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A walking robot called human: lessons to be learned from neural control of locomotion

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Abstract

From what we know at present with respect to the neural control of walking, it can be concluded that an optimal biologically inspired robot could have the following features. The limbs should include several joints in which position changes can be obtained by actuators across the joints. The control of mono- and biarticular actuators should occur at least at three levels: one at direct control of the actuators (equivalent to motoneuron level), the second at indirect control acting at a level which controls whole limb movement (flexion or extension) and the third at a still higher level controlling the interlimb coordination. The limb level circuits should be able to produce alternating flexion and extension movements in the limb by means of coupled oscillator flexor and extensor parts which are mutually inhibitory. The interlimb control level should be able to command the various limb control centers. All three control levels should have some basic feedback circuits but the most essential one is needed at the limb control level and concerns the decision to either flex or extend a given limb. The decision to activate the extensor part of the limb oscillator has to be based on feedback signalling the onset of loading of the limb involved. This should be signalled by means of load sensors in the limb. The decision to activate the flexor part of the limb oscillator has to depend on various types of feedback. The most important requirement is that flexion should only occur when the limb concerned is no longer loaded above a given threshold. The rule for the initiation of limb flexion can be made more robust by adding the requirement that position at the base of the limb (“hip”) should be within a normal end of stance phase range. Hence, human locomotion is thought to use a number of principles which simplify control, just as in other species such as the cat. It is suggested that cat and human locomotion are good models to learn from when designing efficient walking robots. © 2002 Elsevier Science Ltd. All rights reserved.

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1. Why biologically inspired walking robots?

Many four- or six-legged walking robots exist. Only very few bi-pedal robots exist, since they have to face a continuous stability challenge balancing on their feet while contact between foot and ground is not actuated. Motions between feet and ground can only be controlled through coordinated motions of the limbs above. Most currently used walking robots use position or trajectory

control (Wisse et al., 2001). These robots are usually not very energy efficient but they can perform well when used in a predictable environment. An example is the famous robot of Honda Motor Co., which needs 20 kg of batteries to walk for 15 min (Hirai et al., 1998).

Furthermore, such very advanced robots fail when the terrain is irregular or, more generally, when they have to cope with unexpected changes. This type of restrictions has led some robotic engineers to choose alternative approaches. For example, some of them have focussed on using the natural dynamics of the system, thereby developing “passive dynamic walking” (McGeer, 1990). Other robotics engineers have derived their inspiration

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from biologically inspired control methods. In this way, Cruse et al. (1995) and Kimura and Fukuoka (2000) were able to design highly adaptable six- and four-legged robots, respectively. For two-legged robots, there is no reason why a similar biologically inspired robot would not be feasible although, of course, stability issues are quite different for biped vs. quadruped locomotion. This requires that one should learn about the control of human walking. To justify the title of the present paper, “a walking robot called human”, one can state that the regulation of human walking is an excellent example for robotics since man is the ultimate robot. An ideal robot is efficient and can walk long distances without requiring a large supply of energy. Yet, an ideal robot should also be adaptable to changes in the environment. Hence, it is especially important to learn about some of the features, which make human walking into such an efficient, automated yet highly adaptable type of behavior.

To be fair, however, we have to admit that most of our current thinking about the control of locomotion in humans is actually derived from experiments on quadrupeds like cats and requires some extrapolations. But given the strong evidence for maintenance of control principles across species such extrapolations are usually highly justified (see Duysens et al., 2000; Clarac, 1991). Furthermore, many basic similarities between cats and humans have already been demonstrated. A good example is the phase-dependency of reflexes during gait. Perturbations during gait lead to reflex responses but these responses cannot be stereotyped since the motor output and the biomechanical conditions vary at different moments of the step cycle. In the cat, it was found that indeed the responses to identical inputs are very different in various phases of the step cycle (Forssberg et al., 1975; Duysens and Pearson, 1976), a finding that was later confirmed for human locomotion (Yang and Stein, 1990; Duysens et al., 1990).

In general, the purpose of the present review is to summarize some of the findings on the neural control of locomotion of cats and humans in order to provide a basic framework for those interested in applying neural control principles in the construction of walking robots.

2. Control levels

Human and cat locomotion is hierarchically controlled at several levels of the central nervous system, namely the spinal cord, the brainstem and the cerebral cortex. Here we will focus mostly on the lowest level, which is the spinal cord. The reason for this is that we believe this part to be the most robot-like in that the spinal cord can provide the basic control units needed to organize efficient locomotion. Furthermore, it can use

feedback from peripheral sensors in the legs to automatically control gait and respond to unexpected perturbations.

