration between central and peripheral system gradually transforms early, exploration-driven variability into stable, context-specific movement patterns. From this developmental perspective, the human nervous system emerges as a highly plastic and dynamically coupled network, particularly during early life, when interlimb and intersegmental connections are most flexible (Dewolf et al., 2022; Musselman and Yang, 2008). Understanding how sensory feedback and descending control progressively interact to shape coordination not only deepens our insight into the mechanisms of human motor ontogenesis but also offers a foundation for computational and biomechanical modelling approaches— topics addressed in the following section.

4. The Sensory–Cortical integration of interlimb coordination

The neuromotor development in humans is not solely grounded in primitive spinal circuits or elementary reflexes. It relies, non-exhaustively, on the progressive and integrated maturation of various key components: sensory integration through proprioceptive, vestibular, and cutaneous afferents (Clark et al., 2021; Forssberg and Nashner, 1982); myelination of neural pathways (Moulson and Nelson, 2008); and the cortical organization supporting interhemispheric communication (Zandvoort et al., 2022) and top-down control. Together, these processes shape the emergence and refinement of interlimb coordination throughout development. However, how these mechanisms evolve remains poorly understood.

Sensory afferences influence human behavior from birth: olfactory

(Hym et al., 2020), auditory (Hym et al., 2023), and even visual inputs such as optic flow (Forma et al., 2018) can elicit motor responses in newborns. Although these findings highlight early sensory influences on movement, evidence regarding the contribution of other peripheral stimulations, particularly proprioceptive, vestibular, and tactile inputs, remains limited. Yet, these modalities form the backbone of postnatal motor calibration, as they provide continuous feedback about body position, motion, and contact forces. For instance, somatosensory feedback plays a critical role in spatial orientation, postural stabilization, and motor coordination (Frigon et al., 2021). The vestibular system, while its peripheral components are nearly adult-like at birth (Božanić Urbančič et al., 2023), continues to mature centrally through the development of cerebellar control, vestibulospinal pathways, and adaptive postural loops during childhood (Clark et al., 2021).

Young children's ability to effectively combine sensory information from different modalities, such as vision, proprioception, and vestibular feedback, is far from optimal and improves gradually with age (Forssberg and Nashner, 1982). Studies on multisensory integration (MSI) show that children under the age of eight exhibit less mature sensory fusion and reweighting abilities compared to adults (Dionne-Dostie et al., 2015). From the perspective of interlimb coordination, this developmental progression is crucial. As children learn not only to sense their limbs, but also to integrate these signals into a coherent motor framework, their sensorimotor loops become more stable and reliable stabilizing motor timing and bilateral coordination (Verbecque et al., 2016).

The refinement of sensory integration during development is paralleled by major structural and functional changes within the central nervous system. Myelination, which begins prenatally and extends into adolescence, progressively increases the speed and reliability of neural transmission, allowing more precise communication between sensory and motor regions (Moulson and Nelson, 2008). Early-myelinating tracts include primary sensory and motor pathways that support basic postural and locomotor control, whereas associative and prefrontal areas follow a more protracted trajectory, enabling the integration of multisensory feedback and higher-order motor planning. In parallel, the maturation of interhemispheric connectivity through the corpus callosum enhances coordination between homologous cortical areas (Zandvoort et al., 2022). During early development, diffuse callosal connections result in bilateral co-activation and mirrored movements, but progressive myelination and synaptic pruning refine these pathways, promoting hemispheric specialization and independent limb control.

As cortical networks mature, top-down control increasingly modulates spinal CPGs. The progressive recruitment of corticospinal and corticoreticular pathways allows descending commands to fine-tune the timing and phase relationships of limb movements, refining the coordination between upper and lower limbs (Frigon, 2017a). Dominici et al. (2011) demonstrated that infants initially rely on a limited set of spinally organized locomotor modules, which are gradually reorganized under cortical influence into more flexible and adaptive synergies during gait acquisition. Similarly, developmental comparisons across childhood (Zandvoort et al., 2022) indicate that increasing corticospinal drive and enhanced sensorimotor integration coincide with a reduction in motor variability and the emergence of stable, predictive locomotor patterns. Importantly, this increasing cortical modulation should not be interpreted as the late emergence of cortical involvement. Evidence suggests that the sensorimotor cortex is functionally active from early infancy and participates in shaping corticospinal connectivity through self-generated movements and sensory feedback, thereby contributing to the construction of motor circuits rather than merely refining pre-existing spinal programs (Blumberg and Adolph, 2023). Thus, cortical development does not simply impose top-down control on spinal circuits but co-develops with them through reciprocal sensorimotor interactions. Altogether, the maturation of myelination, interhemispheric connectivity, and descending cortical control underpins the developmental shift from a predominantly reactive spinal control to a progressively integrated and cortically modulated system. This integrated evolution supports both the stabilization and adaptability of interlimb coordination, marking a key transition toward mature, anticipatory motor control.

In early development, movement control is dominated by reactive strategies: the child responds to perturbations or environmental constraints through reflex loops directly triggered by sensory afferents (Forssberg and Nashner, 1982). With maturation, predictive control gradually emerges, allowing the nervous system to anticipate perturbations, adjust and synchronize limb movements according to intention and context. For example, a child begins to prepare foot placement, coordinate opposite arm swing, or activate postural muscles even before a disturbance occurs, demonstrating the emergence of anticipatory postural adjustments and the integration of internal models (Verbecque et al., 2016). Recent kinematic analyses of walking further show that young children do not yet anticipate ground contact during step-to-step transitions, and that anticipatory adjustments progressively appear and become more consistent with age and walking speed (Nuñez-Lisboa et al., 2023).

In summary, the maturation of sensory integration and cortical modulation transforms human motor control from a more reactive system to a predictive and adaptive network integrating spinal, sensory, and cortical loops. Building on these findings, computational modelling provides a rigorous framework to test how such early sensorimotor structuration interacts with maturing CPG dynamics, reflex pathways, and cortical modulation to produce the progressively refined interlimb coordination observed across development.

