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Theories of bipedal walking: an odyssey[☆]

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Abstract

In this paper six theories of bipedal walking, and the evidence in support of the theories, are reviewed. They include: evolution, minimising energy consumption, maturation in children, central pattern generators, linking control and effect, and robots on two legs. Specifically, the six theories posit that: (1) bipedalism is the fundamental evolutionary adaptation that sets hominids—and therefore humans—apart from other primates; (2) locomotion is the translation of the centre of gravity along a pathway requiring the least expenditure of energy; (3) when a young child takes its first few halting steps, his or her biomechanical strategy is to minimise the risk of falling; (4) a dedicated network of interneurons in the spinal cord generates the rhythm and cyclic pattern of electromyographic signals that give rise to bipedal gait; (5) bipedal locomotion is generated through global entrainment of the neural system on the one hand, and the musculoskeletal system plus environment on the other; and (6) powered dynamic gait in a bipedal robot can be realised only through a strategy which is based on stability and real-time feedback control. The published record suggests that each of the theories has some measure of support. However, it is important to note that there are other important theories of locomotion which have not been covered in this review. Despite such omissions, this odyssey has explored the wide spectrum of bipedal walking, from its origins through to the integration of the nervous, muscular and skeletal systems.

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1. Introduction

Upright bipedal walking is an important hallmark of the human condition. Despite a highly complex neural control system, human gait is characterised by smooth, regular and repeating movements. The sequence of events that takes place for walking to occur may be summarised as follows: registration and activation of the gait command within the central nervous system; transmission of the gait signals to the peripheral nervous system; contraction of muscles that develop tension; generation of forces at, and moments across, synovial joints; regulation of the joint forces and moments by the rigid skeletal segments based on their anthropometry; movement of the segments in a manner that is recognised as functional gait; and generation of ground

reaction forces (Vaughan et al., 1999). In parallel with this temporal cascade of events—which are based on cause and effect—the sensory feedback system provides real-time information that influences the gait pattern. Despite there being well in excess of 7000 published references on the biomechanics of human gait (Vaughan, 1999), only a handful of papers have considered the underlying *theories* of bipedal walking. The purpose of this review paper, this odyssey, is to consider six theories of bipedal walking and to explore the evidence in support of the theories.

2. Evolution

Bipedalism is the fundamental evolutionary adaptation that sets hominids—and therefore humans—apart from other primates

It was the Roman historian Pliny the Elder who in 75 AD is reputed to have said “Ex Africa semper aliquid novi” which means “Always something new out of Africa”. While he was most probably referring to the

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strange and unusual animals brought from the dark continent, he could not have known that his own ancestors had walked out of the Rift Valley in Africa over 200,000 years BC (Lewin, 1993). This area, commonly referred to as the Cradle of Humankind, was the scene of some extraordinary archaeological discoveries during the 20th century.

Perhaps the most remarkable of these discoveries occurred in 1976 when Mary Leakey exposed the fossilised footprints of human ancestors in Laetoli, East Africa (Leakey and Hay, 1979). The footprints were formed 3.7 million years ago by at least two hominids walking side-by-side over wet volcanic ash (cf. Fig. 1). These trails show that one hominid was larger than the other but, despite the difference in their size, their gaits appeared to be in phase, suggesting that they may even have been walking arm in arm. A careful 3D photogrammetric analysis of the footprints revealed that there was probably a third hominid who followed in the larger of the two sets of prints (Rüther, 1996). The age of these footprints proved that bipedalism existed at least a million years before stone tools and the development of a large brain, thus settling one of the major issues of contention in palaeoanthropology (Leakey and Walker, 1997).

While the footprints at Laetoli provided incontrovertible evidence for the existence of bipedalism in human ancestors, they did not answer the fundamental question of *why* or *how* this form of locomotion evolved. One strategy that has been employed to seek an answer to these questions has been to study the bipedal gait of

non-human primates (Prost, 1980). Tardieu et al. (1993) compared the gaits of a 9-year-old chimpanzee and a 3-year-old child. They hypothesised that one of the necessary changes during the evolution of human bipedalism would be the progressive reduction in the displacement of the whole body centre of gravity. Utilising 3D volumetric measurements of the body segments, based on finite element modelling, they concluded that the trajectory of a human's mass centre was distinguished from that of the chimpanzee not by a lower movement amplitude but by phasic synchronisation of the transverse and vertical displacements. Using cine-radiography, Jenkins (1972) showed that bipedal chimpanzees walk with a femur that is more abducted and flexed than humans. The adducted angulation of the femur allows both humans and *Australopithecus africanus* (an early hominid, with "Lucy" having the most complete record of locomotor morphology) to place the feet directly beneath the whole body centre of gravity, providing a smoother, more efficient gait (Jenkins, 1972; Lewin, 1993).

While there have been studies based on energetic analysis (Rodman and McHenry, 1980; Steudel, 1996) as well as neural control (Dunbar et al., 1986) to try and understand the evolution of bipedalism, one of the most biomechanically insightful approaches has been reported by Crompton et al. (1998). Using the bones of Lucy in a detailed computer simulation, they showed that erect gait (bent-hip and bent-knee) was unlikely to have evolved because of the extra energy required (cf. Fig. 2). Whatever the reasons, it is clear that

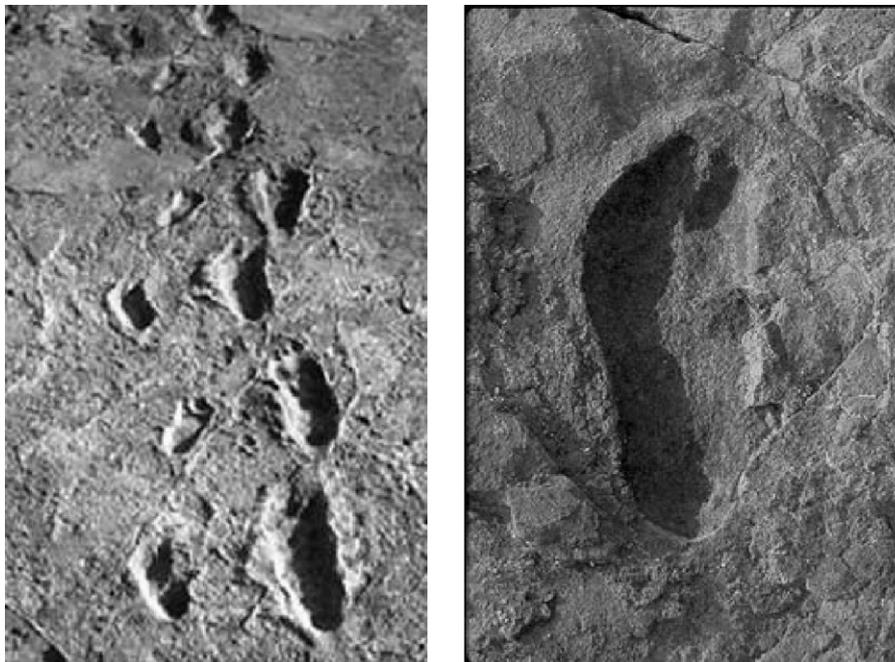


Fig. 1. Fossilised footprints at Laetoli in Tanzania, made 3.7 million years ago by bipedal hominids (Leakey and Hay, 1979). Photographs reproduced by permission of WGBH Boston and John Reader.