How is this achieved? The *spinal cord* contains motoneurons, which activate muscle fibers. These motoneurons can be activated themselves by interneurons (premotoneuronal elements) which are organized in circuits. During locomotion, the various muscles of the leg contract in a typical pattern by activation of the corresponding group of motoneurons. In many species, the cyclical patterns of leg muscle activations can be generated by premotoneuronal spinal networks, referred to as central pattern generators (CPGs). Such networks generate the rhythm and form the pattern of the locomotor bursts of motoneurons (Grillner and Wallen, 1985; Grillner, 1985). For the cat, it is thought that the CPGs are located in the spinal cord and that there is at least one such CPG for each limb. Evidence for the existence of such spinal locomotor CPGs is that the output pattern can persist (as patterned bursts in motor nerve fibers) even when the cats have a transected spinal cord or brainstem and are motionless (“fictive locomotion”, for review see Grillner and Wallen, 1985). In humans, such patterns are rarely generated after spinal transection (Calancie et al., 1994; Roby-Brami and Bussel, 1987) but nevertheless, there is mounting evidence for the existence of spinal generators in man as well (summarized in Duysens and Van de Crommert, 1998). In essence, such CPGs are thought to contain at least two mutually inhibitory parts (“Half Center” model of Brown, 1911a, b). One part can induce flexion in all the joints of a leg, the other produces full limb extension. During the flexion phase of walking, the flexor half-center is active while the extensor half-center is inhibited. The inverse is true for the stance phase. The CPG can be regarded as an oscillating unit, phasically activating flexors and extensors. Through the efferent and afferent pathways, this oscillating unit is in connection with another oscillating unit, i.e. the limb. The CPG has to provide a rather complex output. During the stance phase the knee extensors are active, while the hip flexors and extensors of the stance leg balance the upper body. At the end of the stance phase, an active ankle extension provides the take-off. During the swing phase some flexor muscles are active, since knee flexor activity should be present if more foot clearance is needed. Hip flexor activity is required to adjust the step length. If any, CPG activity during human walking involves multiple centers at different spinal levels for the control of joint flexors and extensors. These centers should mutually affect each other, as can be seen in simulation studies of, for example, Taga (1995).

Feedback occurs through sensors in the leg and it is used to control activity either of individual muscles (feedback to motoneurons) or of groups of muscles

(feedback to pattern generator). This feedback not only serves to control stiffness of individual muscles or joints but also to ensure the stability of the whole system in the sagittal as well as in the frontal plane.

2.1. Feedback control directly to motoneurons

At the *spinal level*, the feedback can occur through specialized reflex pathways to the motoneurons. The best-studied feedback is from the Ia sensory afferents from the muscle spindles. This pathway is potentially very fast because the Ia fibers are the fastest fibers available and they can reach the motoneurons over a single synaps (*monosynaptic reflex*; each synaps causes about 0.5 ms delay). Furthermore, they can provide a sizeable amount of increased impedance and are therefore of interest for robotics. Spindles are very sensitive to stretch and therefore are highly active in different periods of the step cycle, mostly of course when the parent muscle is being stretched (Prochazka et al., 1976, 1977, 1979; Loeb et al., 1977; Loeb and Duysens, 1979). The resulting reflex activation of the parent muscles can or cannot be useful depending on the phase of the step cycle. Stretch reflexes of soleus are useful during the ankle yield in mid-stance but they are not useful during the swing phase, when the ankle moves in dorsiflexion. In contrast, the stretch reflex activation of the hamstrings during swing is useful. It is thought that the resulting muscle contraction contributes to deceleration of hip flexion and knee extension (Smith, 1986). In that period, the hamstrings are rapidly stretched through the combined action of knee extension and hip flexion. In the cat, the resulting stretch evokes a discharge in spindle afferents from these muscles (Prochazka et al., 1976, 1977, 1979; Loeb et al., 1977; Loeb and Duysens, 1979). Therefore, it has been proposed that the activation of hamstrings at the end of the first extension phase during normal gait is caused by stretch reflexes from afferent activity of spindles (Prochazka et al., 1976; Perret and Cabelguen, 1980; Smith, 1986; Wisleder et al., 1990). Typically in the cat, this burst disappears almost completely following removal of sensory input (“deafferentation”; Grillner and Zanger, 1984) while other bursts (i.e. at end stance) remain unaffected. Wisleder et al. (1990) showed that the amplitude of the activation of the hamstrings correlates linearly with the speed of knee extension in the cat. Hence, this provides a good example of an automated regulated braking response at end swing. The exact contribution of these reflexes to the total muscle force is hard to calculate but Van der Helm et al. (2001) showed that as a result of increased reflex gains, the muscle impedance (due to visco-elastic behavior in combination with stretch reflexes) increases by a factor of five.