5. Modelling as an integrative tool

Recent modelling and empirical work converge toward a key principle: interlimb coordination emerges from the dynamic coupling between neural pattern generators, supraspinal control, sensory feedback loops, and the biomechanical body (Fig. 1). Open-ended spontaneous movements in early life already structure sensorimotor information. Using detailed motion capture and musculoskeletal simulation, Kanazawa et al. (2023) showed that newborns and young infants display body-dependent sensorimotor modules and non-random temporal state transitions, indicating that early whole-body activity organizes the building blocks of later coordinated behaviour. In parallel, neuromechanical models demonstrate that rhythmic left–right alternation, phase stabilization, and speed modulation arise only when CPG oscillators, reflex pathways, and body mechanics are integrated into a single hybrid architecture (Van der Noot et al., 2018). Across these studies, a consistent insight emerges coordination is fundamentally a property of the coupled brain–spinal–body system, whose internal organization self-scales with development and experience.

Across vertebrates, the layers of hierarchical control levels form a nested control architecture, with each level contributing distinct but complementary functions (Ijspeert and Daley, 2023b). Brain-level modulation enables voluntary control and task-specific adaptation, CPGs autonomously generate rhythmic patterns even in the absence of sensory feedback, as shown in decerebrate or spinalized animal models (Meehan et al., 2017), while reflex loops provide local feedback for stability and force regulation. At the circuit level, recent computational models based on genetically identified spinal interneuronal populations further specify how these control layers are implemented. In particular, models incorporating commissural and long propriospinal interneurons have shown how specific connectivity patterns can give rise to speed-dependent gait transitions and flexible coordination regimes (Ausborn et al., 2021; Danner et al., 2017), as well as adaptive changes in interlimb coupling (Shinohara et al., 2025). These approaches provide a mechanistic substrate for understanding how spinal circuitry may support the emergence and reorganization of interlimb coordination during development.

A key principle that emerges from modelling and experimental studies is that interlimb coordination depends on the dynamic coupling among these three layers rather than any single level of control. For example, purely reflex-based models replicate walking but fail to modulate speed efficiently (Geyer and Herr, 2010), whereas models relying on CPGs alone produce rhythmic but poorly adaptive movements (Taga, 1995). Dzeladini et al. (2014) demonstrated that combining CPGs with reflex feedback yields human-like gait patterns that flexibly adjust speed and step length, highlighting the necessity of multilevel integration. Such hybrid architectures provide a conceptual framework to interpret the progressive refinement of interlimb coordination during development. Indeed, recent works on human infants further show that isolated neural mechanisms cannot account for the variability in early interlimb coordination underscoring the need for a full multi-level model (Musselman and Yang, 2008; Pang and Yang, 2001). These findings align with neuromechanical modelling work showing that coordination patterns emerge when neural modules are embedded within a biomechanically realistic body. For instance, Lin et al. (Lin et al., 2025) provide empirical evidence that developmental changes in limb musculoskeletal properties significantly contribute to the emerging symmetrisation of locomotor modules, in interaction with the maturation of the neural command.

The role of each layer in the early stage of life remains debated. Through the study of neonates and young infants, it is possible to observe the relative contribution of CPGs and reflexes before cortical modulation becomes dominant. Indeed, neonates and infants display diverse bilaterally coordinated behaviors long before independent walking, revealing most likely early CPG and reflex contributions. Some studies suggest that early interlimb coupling arises from the spontaneous, open-ended movements which give the neural and mechanical substrate for later coordination. For instance, Lamb and Yang (2000) showed that directional changes during infant stepping suggest a CPG basis, whereas neonates exhibit flexible but weakly modulated left–right coupling, consistent with immature supraspinal and sensory influences (Dewolf et al., 2022). This early flexibility likely reflects the initial stage of network organization, where CPGs generate intrinsic rhythmicity and sensory feedback gradually strengthens phase relationships across limbs. The progression from simple bilateral coordination to sophisticated, task-specific interlimb coupling in childhood is thus best viewed as the maturation and integration of all three levels. Therefore, from a developmental perspective, interlimb coordination thus evolves from an intrinsic, spinally driven rhythm to a supraspinally shaped, task-dependent synergy.

Because direct access to infant neural circuits is limited, computational and biomechanical modeling provides a powerful framework to test hypotheses about how these control layers interact across development. Hybrid neuromechanical models (Molkov et al., 2024) that combine biomechanics, CPGs, reflex feedback, and inter-limb coupling have shown that diagonal spinal connections and sensory reafference are essential for stable gait and flexible coordination. Similarly, Di Russo et al. (2023) demonstrated that rhythmic pattern generation alone cannot sustain stable locomotion; reflex feedback introduces inhibitory modulation and context-dependent coupling, which are essential for maintaining adaptive phase relationships between limbs. By systematically manipulating parameters such as sensory delay, coupling strength, or limb growth, these models can replicate developmental changes in interlimb coordination that are otherwise impossible to test experimentally. Moreover, musculoskeletal simulation of growth-related changes (e.g., limb inertia, nerve conduction velocity) offers insight into how maturation influences the interplay of CPGs, reflexes and cortical control, aligning with developmental findings (Sylos-Labini et al., 2020; Teulier et al., 2012). In this sense, modeling serves as an integrative tool bridging mechanistic neural control, biomechanics and developmental motor behavior.

Regarding the modeling for neural control behaviors, there are a staggering number of studies in literature. From a methodological standpoint, computational approaches can be broadly divided into mechanistic (model-based) and data-driven (black-box) frameworks. Mechanistic models, grounded in neural and biomechanical principles, are particularly useful for identifying causal relationships between control levels and behavioural outcomes. Data-driven approaches, based on machine learning or reinforcement algorithms (e.g., CMA-ES, deep RL), excel in reproducing realistic movements and parameter optimization but provide less insight into the underlying mechanisms (Denayer et al., 2025). Integrating these two approaches offers new opportunities: mechanistic models can be tuned using empirical data, while data-driven models can explore the vast parameter space of developmental adaptation.

Crucially, developmental modelling has direct translational value. Interlimb coordination deficits in conditions such as cerebral palsy, spina bifida, or early brain injury likely reflect disruptions at one or more control levels (impaired CPG output, abnormal sensory feedback, or defective supraspinal modulation). By parameterizing models to reflect these impairments, we can test how changes at the brain, spinal or reflex level affect interlimb coupling and gait outcomes and thus guide targeted rehabilitation or neuro-prosthetic control strategies (Arya and Pandian, 2014). Additionally, coupling longitudinal infant motion capture with model predictions could help predict atypical locomotor trajectories and permit early intervention.