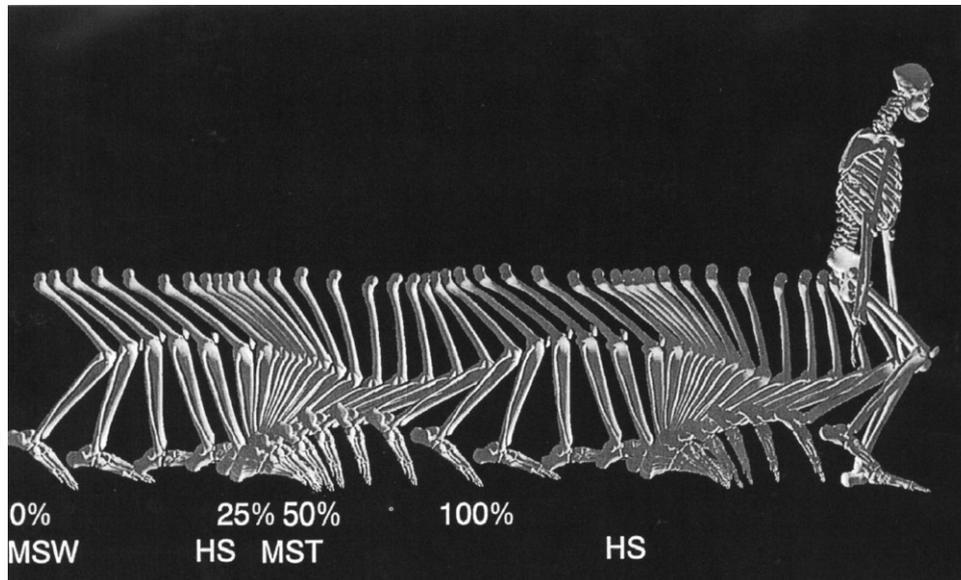


Fig. 2. Computer-simulated animation of “bent-hip bent-knee” walking by an early hominid *Australopithecus aferensis*, a form of gait requiring extra energy (Crompton et al., 1998). Note that MSW = mid-swing; HS = heel strike; and MST = mid-stance, the different phases of the gait cycle.

knuckle-walking African apes and humans share a common ancestor, with bipedalism being a specialised evolutionary adaptation (Lewin, 1993; Richmond and Strait, 2000).

3. Minimising energy consumption

Locomotion is the translation of the centre of gravity along a pathway requiring the least expenditure of energy

The celebrated Irish playwright George Bernard Shaw commented that “There are only two qualities in the world: efficiency and inefficiency, and only two sorts of people: the efficient and the inefficient” (Shaw, 1904). This comment resonates with Fig. 1 in Saunders et al. (1953) where a young boy, holding a piece of chalk against his body at approximately the level of his centre of gravity, scribbles a smooth wavy line on a plate glass window as he walks parallel to it. It was this group from San Francisco which proposed the theory of minimising energy consumption. They started with the concept that human walking could be represented, in a minimal configuration, by a pelvis and two stiff legs that allowed only flexion and extension at the hip joints, a so-called “compass gait”. This model obviously produced a jerky, undulating gait. The subsequent addition of six determinants—pelvic rotation, pelvic tilt, knee flexion during stance, knee and ankle interactions, and lateral displacement of the pelvis—converted this gait into a smooth sinusoidal pattern (Saunders et al., 1953). They postulated that the pathological loss of two or more of

these determinants would lead to a threefold increase in energy consumption.

The biomechanics group at the University of California (San Francisco and Berkeley) did further pioneering work in which they explored the relationship between the basic variables of walking: step length, step rate, and metabolic energy expenditure (Ralston, 1958; Zarrugh et al., 1974). They demonstrated that individuals select a walking speed—the product of step length and step rate—so as to minimise the metabolic energy expended per unit distance travelled. Joint torques, which provide a measure of muscle activity and thus energy consumption, can in the absence of large inertial contributions be estimated as the vector product of the ground reaction force and the moment arm to the joint centre (Vaughan, 1996). As illustrated in Fig. 3, the line of action of the ground reaction force passes close to the ankle, knee and hip joints of the stance limb, thus minimising the joint torques (Alexander, 1992).

The theory of the six determinants by Saunders et al. (1953), which was based on a simple kinematic argument, had a certain logical appeal and has been repeated, almost as proven fact, in subsequent publications (Inman et al., 1981; Vaughan and Sussman, 1993). However, about 15 years ago Pandy and Berme (1988, 1989) began to test the theory, utilising computer simulation techniques, and most recently Anderson and Pandy (2001a, b) have built a remarkable model of bipedal gait based on dynamic optimisation. The human body was modelled as a 10-segment, 23 degree of freedom 3D linkage driven by 54 muscle actuators. The optimisation problem was to solve for the control variables—the muscle excitation patterns—subject to

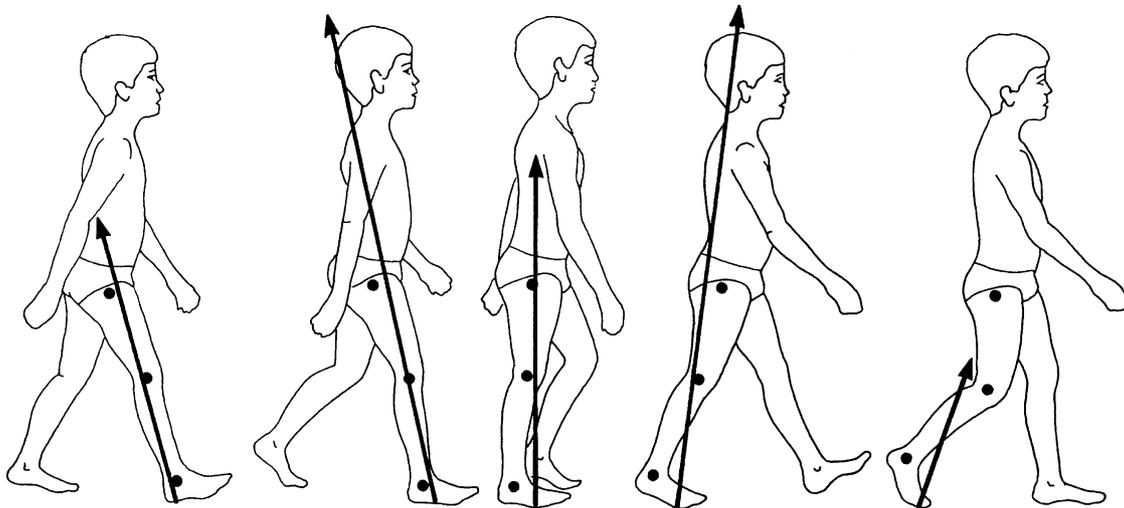


Fig. 3. The ground reaction force (GRF) vector plotted with respect to the hip, knee and ankle joints (Vaughan, 1996). The joint torques (or moments), estimated as the cross product of the force and the lever arms, are minimised because the GRF passes close to the joint centres (Alexander, 1992).

the constraint equations (which were generalised displacements and velocities plus dynamic equations for the skeletal and muscle forces) in order to minimise the cost function which was the total metabolic energy consumed divided by the displacement of the centre of gravity during one gait cycle. Without any a priori knowledge the model predicted joint torques and muscle activation patterns in good agreement with experimental data (cf. Fig. 4).