Does this type of reflex activation exist in humans as well? In humans, the hamstrings are also rapidly

stretched at end swing and there is a large burst of EMG activity in this period (Winter and Yack, 1987). To know whether the end swing EMG activity could partly originate from stretch reflexes, one needs to test stretch reflexes and tendon jerks in this phase of the step cycle. If stretch-induced activity were important, then one would expect that the related reflex responses are larger in that period of the step cycle. This can be investigated by using a special hammer which can provide constant taps in various phases of the step cycle (Dietz et al., 1990). In this way, tendon taps on the distal tendon of the long head of the biceps femoris (BF) elicit stretch responses, the amplitude of which varies as a function of the step cycle (Van de Crommert et al., 1996; Faist et al., 1999). This was done for the distal tendon of the BF in a group of 12 healthy subjects that were walking with the leg ipsilateral to stimulation held stiff (reduced gait) (Van de Crommert et al., 1996). The subjects walked this way in order to reduce movements and to keep stimulation as constant as possible, while still maintaining the basic locomotor output. The results are shown in Fig. 1.

The amplitude of the short-latency BF responses was largest in the end swing period (Van de Crommert et al., 1996). This means that the reflex is facilitated during a period when its contribution is meaningful. The result is

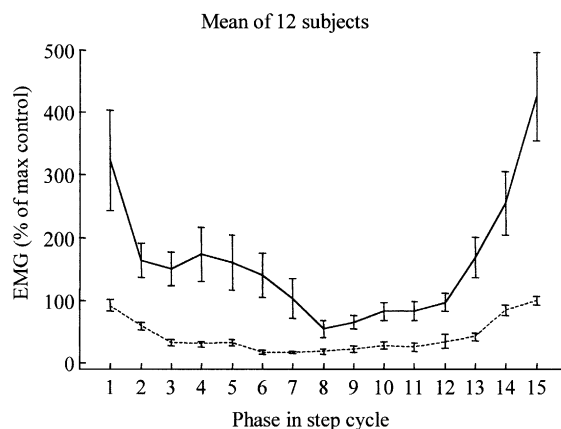


Fig. 1. Phase-dependent modulation of averaged tendon jerk responses in BF of one subject during “reduced gait” on a split-belt treadmill (leg ipsilateral to stimulation was held stiff to reduce movement-induced changes in stimulation). Comparison of control (without stimulation) and reflex (with stimulation; top of figure) at 15 phases of the step cycle (phase 1 is just after touchdown; phase 15 just prior to touchdown). All data points are based on the mean EMG as calculated within a time window set around the responses. The data are normalized with respect to the maximum control activity in the step cycle. The position in the step cycle corresponds to the position of the middle of the responses. Short-latency reflexes were found throughout the whole step cycle but the amplitude was largest in the middle and late-swing phase. The increased amplitude could have only been partly related to a parallel increment in ongoing activity (“control”). It is concluded on the basis of this type of data that the normally occurring BF burst at end swing could be due to stretch-induced activity.

thus conform to the proposed contribution of the stretch reflexes to the BF activity burst at end swing (Prochazka et al., 1976). In other periods, when the effects of the reflex would be inappropriate, the amplitude of the responses is small. This “phase-dependent modulation” of reflexes is a principle very common for all types of reflexes both in man and cat. It can even be found in fictive locomotion and in the spinal cat (transected spinal cord; Schomburg and Behrends, 1978), indicating that the spinal locomotor CPG in each leg has the potential to modulate the transmission in reflex pathways in order to provide appropriate reflex feedback at all times in the step cycle.

2.2. Feedback control of the CPG flexor and extensor centers

Feedback connections to the CPG are especially potent since they allow reflex control of whole limb movements (flexion or extension). In this way, they firstly allow for assistance and reinforcement of ongoing limb extension or flexion during the corresponding stance and swing periods and secondly, they assist in providing automated switching from one of these periods to the other. Hence, contrary to the direct feedback to the motoneurons, the reflex control of the CPG affects timing of the activity periods in muscles and not only their amplitude. The main connections are schematically represented in Fig. 2.