Despite these advances, several key gaps remain. First, most studies have examined neural, sensory, or biomechanical contributions in isolation, limiting our ability to understand how interlimb coordination emerges from their interaction. As a result, there is currently no framework that systematically links observable behavioural variability in early life to its underlying neural and mechanical determinants. Second, existing neuromechanical models are largely derived from adult locomotion and rarely account for developmental changes in body mechanics, sensory delays, or neural maturation, limiting their ability to capture the dynamic reorganization of coordination across growth. The goal of the present review is to highlight why such an integrative, developmentally grounded approach is necessary to understand the emergence of interlimb coordination. In this context, longitudinal modelling of growth-related biomechanical changes and evolving sensory delays will be essential to realistically capture developmental adaptations.

6. Conclusion and perspective

Across early postnatal life, human interlimb coordination progresses from a flexible, largely spinally mediated repertoire to a refined, context-sensitive organisation characteristic of mature gait. This trajectory is not a simple hand-off from one controller to another; rather, it reflects the progressive calibration among descending cortical and brainstem signals, spinal rhythm-generating networks, and sensory pathways as the child's body grows and mechanical constraints evolve (Fig. 2). Together, behavioural, electrophysiological, and modelling evidence converge on a mechanistic view of coordination as an emergent property of multilevel coupling.

This perspective has concrete implications. First, longitudinal assays that perturb coupling (e.g., split-belt, curved walking, or rhythmic upper-limb tasks) can reveal developmental changes in phase control that conventional milestone descriptions miss. Second, hybrid neuromechanical models can connect observable behaviour to latent mechanisms, generate falsifiable predictions, and be tuned with infant data to form personalised developmental "digital twins." Third, this framework is inherently translational: by manipulating specific couplings, clinicians may leverage conserved circuitry to potentiate gait training in conditions such as cerebral palsy or early brain injury.

In sum, interlimb coordination should be framed as a developing system of interacting neural and mechanical processes. Addressing the current fragmentation across levels of analysis requires integrative, developmentally grounded models capable of linking behaviour to mechanism, offering a path toward mechanistic diagnosis and targeted intervention in early life.

Funding

This study was funded by the Fonds de la Recherche Scientifique (F. N.R.S - CDR 40036411) and the FSR- UCLouvain.

Declaration of Competing Interest

The authors have no conflict of interests to declare.

References

Adolph, K.E., Berger, S.E., Leo, A.J., 2011. Developmental continuity? Crawling, cruising, and walking. Dev. Sci. 14, 306. https://doi.org/10.1111/j.1467-7687.2010.00981.x.

Adolph, K.E., Robinson, S.R., 2013. The road to walking. Oxf. Handb. Dev. Psychol. 1. https://doi.org/10.1093/oxfordhb/9780199958450.013.0015.

Arai, T., Ota, K., Funato, T., Tsuchiya, K., Aoyagi, T., Aoi, S., 2024. Interlimb coordination is not strictly controlled during walking. Commun. Biol. 7, 1152. https://doi.org/10.1038/s42003-024-06843-w.

Arya, K.N., Pandian, S., 2014. Interlimb neural coupling: Implications for poststroke hemiparesis. Ann. Phys. Rehabil. Med. 57, 696–713. https://doi.org/10.1016/j.rehab.2014.06.003.

Ausborn, J., Shevtsova, N.A., Danner, S.M., 2021. Computational modeling of spinal locomotor circuitry in the age of molecular genetics. Int. J. Mol. Sci. 22. https://doi.org/10.3390/ijms22136835.

Barbu-Roth, M., Anderson, D.I., Desprès, A., Streeter, R.J., Cabrol, D., Trujillo, M., Campos, J.J., Provasi, J., 2014. Air stepping in response to optic flows that move Toward and Away from the neonate. Dev. Psychobiol. 56, 1142–1149. https://doi.org/10.1002/dev.21174.

Barbu-Roth, M., Siekerman, K., Anderson, D.I., Donnelly, A., Huet, V., Goffinet, F., Teulier, C., 2021. Can optic flow further stimulate treadmill-elicited stepping in newborns? Front. Psychol. 12. https://doi.org/10.3389/fpsyg.2021.665306.

Bekoff, A., Lau, B., 1980. Interlimb coordination in 20-day-old rat fetuses. J. Exp. Zool. 214, 173–175. https://doi.org/10.1002/jez.1402140207.

Bernstein, N.A., 1967. The Coordination and Regulation of Movements. Pergamon Press, Oxford. ⟨https://www.scirp.org/reference/referencespapers?referenceid=1652379⟩ (accessed 3.17.26).

Blumberg, M.S., Adolph, K.E., 2023. Protracted development of motor cortex constrains rich interpretations of infant cognition. Trends Cogn. Sci. 27, 233–245. https://doi.org/10.1016/j.tics.2022.12.014.

Božanić Urbančič, N., Battelino, S., Vozel, D., 2023. Appropriate vestibular stimulation in children and adolescents-a prerequisite for normal cognitive, motor development and bodily homeostasis-a review. Children 11, 2. https://doi.org/10.3390/children11010002.

Brown, T.G., 1911. The intrinsic factors in the act of progression in the mammal. Proc. R. Soc. Lond. B Biol. 84, 308–319.

Brown, T.G., 1914. Ton the nature of the fundamental activity of the nervous centres; together with an analysis of the conditioning rhythmic activity in progression, and a theory of evolution of function in the nervous system. J. Physiol. 48, 18–46.

Brumley, M.R., Roberto, M.E., Strain, M.M., 2012. Sensory feedback modulates quipazine-induced stepping behavior in the newborn rat. Behav. Brain Res. 229, 257–264. https://doi.org/10.1016/j.bbr.2012.01.006.

Butt, S.J.B., Lebret, J.M., Kiehn, O., 2002. Organization of left-right coordination in the mammalian locomotor network. Brain Res. Rev. 40, 107–117. https://doi.org/10.1016/S0165-0173(02)00194-7.

Canton, S., MacLellan, M.J., 2018. Active and passive contributions to arm swing: implications of the restriction of pelvis motion during human locomotion. Hum. Mov. Sci. 57, 314–323. https://doi.org/10.1016/j.humov.2017.09.009.

Catavitello, G., Ivanenko, Y., Lacquaniti, F., 2018. A kinematic synergy for terrestrial locomotion shared by mammals and birds. eLife 7, e38190. https://doi.org/10.7554/eLife.38190.

Cazalets, J.-R., Borde, M., Clarac, F., 1995. Localization and organization of the central pattern generator for hindlimb locomotion in newborn rat. J. Neurosci. 15, 4943–4951. https://doi.org/10.1523/jneurosci.15-07-04943.1995.