4. Maturation in children

When a young child takes its first few halting steps, his or her biomechanical strategy is to minimise the risk of falling

This theory is perhaps best encapsulated in the rhyme by children's author AA Milne: "Whenever I walk in a London street, I'm ever so careful to watch my feet" (Milne, 1924). The speaker was Milne's son Christopher Robin who was determined to step on the squares lest he incur the wrath of the imaginary bears. The whimsy of children's poetry leads to the question: what are the scientific factors that contribute to the development of a mature gait pattern in children?

It is generally accepted that an infant will acquire the ability to sit independently at approximately 6 months, to walk without support between a year and 15 months, and to run at 18 months (Sutherland et al., 1980). During this crucial period, and for the subsequent few years, the child's central nervous system (CNS) will mature in parallel with musculoskeletal growth. These two factors—CNS maturation and musculoskeletal growth—will influence the child's characteristic gait pattern (Vaughan et al., 1997).

As the child grows older, the primary gait variables will change: the width of the walking base gradually diminishes, reciprocal arm-swinging becomes apparent, cadence decreases, while step length, walking velocity and single-limb stance all increase (Beck et al., 1981; Preis et al., 1997; Sutherland et al., 1980; Wheelwright et al., 1993). These changes beg the question: how much of the change can be attributed to CNS maturation and how much to growth of the muscles and long bones? By rendering the gait parameters dimensionless, it should be possible to factor out the effects of growth. Any residual differences that exist, say between 5- and 12-year olds, can then be attributed to CNS maturation alone (Vaughan et al., 1997).

Various methods for scaling (or normalising) children's gait parameters have been proposed, including statistical detrending (O'Malley, 1996) and division by body height (Beck et al., 1981). Hof (1996) has proposed a method that renders *all* parameters dimensionless. His method is based on the simple assumption that taller people tend to walk with longer steps and lower step rates than shorter people, while heavier individuals will exert greater forces and moments than those who are lighter (Hof and Zijlstra, 1997). We have applied this scaling method to a cohort of 204 children aged between 14 and 169 months (1–14 years) and concentrated on four fundamental gait parameters: step length, cadence, step width and single-limb stance time (Langerak et al., 2001; Vaughan et al., 2001). These scaled (dimensionless) parameters change between 14 and 60 months but are invariant after 80 months of age (cf. Fig. 5). Scaled step length, cadence and single-limb stance time all increase, while step width decreases, suggesting that the child becomes more confident—and therefore willing to take more risks—as the CNS matures. These data provide support for a *risk aversion hypothesis*, in which

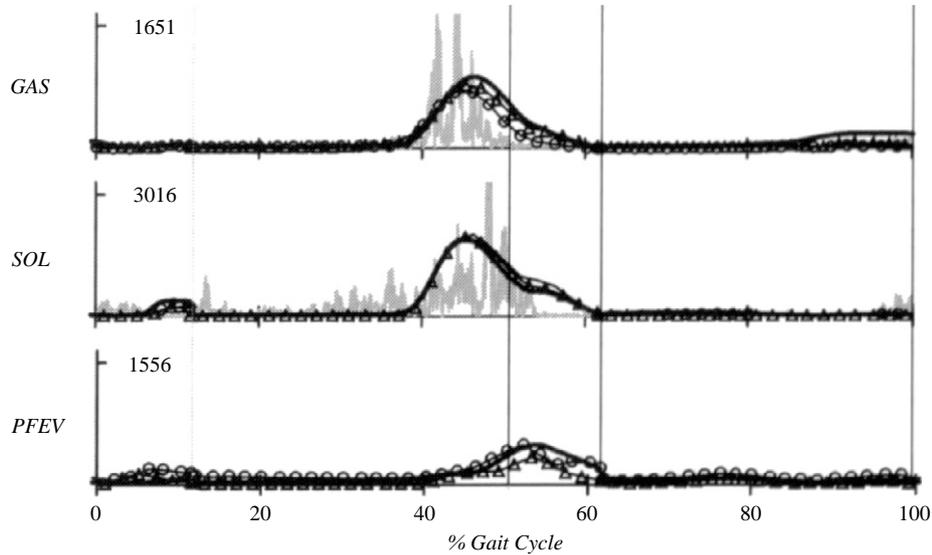


Fig. 4. Forces generated by muscles crossing the ankle joint are derived by optimisation theory (minimum energy consumption) and compared to actual electromyographic activity (Anderson and Pandy, 2001a). Note that the vertical scale is in Newton while GAS = gastrocnemius, SOL = soleus, and PFEV = peroneus brevis and longus.

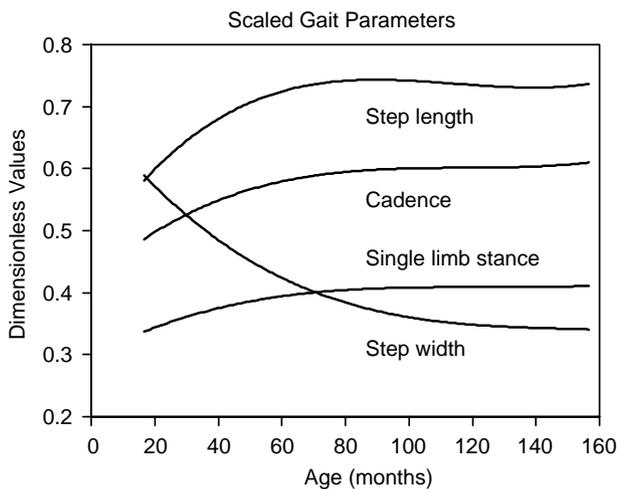


Fig. 5. Fundamental gait parameters, scaled according to Hof (1996), change during the first 6 years (72 months) of life and are thereafter invariant with age (Vaughan et al., 2001).

the young infant seeks to minimise the risk of falling by maintaining a shorter step length, lower cadence, wider step width and lower single-limb stance time (cf. Fig. 6).

5. Central pattern generators

A dedicated network of interneurons in the spinal cord generates the rhythm and cyclic pattern of electromyographic signals that give rise to bipedal gait

Francis Crick, who in 1962 shared the Nobel Prize for co-discovering the structure of deoxyribonucleic acid (DNA) and subsequently turned his attention to neuroscience, said “I myself find it difficult at times to

avoid the idea of the homunculus—a little man directing it all. As Lewis Carroll’s *Alice* might have phrased it, you’re nothing but a pack of neurons” (Voll, 1994). In the context of human locomotion, this statement conjures up the image of the little man, illustrated in Fig. 1.9 on page 11 of the book by Inman et al. (1981), controlling the actions of the tibialis anterior and triceps surae muscles during the stance phase of the gait cycle.