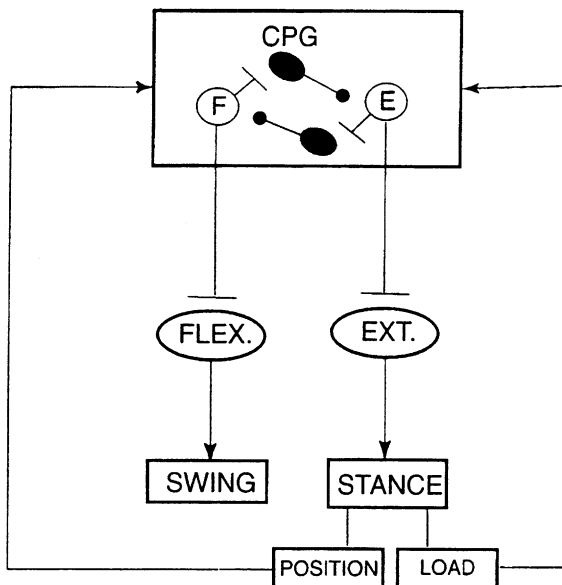


Fig. 2. Schematic representation of the current hypothesis about the reflex regulation of gait. The CPG contains F and E: flexor and extensor half-center, controlling flexors (Flex.) and extensors (Ext.), respectively. For further explanation, see text.

2.2.1. Contribution of reflexes to activity of the extensor center of the CPG

When a limb has to counteract gravity, several reflexes assist the activation of antigravity muscles (often referred to as “extensors” in the physiological literature) and prevent the flexor muscles to initiate the flexion phase. Load-sensitive proprioceptors in the leg provide a signal which leads to a reflex which reinforces the activity in the extensor part of the CPG, thereby initiating or enhancing contraction in antigravity muscles and delaying the switch to the ensuing flexion phase. Load sensors in extensors inhibit the flexor half-center (see Fig. 2) during the stance phase (Pearson and Duysens, 1976; Duysens and Pearson, 1980). The function is clear. Load on the stance limb must be decreasing and load-related afferent discharge must fall below a given threshold level, before swing can be initiated. Or inversely, limb support has to be maintained until sufficient unloading has taken place. Model studies showed that such positive feedback does not lead to instability (Prochazka et al., 1997a, b).

Both for cats and humans, the main load sensors are thought to be the foot-sole mechanoreceptors and the Golgi Tendon Organs (GTO) of antigravity muscles (see Pearson, 1995; Duysens et al., 2000 for review). Activation of these receptors yields direct access to the CPG. In animal studies (including those on cats), it was shown that stimulation of these sensory fibers can reinforce ongoing activity in antigravity muscles. In addition, the switch to the ensuing swing phase is delayed by the inhibitory action of the extensor half-center (HC) on the flexor HC (see Fig. 2).

For foot-sole afferents, this was first demonstrated in 1976 (Duysens and Pearson, 1976) while for GTOs, the first evidence was obtained in 1980 (Duysens and Pearson, 1980). Since then, many studies have confirmed and extended these initial observations (Conway et al., 1987, 1994; Whelan et al., 1995; Pearson et al., 1992; Pearson and Collins, 1993; for review, see Duysens et al., 2000).

Finally, it should be mentioned that in these studies, the sensory fibers from muscles and skin have been studied separately but that it is not at all certain whether the pathways involved operate completely separately. In fact, some studies have shown convergence of GTO and skin input onto spinal interneurons (Lundberg et al., 1975). It is likely that, from the viewpoint of the CPG, the main message of interest is whether the limb is loaded or not, irrespective of the type of afferents involved. In this respect, the role of the contralateral limb should also be considered. Clinical observations (Harkema, personal communication) point to the importance of loading of one leg as a condition for the initiation of the swing phase of the other leg but the mechanisms underlying these interlimb effects have not yet been revealed.