Choi, J.T., Bastian, A.J., 2007. Adaptation reveals independent control networks for human walking. Nat. Neurosci. 10, 1055–1062. https://doi.org/10.1038/nn1930.

Clark, J.E., Pate, R., Rine, R.M., Christy, J., Dalton, P., Damiano, D.L., Daniels, S., Holmes, J.M., Katzmarzyk, P.T., Magasi, S., McCreery, R., McIver, K., Newell, K.M., Sanger, T., Sugden, D., Taveras, E., Hirschfeld, S., 2021. NCS assessments of the motor, sensory, and physical health domains. Front. Pedia 9. https://doi.org/10.3389/fped.2021.622542.

Côté, M.-P., Murray, L.M., Knikou, M., 2018. Spinal control of locomotion: individual neurons, their circuits and functions. Front. Physiol. 9, 2018.

Courtine, G., Schieppati, M., 2004. Tuning of a basic coordination pattern constructs straight-ahead and curved walking in humans. J. Neurophysiol. 91, 1524–1535. https://doi.org/10.1152/jn.00817.2003.

Cowley, K.C., Schmidt, B.J., 1994. A comparison of motor patterns induced by N-methyl-d-aspartate, acetylcholine and serotonin in the in vitro neonatal rat spinal cord. Neurosci. Lett. 171, 147–150. https://doi.org/10.1016/0304-3940(94)90626-2.

Danner, S.M., Shevtsova, N.A., Frigon, A., Rybak, I.A., 2017. Computational modeling of spinal circuits controlling limb coordination and gaits in quadrupeds. Elife 6. https://doi.org/10.7554/eLife.31050.

Dedieu, P., Zanone, P.-G., 2012. Effects of gait pattern and arm swing on intergirdle coordination. Hum. Mov. Sci. 31, 660–671. https://doi.org/10.1016/j.humov.2011.07.009.

Denayer, M., Alfio, E., Díaz, M.A., Sartori, M., De Groote, F., De Pauw, K., Verstraten, T., 2025. A PRISMA systematic review through time on predictive musculoskeletal simulations. J. Neuroeng. Rehabil. 22, 149. https://doi.org/10.1186/s12984-025-01686-w.

Dewolf, A., La Scaleia, V., Fabiano, A., Sylos-Labini, F., Mondi, V., Picone, S., Di Paolo, A., Paolillo, P., Ivanenko, Y., Lacquaniti, F., 2022. Left–right locomotor coordination in human neonates. J. Neurosci. 42, 6566.

Dewolf, Arthur H., Sylos Labini, F., Ivanenko, Y., Lacquaniti, F., 2020. Development of locomotor-related movements in early infancy. Front. Cell Neurosci. 14, 623759. https://doi.org/10.3389/fncel.2020.623759.

Dewolf, Arthur Henri, Sylos-Labini, F., Cappellini, G., Lacquaniti, F., Ivanenko, Y., 2020. Emergence of different gaits in infancy: relationship between developing neural circuitries and changing biomechanics. Front. Bioeng. Biotechnol. 8. https://doi.org/10.3389/fbioe.2020.00473.

Di Russo, A., Stanev, D., Sabnis, A., Danner, S.M., Ausborn, J., Armand, S., Ijspeert, A., 2023. Investigating the roles of reflexes and central pattern generators in the control and modulation of human locomotion using a physiologically plausible neuromechanical model. J. Neural Eng. 20, 066006. https://doi.org/10.1088/1741-2552/acfdcc.

Dietz, V., Fouad, K., Bastiaanse, C.M., 2001. Neuronal coordination of arm and leg movements during human locomotion. Eur. J. Neurosci. 14, 1906–1914. https://doi.org/10.1046/j.0953-816x.2001.01813.x.

Dietz, V., Michel, J., 2009. Human Bipeds Use Quadrupedal Coordination during Locomotion. Ann. N. Y. Acad. Sci. 1164, 97–103. https://doi.org/10.1111/j.1749-6632.2008.03710.x.

Dietz, V., Zijlstra, W., Duysens, J., 1994. Human neuronal interlimb coordination during split-belt locomotion. Exp. Brain Res. 101, 513–520. https://doi.org/10.1007/BF00227344.

Dionne-Dostie, E., Paquette, N., Lassonde, M., Gallagher, A., 2015. Multisensory integration and child neurodevelopment. Brain Sci. 5, 32–57. https://doi.org/10.3390/brainsci5010032.

Disselhorst-Klug, C., Heinze, F., Breitbach-Faller, N., Schmitz-Rode, T., Rau, G., 2012. Introduction of a method for quantitative evaluation of spontaneous motor activity development with age in infants. Exp. Brain Res. 218, 305–313. https://doi.org/10.1007/s00221-012-3015-x.

Dolinskaya, I.Y., Solopova, I.A., Zhvansky, D.S., Keshishian, E.S., Ivanenko, Y., 2021. Increasing muscle activity correlations during spontaneous movements in the first six months of life. Neurosci. Lett. 756. https://doi.org/10.1016/j.neulet.2021.135957.

Domellöf, E., Rönnqvist, L., Hopkins, B., 2007. Functional asymmetries in the stepping response of the human newborn: a kinematic approach. Exp. Brain Res. 177, 324–335. https://doi.org/10.1007/s00221-006-0675-4.

Dominici, N., Ivanenko, Y.P., Cappellini, G., Zampagni, M.L., Lacquaniti, F., 2010. Kinematic strategies in newly walking toddlers stepping over different support surfaces. J. Neurophysiol. 103, 1673–1684. https://doi.org/10.1152/jn.00945.2009.

Dominici, N., Ivanenko, Y.P., Cappellini, G., d'Avella, A., Mondì, V., Cicchese, M., Fabiano, A., Silei, T., Di Paolo, A., Giannini, C., Poppele, R.E., Lacquaniti, F., 2011. Locomotor primitives in newborn babies and their development. Science 334, 997–999. https://doi.org/10.1126/science.1210617.

Donker, S.F., Beek, P.J., Wagenaar, R.C., Mulder, T., 2001. Coordination between arm and leg movements during locomotion. J. Mot. Behav. 33, 86–102. https://doi.org/10.1080/00222890109601905.

Dzeladini, F., van den Kieboom, J., Ijspeert, A., 2014. The contribution of a central pattern generator in a reflex-based neuromuscular model. Front. Hum. Neurosci. 8, 2014.