Beginning with the pioneering research on mammalian walking almost a century ago by Brown (1911), it has become increasingly evident that rhythmic movements such as locomotion are generated by neuronal circuits that, in the isolated CNS, can generate neural activity patterns which closely resemble those observed in nearly intact animals (Delcomyn, 1980). Grillner (1985) suggested that there are a number of neuronal modules, which he referred to as central pattern generators (CPGs), that can be made to produce a rhythmic output. He further speculated on the unit CPG hypothesis, suggesting a versatile motor organisation able to combine different components in a variety of ways. Although detailed circuits that underlie vertebrate locomotion are now available for larval frogs and the lamprey (Vaughan et al., 1996), is there evidence to prove that CPGs exist in humans?

In a review of gait after spinal cord injury (SCI), Pinter and Dimitrijevic (1999) have provided two examples for the existence of the CPG in humans. In the case of incomplete SCI, the human lumbar cord isolated from brain influence can be trained to respond with rhythmic, locomotor-like EMG activity to peripheral afferents which are activated by externally induced stepping movements where the subject was suspended over a moving treadmill (cf. Fig. 7a). They also

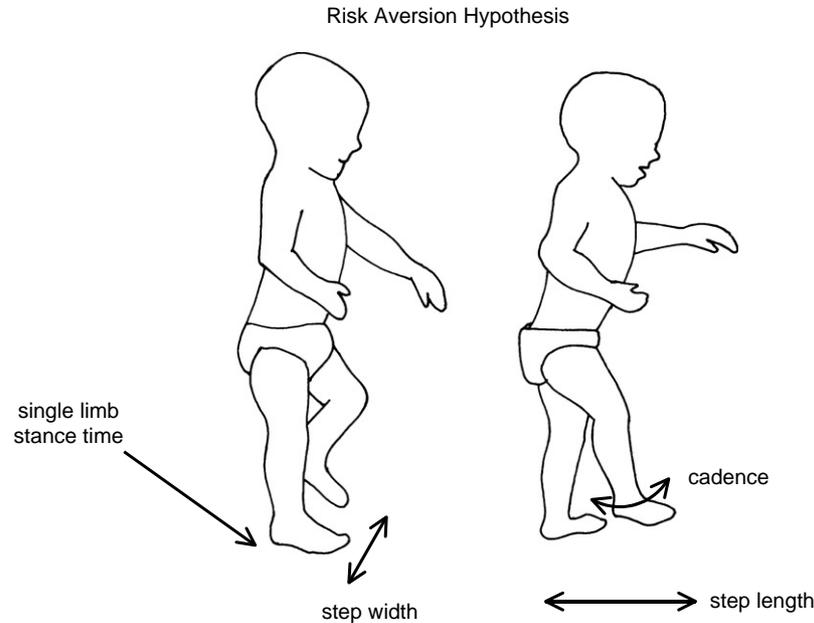


Fig. 6. When learning to walk, young infants adopt a biomechanical strategy of minimising risk by maintaining a shorter step length, lower cadence, wider step width and lower single-limb stance time (Langerak et al., 2001). The gait parameters have been scaled according to Hof (1996).

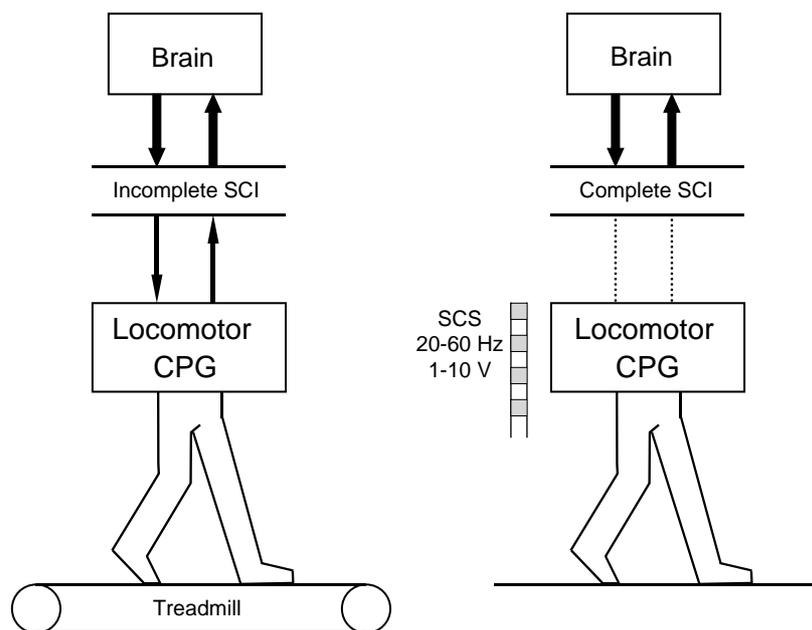


Fig. 7. Stepping movements, providing evidence of a central pattern generator (CPG), can be induced in patients with spinal cord injury (SCI) using: (a) mechanical stimulation via a treadmill; and (b) spinal cord stimulation or SCS (Pinter and Dimitrijevic, 1999).

conducted a study on six subjects with complete long-standing SCI in which an electrical train of stimuli were applied epidurally over the second lumbar segment of the spinal cord (cf. Fig. 7b). This stimulation induced rhythmic, alternating stance and swing phases of the lower limbs (Dimitrijevic et al., 1998).

Olree and Vaughan (1995) performed a principal components (or factor) analysis on the EMG patterns of

16 muscles (eight bilateral pairs) in ten normal subjects. They established two primary factors, named *loading response* and *propulsion*, which correspond with important phases in the gait cycle (cf. Fig. 8). They also discovered a third factor, which they called the *coordinating factor*, that appeared to maintain the phase shift between the left and right legs. Their findings suggest that the CNS solves the problem of high

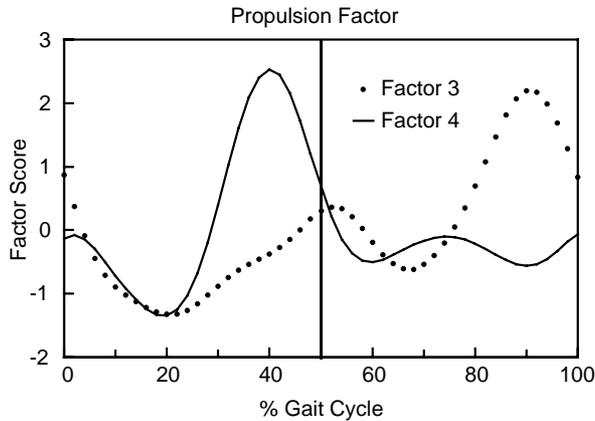


Fig. 8. Eigenvectors, or factor analysis scores, plotted as a function of the gait cycle (Olee and Vaughan, 1995). Factors 3 and 4 are the propulsion factors and correspond closely to the electromyographic signals of the left and right gastrocnemius muscles, respectively.

dimensionality by generating just a few fundamental signals which control *all* the major muscle groups in both legs. There have been other recent studies utilising EMG in both infants and adults that have provided support for the hypothesis that a single locomotor CPG controls both forward and backward walking (Lamb and Yang, 2000; van Deursen et al., 1998).

6. Linking control and effect

Bipedal locomotion is generated through global entrainment of the neural system on the one hand, and the musculoskeletal system plus environment on the other

Charles Scott Sherrington, who won a Nobel Prize for his contributions to neuroscience in 1932, said “Swiftly the brain becomes an enchanted loom, where millions of flashing shuttles weave a dissolving pattern, always a meaningful pattern though never an abiding one; a shifting harmony of sub-patterns” (Sherrington, 1941). This analogy between the functioning of the brain and a machine was a mathematical construct described almost 60 years ago by McCulloch and Pitts (1943). They pioneered the field of artificial neural networks (ANNs) and, although there was some activity in the 1960s (Rosenblatt, 1961; Minsky and Papert, 1969), ANNs only became widely accepted as an area of serious research endeavour during the 1980s with the efforts of Hopfield (1982), Anderson (1983), Rumelhart et al. (1986) and others. As the name implies, an ANN is a group of many neurons (or processing elements) that are interconnected and distributed in layers. An ANN normally operates in two states: *learning*, where a process of changes in the synaptic weights occurs; and *recall*, where an input stimulus generates an output signal (Rumelhart et al., 1986).

While ANNs were originally utilised in pattern recognition problems, their application to the study of real biological systems began to appear in the early 1990s (Srinivasan et al., 1992; Sepulveda et al., 1993). The argument had thus come full circle: ANNs, inspired by the example of the central nervous system, now had the potential to help elucidate how the CNS itself functioned (Vaughan, 1997). Sepulveda et al. (1993) built an ANN in which 16 EMG signals were used as the input signals and three joint torques were generated as output. Once the network had been successfully trained, a series of simulations were conducted. A 30% reduction in the magnitude of the soleus EMG led to a significant reduction in the plantar flexor moment at the ankle joint (cf. Fig. 9), a prediction that is consistent with our understanding of ankle biomechanics. Recognising the potential of ANNs to control muscle activation patterns, Popovic et al. (1993) developed a network which they tested on chronic spinalised cats. Other researchers have built on this basic science platform and have used ANN models and functional electrical stimulation to rehabilitate the gait of human subjects (Graupe and Kordylewski, 1995; Sepulveda and Cliquet, 1995).

While the aforementioned models linked the controller (neural system) and the effector (mechanical system), they lacked true integration with feedback influencing the real-time performance of the model (Vaughan, 1997). One of the most intriguing models of bipedal walking is that developed by Taga et al. (1991). A pair of CPGs, modelled by an ANN, controlled the muscles of the trunk plus the left and right hip, knee and ankle joints. Their biped consisted of eight segments, 10 degrees of freedom and 19 muscle actuators. A series of

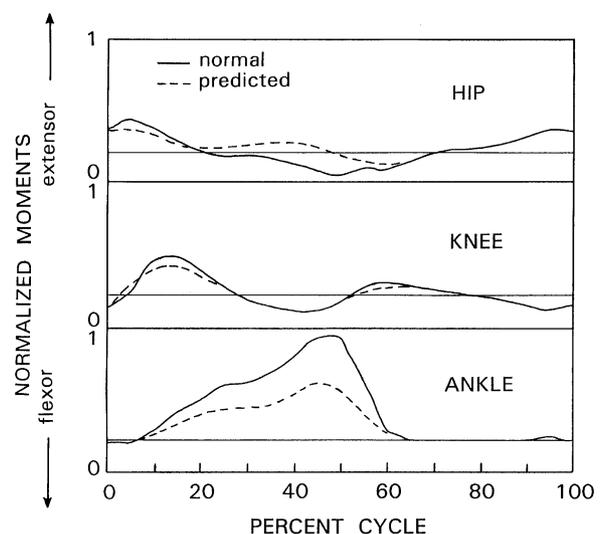


Fig. 9. An artificial neural network, designed to link 16 electromyographic signals and three joint moments, predicts the effect of a 30% reduction in the soleus activity (cf. dashed line), showing a significant decrease in the plantar flexor moment at the ankle during the push-off phase (Sepulveda et al., 1993).

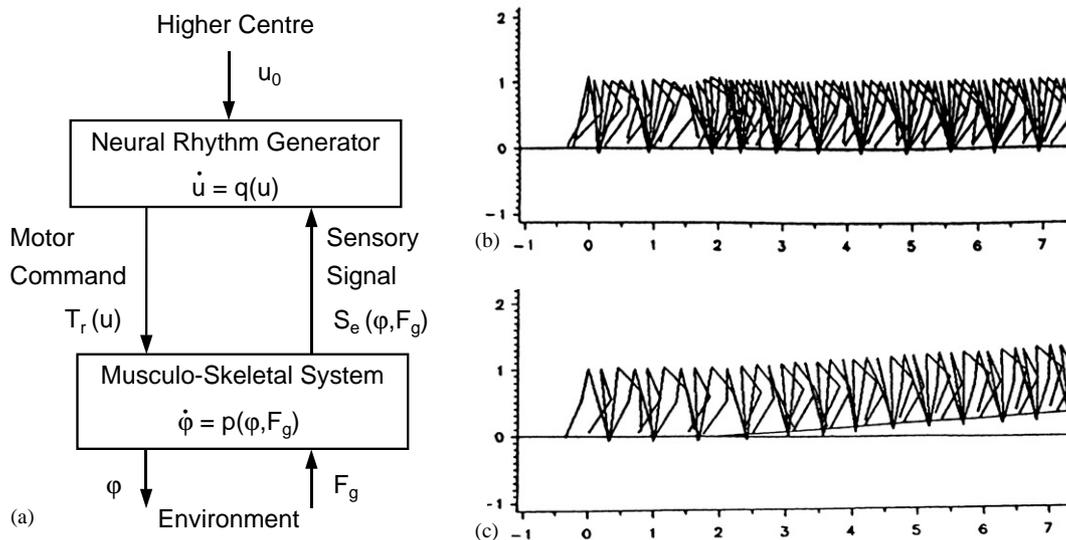


Fig. 10. (a) A model of the locomotor system links control and effect with coupled differential equations (Taga, 1995). Global entrainment of the neural system on the one hand, and the musculoskeletal system plus environment on the other, generates bipedal gait on (b) the level and can adapt to (c) an uphill pathway.

coupled differential equations defined both the neural rhythms (CPGs) and the mechanics of the musculoskeletal system (cf. Fig. 10a). Once the model had been trained, it not only produced level gait under normal conditions (cf. Fig. 10b), but it also adapted to environmental perturbations such as uneven terrain or increased carrying load (cf. Fig. 10c). Taga (1995) demonstrated that the speed of walking could be controlled by a single parameter which drove the neural oscillators, and the step cycle could be entrained by a rhythmic input to the oscillators.