Einspieler, C., Prayer, D., Marschik, P.B., 2021. Fetal movements: the origin of human behaviour. Dev. Med. Child Neurol. 63, 1142–1148. https://doi.org/10.1111/dmcn.14918.

Fagard, J., 1998. Changes in grasping skills and the emergence of bimanual coordination during the first year of life. The Psychobiology of the Hand. Clinics in Developmental Medicine No. 147, Mac Keith Press, London NW3 5RN, England, pp. 123–143.

Forma, V., Anderson, D.I., Goffinet, F., Barbu-Roth, M., 2018. Effect of optic flows on newborn crawling. Dev. Psychobiol. 60, 497–510. https://doi.org/10.1002/dev.21634.

Forma, V., Anderson, D.I., Provasi, J., Soyez, E., Martial, M., Huet, V., Granjon, L., Goffinet, F., Barbu-Roth, M., 2019. What does prone skateboarding in the newborn tell us about the ontogeny of human locomotion? Child Dev. 90, 1286–1302. https://doi.org/10.1111/cdev.13251.

Forssberg, H., 1985. Ontogeny of human locomotor control I. Infant stepping, supported locomotion and transition to independent locomotion. Exp. Brain Res. 57, 480–493. https://doi.org/10.1007/BF00237835.

Forssberg, H., Nashner, L.M., 1982. Ontogenetic development of postural control in man: adaptation to altered support and visual conditions during stance. J. Neurosci. 2, 545–552. https://doi.org/10.1523/jneurosci.02-05-00545.1982.

Frigon, A., 2012. Central pattern generators of the mammalian spinal cord. Neuroscientist 18, 56–69. https://doi.org/10.1177/1073858410396101.

Frigon, A., 2017a. The neural control of interlimb coordination during mammalian locomotion. J. Neurophysiol. 117, 2224–2241. https://doi.org/10.1152/jn.00978.2016.

Frigon, A., 2017b. The neural control of interlimb coordination during mammalian locomotion. J. Neurophysiol. 117, 2224–2241. https://doi.org/10.1152/jn.00978.2016.
Frigon, A., Akay, T., Prilutsky, B.I., 2021. Control of mammalian locomotion by somatosensory feedback. Compr. Physiol. 12 2877–2947. https://doi.org/10.1002/cphy.c210020.
Geyer, H., Herr, H., 2010. A muscle-reflex model that encodes principles of legged mechanics produces human walking dynamics and muscle activities. IEEE Trans. Neural Syst. Rehabil. Eng. 18, 263–273. https://doi.org/10.1109/TNSRE.2010.2047592.
Gonçalves, A.I., Zavatone-Veth, J.A., Carey, M.R., Clark, D.A., 2021. Parallel locomotor control strategies in mice and flies. arXiv:2112.12227 [q-bio].
Gosgnach, S., 2023. Spinal inhibitory interneurons: regulators of coordination during locomotor activity. Front. Neural Circuits 17, 2023.
Gosgnach, S., 2025. The mammalian locomotor CPG: revealing the contents of the black box. J. Neurophysiol. 133, 472–478. https://doi.org/10.1152/jn.00238.2024.
Goulding, M., 2009. Circuits controlling vertebrate locomotion: moving in a new direction. Nat. Rev. Neurosci. 10, 507–518. https://doi.org/10.1038/nrn2608.
Grillner, S., El Manira, A., 2020. Current principles of motor control, with special reference to vertebrate locomotion. Physiol. Rev. 100, 271–320. https://doi.org/10.1152/physrev.00015.2019.
Grillner, S., Zangger, P., 1979. On the central generation of locomotion in the low spinal cat. Exp. Brain Res. 34, 241–261. https://doi.org/10.1007/BF00235671.
Guertin, P.A., 2009. The mammalian central pattern generator for locomotion. Brain Res. Rev. 62, 45–56. https://doi.org/10.1016/j.brainresrev.2009.08.002.
Hadders-Algra, M., 2010. Variation and variability: key words in human motor development. Phys. Ther. 90, 1823–1837. https://doi.org/10.2522/ptj.20100006.
Hägglund, M., Dougherty, K.J., Borgius, L., Itohara, S., Iwasato, T., Kiehn, O., 2013. Optogenetic dissection reveals multiple rhythmogenic modules underlying locomotion. Proc. Natl. Acad. Sci. USA 110, 11589–11594. https://doi.org/10.1073/pnas.1304365110.
Hamburger, V., 1973. Anatomical and physiological basis of embryonic motility in birds and mammals. In: Gottlieb, G. (Ed.), Studies on the Development of Behavior and the Nervous System, Behavioral Embryology. Elsevier, pp. 51–76. https://doi.org/10.1016/B978-0-12-609301-8.50009-X.
Hinnekens, E., Berret, B., Morard, E., Do, M.-C., Barbu-Roth, M., Teulier, C., 2024. Optimization of modularity during development to simplify walking control across multiple steps. Front. Neural Circuits 17. https://doi.org/10.3389/fncir.2023.1340298.
Hiraoka, K., 2021. Phase-dependent crossed inhibition mediating coordination of anti-phase bilateral rhythmic movement: a mini review. Front. Hum. Neurosci. 15. https://doi.org/10.3389/fnhum.2021.668442.
Hiraoka, K., Chujyo, Y., Hatano, S., Fukuhara, K., Yamanaka, Y., 2014. Effects of contralateral movement on the soleus H-reflex during in-phase and antiphase movements of the ankles. Mot. Control 18, 88–100. https://doi.org/10.1123/mc.2013-0029.
Hym, C., Dumuids, M.-V., Anderson, D.I., Forma, V., Provasi, J., Brière-Dollat, C., Granjon, L., Gervain, J., Nazzi, T., Barbu-Roth, M., 2023. Newborns modulate their crawling in response to their native language but not another language. Dev. Sci. 26, e13248. https://doi.org/10.1111/desc.13248.
Hym, C., Forma, V., Anderson, D.I., Provasi, J., Granjon, L., Huet, V., Carpe, E., Teulier, C., Durand, K., Schaal, B., Barbu-Roth, M., 2020. Newborn crawling and rooting in response to maternal breast odor. Dev. Sci., e13061 https://doi.org/10.1111/desc.13061.
Ijspeert, A.J., Daley, M.A., 2023a. Integration of feedforward and feedback control in the neuromechanics of vertebrate locomotion: a review of experimental, simulation and robotic studies. J. Exp. Biol. 226, jeb245784. https://doi.org/10.1242/jeb.245784.
Ijspeert, A.J., Daley, M.A., 2023b. Integration of feedforward and feedback control in the neuromechanics of vertebrate locomotion: a review of experimental, simulation and robotic studies. J. Exp. Biol. 226, jeb245784. https://doi.org/10.1242/jeb.245784.
Ivanenko, Y.P., Dominici, N., Cappellini, G., Di Paolo, A., Giannini, C., Poppele, R.E., Lacquaniti, F., 2013. Changes in the spinal segmental motor output for stepping during development from infant to adult. J. Neurosci. 33, 3025–3036a.
Ivanenko, Y.P., Grasso, R., Zago, M., Molinari, M., Scivoletto, G., Castellano, V., Macellari, V., Lacquaniti, F., 2003. Temporal components of the motor patterns expressed by the human spinal cord reflect foot kinematics. J. Neurophysiol. 90, 3555–3565. https://doi.org/10.1152/jn.00223.2003.
Johnston, D.W., Nicholls, M.E.R., Shah, M., Shields, M.A., 2013. Handedness, health and cognitive development: evidence from children in the National Longitudinal Survey of Youth. J. R. Stat. Soc. 176, 841–860 (Series A (Statistics in Society)).
Juvin, L., Gal, J.-P.L., Simmers, J., Morin, D., 2012. Cervicolumbar coordination in mammalian quadrupedal locomotion: role of spinal thoracic circuitry and limb sensory inputs. J. Neurosci. 32, 953–965. https://doi.org/10.1523/JNEUROSCI.4640-11.2012.
Kanazawa, H., Yamada, Y., Tanaka, K., Kawai, M., Niwa, F., Iwanaga, K., Kuniyoshi, Y., 2023. Open-ended movements structure sensorimotor information in early human development. Proc. Natl. Acad. Sci. 120, e2209953120. https://doi.org/10.1073/pnas.2209953120.
Kanemaru, N., Watanabe, H., Taga, G., 2012. Increasing selectivity of interlimb coordination during spontaneous movements in 2- to 4-month-old infants. Exp. Brain Res. 218, 49–61. https://doi.org/10.1007/s00221-012-3001-3.
Kiehn, O., 2016. Decoding the organization of spinal circuits that control locomotion. Nat. Rev. Neurosci. 17, 224–238. https://doi.org/10.1038/nrn.2016.9.
Kjaerulff, O., Kiehn, O., 1996. Distribution of networks generating and coordinating locomotor activity in the neonatal rat spinal cord In vitro: a lesion study. J. Neurosci. 16, 5777–5794. https://doi.org/10.1523/jneurosci.16-18-05777.1996.
Kleven, G.A., Lane, M.S., Robinson, S.R., 2004. Development of interlimb movement synchrony in the rat fetus. Behav. Neurosci. 118, 835–844. https://doi.org/10.1037/0735-7044.118.4.835.
Klishko, A.N., Harnie, J., Hanson, C.E., Rahmati, S.M., Rybak, I.A., Frigon, A., Prilutsky, B.I., 2024. EFFECTS OF SPINAL TRANSECTION AND LOCOMOTOR SPEED ON MUSCLE SYNERGIES OF THE CAT HINDLIMB. bioRxiv 2024.09.19.613891. https://doi.org/10.1101/2024.09.19.613891.
Koster, R.A.J., Zandvoort, C.S., Kerkman, J.N., Daffertshofer, A., Dominici, N., 2025. Exploring the cortical involvement in sensorimotor integration during early stages of independent walking. Exp. Brain Res. 243, 153. https://doi.org/10.1007/s00221-025-07099-4.
La Scaleia, V., Ivanenko, Y., Fabiano, A., Sylos-Labini, F., Cappellini, G., Picone, S., Paolillo, P., Di Paolo, A., Lacquaniti, F., 2018. Early manifestation of arm-leg coordination during stepping on a surface in human neonates. Exp. Brain Res. 236, 1105–1115. https://doi.org/10.1007/s00221-018-5201-y.
Lafreniere-Roula, M., McCrea, D.A., 2005. Deletions of rhythmic motoneuron activity during fictive locomotion and scratch provide clues to the organization of the mammalian central pattern generator. J. Neurophysiol. 94, 1120–1132. https://doi.org/10.1152/jn.00216.2005.
Lamb, T., Yang, J.F., 2000. Could different directions of infant stepping be controlled by the same locomotor central pattern generator? J. Neurophysiol. 83, 2814–2824. https://doi.org/10.1152/jn.2000.83.5.2814.
Ledebt, A., 2000. Changes in arm posture during the early acquisition of walking. Infant Behav. Dev. 23, 79–89. https://doi.org/10.1016/S0163-6383(00)00027-8.
Lin, J., Ha, S.C.W., Zhang-Lea, J.H., Chan, Z.Y.S., Fang, K., Guo, X., He, B., Lau, K.Y.S., Chan, R.H.M., Cheung, R.T.H., Chen, C.-Y., Cheung, V.C.K., 2025. Functional symmetrization of neuromotor modules during locomotor development in human infants. Commun. Biol. 8, 1782. https://doi.org/10.1038/s42003-025-09198-y.
MacLellan, M.J., Ivanenko, Y.P., Catavitello, G., La Scaleia, V., Lacquaniti, F., 2013. Coupling of upper and lower limb pattern generators during human crawling at different arm/leg speed combinations. Exp. Brain Res. 225, 217–225. https://doi.org/10.1007/s00221-012-3364-5.
Maxwell, D.J., Soteropoulos, D.S., 2020. The mammalian spinal commissural system: properties and functions. J. Neurophysiol. 123, 4–21. https://doi.org/10.1152/jn.00347.2019.
McCrea, D.A., Rybak, I.A., 2008. Organization of mammalian locomotor rhythm and pattern generation. Brain Res Rev. 57, 134–146. https://doi.org/10.1016/j.brainresrev.2007.08.006.
McGraw, M.B., 1939. Swimming behavior of the human infant. J. Pediatr. 15, 485–490. https://doi.org/10.1016/S0022-3476(39)80003-8.
McGraw, M.B., 1940. Neuromuscular development of the human infant as exemplified in the achievement of erect locomotion. J. Pediatr. 17, 747–771. https://doi.org/10.1016/S0022-3476(40)80021-8.
Meehan, C.F., Mayr, K.A., Manuel, M., Nakanishi, S.T., Whelan, P.J., 2017. Decerebrate mouse model for studies of the spinal cord circuits. Nat. Protoc. 12, 732–747. https://doi.org/10.1038/nprot.2017.001.
Mesquita, R.M., Willems, P.A., Dewolf, A.H., Catavitello, G., 2024. Kinetics and mechanical work done to move the body centre of mass along a curve. PLoS One 19, e0298790. https://doi.org/10.1371/journal.pone.0298790.
Meyns, P., Bruijn, S.M., Duysens, J., 2013. The how and why of arm swing during human walking. Gait Posture 38, 555–562. https://doi.org/10.1016/j.gaitpost.2013.02.006.
Miller, S., Van der Burg, J., Van der Meché, F.G.A., 1975. Coordination of movements of the hindlimbs and forelimbs in different forms of locomotion in normal and decerebrate cats. Brain Res. 91, 217–237. https://doi.org/10.1016/0006-8993(75)90544-2.
Minetti, A.E., 1998. The biomechanics of skipping gaits: a third locomotion paradigm? Proc. R. Soc. Lond. Ser. B Biol. Sci. 265, 1227–1233. https://doi.org/10.1098/rspb.1998.0424.
Molkov, Y.I., Yu, G., Ausborn, J., Bouvier, J., Danner, S.M., Rybak, I.A., 2024. Sensory feedback and central neuronal interactions in mouse locomotion. R. Soc. Open Sci. 11, 240207. https://doi.org/10.1098/rsos.240207.
Mortin, L.I., Stein, P.S.G., 1989. Spinal cord segments containing key elements of the central pattern generators for three forms of scratch reflex in the turtle. J. Neurosci. 9, 2285–2296. https://doi.org/10.1523/jneurosci.09-07-02285.1989.
Moulson, M.C., Nelson, C.A., 2008. Neurological development. Encyclopedia of Infant and Early Childhood Development. Elsevier, pp. 414–424. https://doi.org/10.1016/B978-012370877-9.00109-2.
Musselman, K.E., Yang, J.F., 2008. Interlimb coordination in rhythmic leg movements: spontaneous and training-induced manifestations in human infants. J. Neurophysiol. 100, 2225–2234. https://doi.org/10.1152/jn.90532.2008.
Nuñez-Lisboa, M., Bastien, G.J., Schepens, B., Lacquaniti, F., Ivanenko, Y., Dewolf, A.H., 2023. Effect of age and speed on the step-to-step transition strategies in children. J. Biomech. 157, 111704. https://doi.org/10.1016/j.jbiomech.2023.111704.
Nùñez-Lisboa, M., Valero-Breton, M., Dewolf, A.H., 2023. Unraveling age-related impairment of the neuromuscular system: exploring biomechanical and neurophysiological perspectives. Front Physiol. 14, 1194889. https://doi.org/10.3389/fphys.2023.1194889.
Ossmy, O., Adolph, K.E., 2020. Real-time assembly of coordination patterns in human infants. Curr. Biol. 30, 4553–4562.e4. https://doi.org/10.1016/j.cub.2020.08.073.
Pang, M.Y.C., Yang, J.F., 2001. Interlimb co-ordination in human infant stepping. J. Physiol. 533, 617–625. https://doi.org/10.1111/j.1469-7793.2001.0617a.x.
Patrick, S.K., Noah, J.A., Yang, J.F., 2012. Developmental constraints of quadrupedal coordination across crawling styles in human infants. J. Neurophysiol. 107, 3050–3061. https://doi.org/10.1152/jn.00029.2012.