7. Robots on two legs

Powered dynamic gait in a bipedal robot can be realised only through a strategy which is based on stability and real-time feedback control

Five decades ago Isaac Asimov, the science fiction writer (who also held a doctorate in chemistry) formulated his three laws of robotics. The second of these stated that “A robot must obey the orders given it by human beings”. One of these orders would no doubt have been to walk, a natural extension of the original function of a “robot”, first introduced to the English language by the playwright Karel Capek in 1921. Based on his mother tongue of Czech, a *robota* is defined as a worker of forced labour. Over 30 years before Capek coined the term robot, George Fallis in the USA invented a bipedal walking toy (Fallis, 1888). The central claim of his patent stated “This invention consists of a toy which is designed to simulate the human frame and which is a combined pendulum and rocker construction, whereby when placed upon an

inclined plane it will be caused by the force of its own gravity to automatically step out and walk down the said plane” (cf. Fig. 11).

What Fallis had described was a *passive* bipedal robot, where the word “passive” connotes the lack of *active* power. Another feature of the Fallis walker was that its gait was almost certainly *static*, in the sense that its centre of gravity was always located within its base of support. This is in contrast to *dynamic* walking where the centre of gravity falls outside the support base during the transition from one foot to the other. The passive vs. active debate is an interesting one, as is the discourse on static vs. dynamic gait. A little over 10 years ago McGeer (1990) demonstrated that a passive walker based on the Fallis design, despite the lack of any form of feedback control, could achieve dynamic gait. His work has led to more recent efforts to explore the potential of passive gait to provide biomechanical insight (Garcia et al., 1998; Kuo, 2001). The first theoretical attempts to describe the mechanics of an active bipedal robot were made over 30 years ago (McGhee, 1968; Vukobratovic, 1970; Frank, 1970). A group at Waseda University in Japan, led by Kato et al. (1974), are generally acknowledged to have been the first to design and implement a successful active walker. However, it employed a static gait pattern, with active walking in a bipedal robot only being achieved in the late 1980s (Zheng, 1989).

The most recent breakthroughs in implementing active dynamic gait in bipedal robots have been made by the Japanese companies Honda (2002) and Sony (2002). Both Honda’s ASIMO (mass 43 kg, height 1.2 m, velocity 0.44 m/s) and Sony’s SDR-3X (mass 5 kg, height 0.5 m, velocity 0.25 m/s) are anthropomorphic

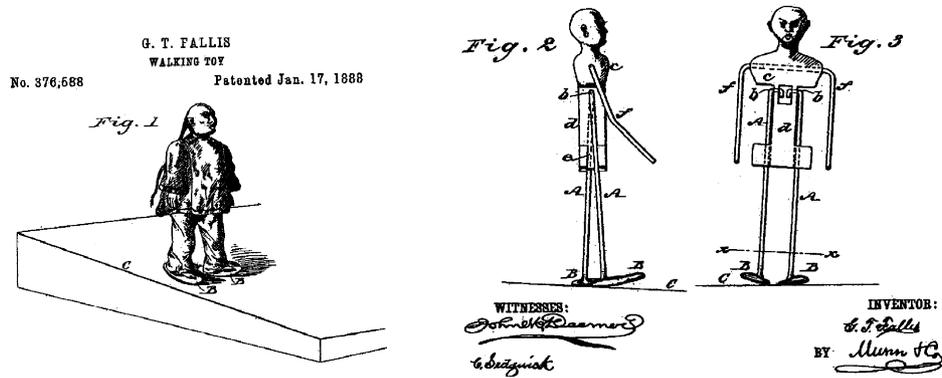


Fig. 11. The first three drawings of the patent by Fallis (1888) demonstrating how a bipedal toy is able to walk when powered only by gravity. Reproduced with the permission of the United States Patent and Trademark Office. I am indebted to Andy Ruina of Cornell University whose research group made the patent available on their web-site.

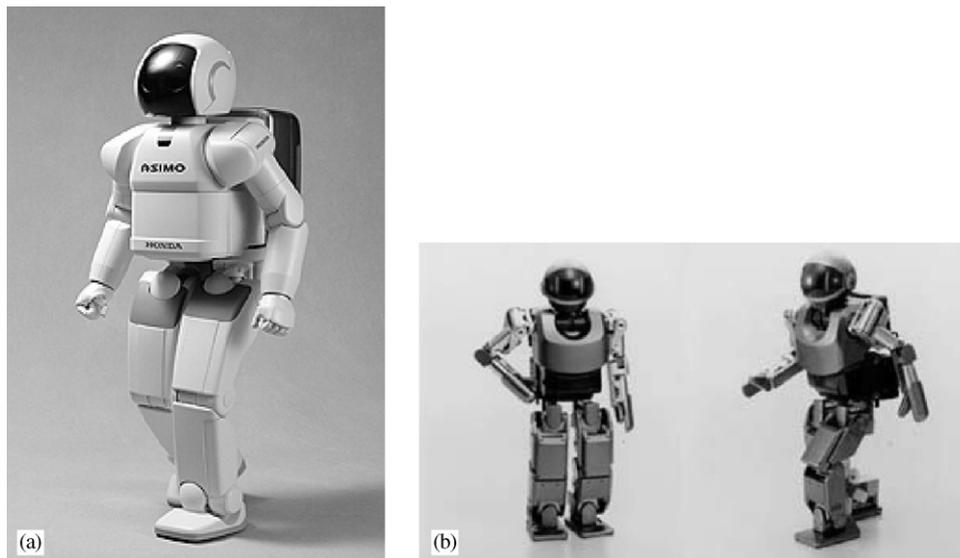


Fig. 12. Two anthropomorphic bipedal robots, each with 24 degrees of freedom, that demonstrate powered dynamic gait utilising real-time feedback control: (a) ASIMO manufactured by Honda (2002); and (b) SDR-3X manufactured by Sony (2002). Both photographs have been reproduced with the permission of the respective companies.

robots with 24 degrees of freedom (cf. Fig. 12). Both have joint torque actuators, sophisticated feedback via accelerometers and rate sensors, plus an onboard computer to provide real-time control. As is evident from videos of the robots, their gait—which includes stair climbing—is not only stable but very similar to that of humans whom they have been designed to mimic. To be sure, robots on two legs have come a long way since Fallis' invention in the late 19th century.

8. Concluding remarks

There are, of course, other important theories of locomotion that have not been considered in this review. These include: the dynamic similarity hypothesis, where the Froude number—the dimensionless ratio of velocity

squared to the product of leg length and the acceleration due to gravity—is constant (Alexander and Jayes, 1983); the theory of the spinal engine, which posits that the lumbar spine is the key structure necessary for land-based locomotion, with the pelvis being driven by the spine (Gracovetsky, 1985); and dynamic systems theory, which postulates that new forms of behaviour—such as infant locomotion—will emerge from the cooperative interactions of multiple components within a task context (Thelen and Ulrich, 1991). Despite these omissions, the odyssey has covered a wide spectrum, from the evolution of bipedal walking through to the integration of the nervous, muscular, and skeletal systems.