Pearson, K.G., Rossignol, S., 1991. Fictive motor patterns in chronic spinal cats. J. Neurophysiol. 66, 1874–1887. https://doi.org/10.1152/jn.1991.66.6.1874.

Picton, L., Pallucchi, I., Fontanel, P., Bertuzzi, M., Song, J., El Manira, A., 2025. Circuit Modules for Flexible Locomotion. Annu. Rev. Neurosci. https://doi.org/10.1146/annurev-neuro-112723-061241.

Piek, J.P., 2002. The role of variability in early motor development. Infant Behav. Dev. 25, 452–465. https://doi.org/10.1016/S0163-6383(02)00145-5.

Pontzer, H., Holloway IV, J.H., Raichlen, D.A., Lieberman, D.E., 2009. Control and function of arm swing in human walking and running (Journal of Experimental Biology 212 (523-534)). J. Exp. Biol. 212, 894. https://doi.org/10.1242/jeb.030478.

Prokop, T., Berger, W., Zijlstra, W., Dietz, V., 1995. Adaptational and learning processes during human split-belt locomotion: interaction between central mechanisms and afferent input. Exp. Brain Res. 106, 449–456. https://doi.org/10.1007/BF00231067.

Robinson, S.R., Smotherman, W.P., 1987. Environmental determinants of behaviour in the rat fetus. II. The emergence of synchronous movement. Anim. Behav. 35, 1652–1662. https://doi.org/10.1016/S0003-3472(87)80058-1.

Shinohara, K., Ambe, Y., Kim, Y., Mano, F., Ramalingasetty, S.T., Lockhart, A.B., Markin, S.N., Ausborn, J., Rybak, I.A., Danner, S.M., Aoi, S., 2025. Mechanisms of adaptive interlimb coordination to sudden ground loss: a neuromusculoskeletal modeling study. bioRxiv 2025.11.11.687930. https://doi.org/10.1101/2025.11.11.687930.

Siekerman, K., Barbu-Roth, M., Anderson, D.I., Donnelly, A., Goffinet, F., Teulier, C., 2015. Treadmill stimulation improves newborn stepping. Dev. Psychobiol. 57, 247–254. https://doi.org/10.1002/dev.21270.

Solopova, I.A., Selionov, V.A., Blinov, E.O., Zhvansky, D.S., Ivanenko, Y.P., 2017. Rhythmic wrist movements facilitate the soleus H-reflex and non-voluntary air-stepping in humans. Neurosci. Lett. 638, 39–45. https://doi.org/10.1016/j.neulet.2016.12.007.

Solopova, I.A., Zhvansky, D.S., Dolinskaya, I.Y., Keshishian, E.S., Selionov, V.A., Sylos-Labini, F., Lacquaniti, F., Ivanenko, Y., 2019. Muscle responses to passive joint movements in infants during the first year of life. Front Physiol. 10, 1158. https://doi.org/10.3389/fphys.2019.01158.

Stein, P.S., McCullough, M.L., 1998. Example of 2:1 interlimb coordination during fictive rostral scratching in a spinal turtle. J. Neurophysiol. 79, 1132–1134. https://doi.org/10.1152/jn.1998.79.2.1132.

Stergiou, N., Decker, L.M., 2011. Human movement variability, nonlinear dynamics, and pathology: is there a connection? Hum. Mov. Sci. 30, 869–888. https://doi.org/10.1016/j.humov.2011.06.002.

Stergiou, N., Harbourne, R., Cavanaugh, J., 2006. Optimal movement variability: a new theoretical perspective for neurologic physical therapy. J. Neurol. Phys. Ther. 30, 120–129. https://doi.org/10.1097/01.npt.0000281949.48193.d9.

Sylos-Labini, F., Ivanenko, Y.P., MacLellan, M.J., Cappellini, G., Poppele, R.E., Lacquaniti, F., 2014. Locomotor-like leg movements evoked by rhythmic arm movements in humans. PLoS One 9, e90775. https://doi.org/10.1371/journal.pone.0090775.

Sylos-Labini, F., La Scaleia, V., Cappellini, G., Fabiano, A., Picone, S., Keshishian, E.S., Zhvansky, D.S., Paolillo, P., Solopova, I.A., d'Avella, A., Ivanenko, Y., Lacquaniti, F., 2020. Distinct locomotor precursors in newborn babies. Proc. Natl. Acad. Sci. 117, 9604–9612. https://doi.org/10.1073/pnas.1920984117.

Sylos-Labini, F., La Scaleia, V., Cappellini, G., Dewolf, A., Fabiano, A., Solopova, I.A., Mondì, V., Ivanenko, Y., Lacquaniti, F., 2022. Complexity of modular neuromuscular control increases and variability decreases during human locomotor development. Commun. Biol. 5, 1256. https://doi.org/10.1038/s42003-022-04225-8.

Sylos-Labini, F., Magnani, S., Cappellini, G., La Scaleia, V., Fabiano, A., Picone, S., Paolillo, P., Di Paolo, A., Lacquaniti, F., Ivanenko, Y., 2017. Foot placement characteristics and plantar pressure distribution patterns during stepping on ground in neonates. Front. Physiol. 8. https://doi.org/10.3389/fphys.2017.00784.

Taga, G., 1995. A model of the neuro-musculo-skeletal system for human locomotion. Biol. Cybern. 73, 113–121. https://doi.org/10.1007/BF00204049.

Teulier, C., Sansom, J.K., Muraszko, K., Ulrich, B.D., 2012. Longitudinal changes in muscle activity during infants' treadmill stepping. J. Neurophysiol. 108, 853–862. https://doi.org/10.1152/jn.01037.2011.

Thelen, E., Fisher, D.M., 1982. Newborn stepping: an explanation for a "disappearing" reflex. Dev. Psychol. 18, 760–775. https://doi.org/10.1037/0012-1649.18.5.760.

Thelen, E., Fisher, D.M., Ridley-Johnson, R., Griffin, N.J., 1982. Effects of body build and arousal on newborn infant stepping. Dev. Psychobiol. 15, 447–453. https://doi.org/10.1002/dev.420150506.

Thelen, E., Smith, L.B., 1994. A Dynamic Systems Approach to the Development of Cognition and Action, A Dynamic Systems Approach to the Development of Cognition and Action. The MIT Press, Cambridge, MA, US.

Ting, L.H., Raasch, C.C., Brown, D.A., Kautz, S.A., Zajac, F.E., 1998. Sensorimotor state of the contralateral leg affects ipsilateral muscle coordination of pedaling. J. Neurophysiol. 80, 1341–1351. https://doi.org/10.1152/jn.1998.80.3.1341.

Van de Walle, P., Meyns, P., Desloovere, K., De Rijck, J., Kenis, J., Verbecque, E., Van Criekinge, T., Hallemans, A., 2018. Age-related changes in arm motion during typical gait. Gait Posture 66, 51–57. https://doi.org/10.1016/j.gaitpost.2018.07.176.

Van der Noot, N., Ijspeert, A.J., Ronsse, R., 2018. Bio-inspired controller achieving forward speed modulation with a 3D bipedal walker. Int. J. Robot. Res. 37, 168–196. https://doi.org/10.1177/0278364917743320.

Verbecque, E., Vereeck, L., Hallemans, A., 2016. Postural sway in children: a literature review. Gait Posture 49, 402–410. https://doi.org/10.1016/j.gaitpost.2016.08.003.

Wannier, T., Bastiaanse, C., Colombo, G., Dietz, V., 2001. Arm to leg coordination in humans during walking, creeping and swimming activities. Exp. Brain Res. 141, 375–379. https://doi.org/10.1007/s002210100875.

Whelan, P., Bonnot, A., O'Donovan, M.J., 2000. Properties of rhythmic activity generated by the isolated spinal cord of the neonatal mouse. J. Neurophysiol. 84, 2821–2833. https://doi.org/10.1152/jn.2000.84.6.2821.

Yang, J.F., Lamont, E.V., Pang, M.Y.C., 2005. Split-belt treadmill stepping in infants suggests autonomous pattern generators for the left and right leg in humans. J. Neurosci. 25, 6869–6876. https://doi.org/10.1523/JNEUROSCI.1765-05.2005.

Yang, J.F., Mitton, M., Musselman, K.E., Patrick, S.K., Tajino, J., 2015. Characteristics of the developing human locomotor system: Similarities to other mammals. Dev. Psychobiol. 57, 397–408. https://doi.org/10.1002/dev.21289.

Yang, J.F., Stephens, M.J., Vishram, R., 1998. Infant stepping: a method to study the sensory control of human walking. J. Physiol. 507, 927–937. https://doi.org/10.1111/j.1469-7793.1998.927bs.x.

Zandvoort, C.S., Daffertshofer, A., Dominici, N., 2022. Cortical contributions to locomotor primitives in toddlers and adults. iScience 25, 105229. https://doi.org/10.1016/j.isci.2022.105229.

Zanone, P.G., Kelso, J.A., 1997. Coordination dynamics of learning and transfer: collective and component levels. J. Exp. Psychol. Hum. Percept. Perform. 23, 1454–1480. https://doi.org/10.1037//0096-1523.23.5.1454.

Zehr, E.P., Duysens, J., 2004. Regulation of arm and leg movement during human locomotion. Neuroscientist 10, 347–361. https://doi.org/10.1177/1073858404264680.