While it is highly unlikely that a single, unifying theory of bipedal walking exists, there are interesting ways in which the six theories reviewed in this paper

overlap with one another. For example, the risk aversion hypothesis proposed for the maturation of gait in young infants (cf. Fig. 6) explains the historical development of an active bipedal robot, in moving from a static to a dynamic mode of walking. In addition, the central pattern generator theory has been included by Taga (1995) in his theory linking control and effect, while it should also be feasible to extend his model so that it incorporates the minimum energy consumption features of the model by Anderson and Pandy (2001a). With the computational resources available today, large-scale models of the human body can be used to produce realistic simulations of bipedal walking that are an order of magnitude more complex than those produced just a decade ago (Pandy, 2001).

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References

- Alexander, R.M., 1992. *The Human Machine*. Columbia University Press, New York, pp. 176.
- Alexander, R.M., Jayes, A.S., 1983. A dynamic similarity hypothesis for the gaits of quadrupedal mammals. *Journal of Zoology (London)* 202, 577–582.
- Anderson, J.A., 1983. Cognitive and psychological computation with neural models. *IEEE Transactions on Systems, Man and Cybernetics*, 13, 799–815.
- Anderson, F.C., Pandy, M.G., 2001a. Static and dynamic optimization solutions for gait are practically equivalent. *Journal of Biomechanics* 34, 153–161.
- Anderson, F.C., Pandy, M.G., 2001b. Dynamic optimization of human walking. *Journal of Biomechanical Engineering* 123 (5), 381–390.
- Beck, R.J., Andriacchi, T.P., Kuo, K.N., Fermier, R.W., Galante, J.O., 1981. Changes in gait patterns of growing children. *Journal of Bone and Joint Surgery* 63-A (9), 1452–1457.
- Brown, T.G., 1911. The intrinsic factors in the act of progression in the mammal. *Proceedings of the Royal Society: London* 84, 308–319.
- Crompton, R.H., Yu, L., Weijie, W., Gunther, M., Savage, R., 1998. The mechanical effectiveness of erect and “bent-hip, bent-knee” bipedal walking in *Australopithecus afarensis*. *Journal of Human Evolution* 35 (1), 55–74.
- Delcomyn, F., 1980. Neural basis of rhythmic behavior in animals. *Science* 210, 492–498.
- Dimitrijevic, M.R., Gerasimenko, Y., Pinter, M.M., 1998. Effect of reduced afferent input on lumbar CPG in spinal cord injury subjects. *Society for Neuroscience* 24, 623–624.
- Dunbar, D.C., Horak, F.B., MacPherson, J.M., Rushmer, D.S., 1986. Neural control of quadrupedal and bipedal stance: implications for the evolution of erect posture. *American Journal of Physical Anthropology* 69 (1), 93–105.
- Fallis, G.T., 1888. Walking toy. United States Patent Number 376,588, Washington, DC.
- Frank, A.A., 1970. An approach to the dynamic analysis and synthesis of biped locomotion machines. *Medical and Biological Engineering* 8, 465–476.
- Garcia, M., Chatterjee, A., Ruina, A., Coleman, M., 1998. The simplest walking model: stability, complexity, and scaling. *Journal of Biomechanical Engineering* 120 (2), 281–288.
- Gracovetsky, S., 1985. An hypothesis for the role of the spine in human locomotion: a challenge to current thinking. *Journal of Biomedical Engineering* 7, 205–216.
- Graupe, D., Kordylewski, H., 1995. Artificial neural network control of FES in patients for patient responsive ambulation. *IEEE Transactions on Biomedical Engineering* 42 (7), 699–707.
- Grillner, S., 1985. Neurological bases of rhythmic motor acts in vertebrates. *Science* 228, 143–149.
- Hof, A.L., 1996. Scaling gait data to body size. *Gait & Posture* 4, 222–223.
- Hof, A.L., Zijlstra, W., 1997. Comment on “Normalization of temporal-distance parameters in pediatric gait”. *Journal of Biomechanics* 30 (3), 299–302.
- Honda, 2002. Humanoid robot. <http://world.honda.com/robot/>
- Hopfield, J.J., 1982. Neural networks and physical systems with emergent collective computational abilities. *Proceedings of the National Academy of Sciences of the USA* 79, 2554–2558.
- Inman, V.T., Ralston, H.J., Todd, F., 1981. *Human Walking*. Williams and Wilkins, Baltimore, pp. 154.
- Jenkins, F.A., 1972. Chimpanzee bipedalism: cineradiographic analysis and implications for the evolution of gait. *Science* 178 (63), 877–879.
- Kato, I., Ohteru, S., Kobayashi, H., Shirai, K., Uchiyama, A., 1974. Information-power machine with senses and limbs. In: *Theory and Practice of Robots and Manipulation*. Springer, New York, pp. 11–24.
- Kuo, A.D., 2001. A simple model of bipedal walking predicts the preferred speed-step length relationship. *Journal of Biomechanical Engineering* 123 (3), 264–269.
- Lamb, T., Yang, J.F., 2000. Could different directions of infant stepping be controlled by the same locomotor central pattern generator? *Journal of Neurophysiology* 83 (5), 2814–2824.
- Langerak, N., Leskens, H., Deib, G., Martinez, F., Vaughan, C.L., 2001. At what age is a child’s gait mature? In: Müller, R., Gerber, H., Stacoff, A. (Eds.), *Proceedings of XVIIIth Congress of International Society of Biomechanics*. Zürich, Switzerland, pp. 25–26.
- Leakey, M.D., Hay, R.L., 1979. Pliocene footprints in the Laetoli Beds at Laetoli northern Tanzania. *Nature* 278, 317–323.
- Leakey, M., Walker, A., 1997. Early hominid fossils from Africa. *Scientific American* 276 (6), 74–79.
- Lewin, R., 1993. *The Origin of Modern Humans*. Scientific American Library, New York, pp. 204.
- McCulloch, W.S., Pitts, W., 1943. A logical calculus of the ideas immanent in nervous activity. *Bulletin of Mathematical Biophysics* 5, 115–133.
- McGeer, T., 1990. Passive dynamic walking. *International Journal of Robotics Research* 9, 62–82.
- McGhee, R., 1968. Some finite state aspects of legged locomotion. *Mathematical Biosciences* 2, 67–84.
- Milne, A.A., 1924. *Lines and squares*. In: *When We Were Very Young*. Methuen Children’s Books, London.
- Minsky, M., Papert, S., 1969. *Perceptrons*. MIT Press, Cambridge, MA.
- Oiree, K.S., Vaughan, C.L., 1995. Fundamental patterns of bilateral muscle activity in human locomotion. *Biological Cybernetics* 73 (5), 409–414.
- O’Malley, M.J., 1996. Normalization of temporal-distance parameters in pediatric gait. *Journal of Biomechanics* 29 (5), 619–625.
- Pandy, M.G., 2001. Computer modeling and simulation of human movement. *Annual Reviews in Biomedical Engineering* 3, 245–273.

- Pandy, M.G., Berme, N., 1988. A numerical method for simulating the dynamics of human walking. *Journal of Biomechanics* 21, 1043–1051.
- Pandy, M.G., Berme, N., 1989. Quantitative assessment of gait determinants during single stance via a three-dimensional model: 1. Normal gait. *Journal of Biomechanics* 22, 725–733.
- Pinter, M.M., Dimitrijevic, M.R., 1999. Gait after spinal cord injury and the central pattern generator for locomotion. *Spinal Cord* 37 (8), 531–537.
- Popovic, D.B., Stein, R.B., Jovanovic, K.L., Dai, R., Kostov, A., Armstrong, W.W., 1993. Sensory nerve recording for closed-loop control to restore motor functions. *IEEE Transactions on Biomedical Engineering* 40 (10), 1024–1031.
- Preis, S., Klemms, A., Muller, K., 1997. Gait analysis by measuring ground reaction forces in children: changes to an adaptive gait pattern between the ages of one and five years. *Developmental Medicine and Child Neurology* 9 (4), 228–233.
- Prost, J.H., 1980. Origin of bipedalism. *American Journal of Physical Anthropology* 52 (2), 175–189.
- Ralston, H.J., 1958. Energy-speed relation and optimal speed during level walking. *Internationale Zeitschrift für angewandte Physiologie* 17, 277–283.
- Richmond, B.G., Strait, D.S., 2000. Evidence that humans evolved from a knuckle-walking ancestor. *Nature* 404, 382–385.
- Rodman, P.S., McHenry, H.M., 1980. Bioenergetics and the origin of hominid bipedalism. *American Journal of Physical Anthropology* 52 (1), 103–106.
- Rosenblatt, F., 1961. *Principles of Neurodynamics*. Spartan Books, Washington, DC.
- Rumelhart, D.E., Hinton, G.E., Williams, R.J., 1986. Learning representations by back propagation errors. *Nature* 323, 533–536.
- Rüther, H., 1996. Part IX. Report on the photogrammetric field campaign. In: *Laetoli Project: Conservation of the Hominid Trackway Site at Laetoli, Tanzania*, Getty Conservation Institute, New York, pp. 66–105.
- Saunders, J.B., Inman, V.T., Eberhart, H.D., 1953. The major determinants in normal and pathological gait. *Journal of Bone and Joint Surgery* 35-A, 543–558.
- Sepulveda, F., Cliquet, A., 1995. An artificial neural system for closed loop control of locomotion produced via neuromuscular stimulation. *Artificial Organs* 19 (3), 231–237.
- Sepulveda, F., Wells, D., Vaughan, C.L., 1993. A neural network representation of electromyography and joint dynamics in human gait. *Journal of Biomechanics* 26, 101–109.
- Shaw, G.B., 1904. Act IV. John Bull's Other Island, Constable London.
- Sherrington, C.S., 1941. *Man on his nature*. The Gifford Lectures, MacMillan, New York, p. 178.
- Sony, 2002. Sony develops small biped entertainment robot. <http://www.sony.co.jp/en/>
- Srinivasan, S., Gander, R.E., Wood, H.C., 1992. A movement pattern generator model using artificial neural networks. *IEEE Transactions in Biomedical Engineering* 39 (7), 716–722.
- Studel, K., 1996. Limb morphology bipedal gait and the energetics of hominid locomotion. *American Journal of Physical Anthropology* 99 (2), 345–355.
- Sutherland, D.H., Olshen, R., Cooper, L., Woo, S.L., 1980. The development of mature gait. *Journal of Bone and Joint Surgery* 62 (3), 336–353.
- Taga, G., 1995. A model of the neuro-musculo-skeletal system for human locomotion. I. Emergence of basic gait. *Biological Cybernetics* 73 (2), 97–111.
- Taga, G., Yamaguchi, Y., Shimizu, H., 1991. Self-organized control of bipedal locomotion by neural oscillators in unpredictable environment. *Biological Cybernetics* 65 (3), 147–159.
- Tardieu, C., Aurengo, A., Tardieu, B., 1993. New method of 3D analysis of bipedal locomotion for the study of displacements of the body and body-parts centers of mass in man and non-human primates: evolutionary framework. *American Journal of Physical Anthropology* 90 (4), 455–476.
- Thelen, E., Ulrich, B.D., 1991. Hidden skills: a dynamic systems analysis of treadmill stepping during the first year. *Monographs of the Society for Research in Child Development* 56 (1), 1–104.
- van Deursen, R.W., Flynn, T.W., McCrory, J.L., Morag, E., 1998. Does a single control mechanism exist for both forward and backward walking? *Gait & Posture* 7 (3), 214–224.
- Vaughan, C.L., 1996. Are joint torques the Holy Grail of human gait analysis? *Human Movement Science* 15, 423–443.
- Vaughan, C.L., 1997. Neural network models of the locomotor apparatus. In: Allard, P., Cappozzo, A., Lundberg, A., Vaughan, C.L. (Eds.), *Three-dimensional Analysis of Human Locomotion*. Wiley, Chichester, UK, pp. 259–280.
- Vaughan, C.L., 1999. *Biomechanics of Human Gait: an electronic bibliography*, 4th Edition, ISBN 0 620 23559 4, Kiboho Publishers, Cape Town.
- Vaughan, C.L., Brooking, G.D., Olree, K.S., 1996. Exploring new strategies for controlling multiple muscles in human locomotion. In: Harris, G.F., Smith, P.A. (Eds.), *Human Motion Analysis. Current Applications and Future Directions*. IEEE Press, New York, NY, pp. 93–113.
- Vaughan, C.L., Damiano, D.L., Abel, M.F., 1997. Gait of normal children and those with cerebral palsy. In: Allard, P., Cappozzo, A., Lundberg, A., Vaughan, C.L. (Eds.), *Three-dimensional Analysis of Human Locomotion*. Wiley, Chichester, UK, pp. 335–361.
- Vaughan, C.L., Davis, B.L., O'Connor, J.C., 1999. *Dynamics of Human Gait*, 2nd Edition, Kiboho Publishers, Cape Town, pp. 155.
- Vaughan, C.L., Langerak, N., Deib, G., Leskens, H., Martinez, F., 2001. The acquisition of mature gait patterns in children. In: *Proceedings of IX Congresso Brasileiro de Biomechanica*. Gramado, Brazil, pp. 9–13.
- Vaughan, C.L., Sussman, M.D., 1993. Human gait: from clinical interpretation to computer simulation. In: Grabiner, M.D. (Ed.), *Current Issues in Biomechanics*. Human Kinetics, Champaign, IL, pp. 53–68.
- Voll, D., 1994. Soul searching with Francis Crick. *Omni Magazine* 16 (2), 46–53.
- Vukobratovic, M., 1970. On the stability of biped locomotion. *IEEE Transactions on Biomedical Engineering* 17 (1), 25–36.
- Wheelwright, E.F., Minns, R.A., Law, H.T., Elton, R.A., 1993. Temporal and spatial parameters of gait in children. I: Normal control data. *Developmental Medicine and Child Neurology* 35, 102–113.
- Zarrugh, M.Y., Todd, F.N., Ralston, H.J., 1974. Optimisation of energy expenditure during level walking. *European Journal of Applied Physiology* 33, 293–306.
- Zheng, Y.F., 1989. Acceleration compensation for biped robots to reject external disturbances. *IEEE Transactions on Systems, Man, and Cybernetics* 19 (1), 74–84.