2.2.2. Contribution of reflexes to activity of the flexor center of the CPG

The flexor part of the CPG is activated mainly by two types of sensory input, which are usually both present at the end of the stance phase. First, when the leg is unloaded and load signals weaken, there is a disinhibition (release of inhibition) of the flexor center of the CPG. This simply follows from the termination of the activation of the extensor part of the CPG by load receptors (see Fig. 2). Second, there is a powerful excitatory signal to the flexor part of the CPG through signals related to the position of the limb at end stance. In particular, a lengthening of hip flexor muscles occurs at the end of the stance phase. Sherrington (1910) showed that dropping the leg to an extended position elicits a flexion movement such as that which occurs in the swing phase. Shik and Orlovsky (1965) induced a prolongation of the stance phase by raising the anterior or posterior part of a normal dog walking on a treadmill so that the raised limbs could not reach full extension. They concluded that the onset of threshold extension of joints of the limb was a prerequisite for the initiation of the swing phase. Later, Grillner and his colleagues were able to show that it was primarily hip extension which was the important cue (Andersson and Grillner, 1981, 1983). In spinal cats (cats with transected spinal cord), they found that hip extension resulted in initiation of the swing phase of stepping (hip extension excursion had to reach the angle as normally seen at the end of the stance phase). In contrast, when the hip of one limb was manually flexed during treadmill walking, the stepping movement disappeared. Hence, they concluded that afferent signals from the hip were important for the initiation of the swing phase. Andersson and Grillner (1983) further showed that these effects are due to hip afferents signals having direct access to the CPG. Small-amplitude sinusoidal hip movement of a partially denervated hindlimb was used for resetting and/or entraining the locomotor rhythm. The receptors involved have been identified as well. Kriellaars et al. (1994) showed that entrainment relied on stretch of hip muscles. Joint denervation or anesthesia of the hip joints, procedures which eliminate joint afferents, did not block the entrainment. Hiebert et al. (1996) used selective stretches of hindlimb muscles to confirm that the flexor phase induction was indeed related to stretch of hip flexors.

The hip position feedback, described above is complimentary to the unloading signal. It prevents limb flexion when a human or robot limb is suddenly unloaded in mid-stance (“foot in hole” condition). Furthermore, an additional important “IF–THEN” condition is that another limb has started to accept weight.

It should be emphasized that the rules presented here apply only to the walking mode in which the unloading

of one limb coincides with increased loading of another limb. In the running mode, the robots have to switch to open-loop control mode. For this, one could again use biologically inspired principles but these are beyond the limits of the present paper.

3. Higher (supraspinal) control level

It should be added that most of the experiments described in the previous sections were performed on cats in which either the spinal cord or the brainstem was transected. Furthermore, in most of these experiments, there has been some type of reduction of sensory inputs (partial denervation is the practice of cutting some nerves to reduce unwanted inputs). These manipulations have accentuated the effects on the CPG but they have created some naïve hopes in researchers wanting to replicate this type of results in intact humans (Capaday, 2000). In the intact cat or human, there are many competing sources which can influence phase-switching and the manipulation of one single source is usually not potent enough to induce changes in the duration of the step cycle (Duysens and Stein, 1978). Furthermore, in both cat and human, it is known that higher centers in the brainstem or cortex can produce changes in the transmission of spinal reflexes. Hence, humans consist actually of several robots at the same time, corresponding to the different layers of neural control. The higher level robot can influence the way the lower level controllers are interacting. The “spinal robot”, explained in the present paper, provides the lowest basic robot level. This level is presumably what one uses when one is making long walks and hardly is aware that one is walking. This automated level of walking can easily be combined with other tasks such as talking to a companion. However, as one grows older, one realizes that walking becomes less automated as it is much harder or even impossible for some elderly to combine such different tasks (Lundin-Olsson et al., 1997). Similarly, patients with a knee prosthesis walk apparently normally unless they are asked to perform a double task (cognitive load; De Visser et al., 1998).

It is clear that under these conditions, the control of the walking behavior requires a high degree of conscious control. How much of the spinal robot is still used under these conditions is an open question. Nevertheless, this should not discourage attempts to model the spinal robot since its achievements are impressive enough to be a useful example for engineers designing artificial walking robots. For example, the application of some of the principles governing gait of the “spinal robot” (limb unloading and hip extension at end stance) have already proven extremely useful for the design of training programs to restore gait not only in cats with transected spinal cord but also in patients with spinal

cord injury (Dietz et al., 1994, 1995; Harkema et al., 1997; Dobkin et al., 1995; Wernig et al., 1995, 1999).

4. Conclusion

In cat, and presumably also in humans, gait is regulated through feedback from load receptors onto the so-called central pattern generators (CPG), circuits involved in the generation of rhythmic locomotor output. Load-detecting receptors play an important role in the control of the intensity and duration of the stance phase in the step cycle. This is achieved through reflexes that are not apparent in the immobile animal. Reinforcing force feedback assists the muscle activity of extensors in this period and suppresses flexor activity. As long as the limb is loaded, the onset of the next flexion should be delayed. It is suggested that these principles can be useful in the design of walking robots.

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References

- Andersson, O., Grillner, S., 1981. Peripheral control of the cat's step cycle. I. Phase dependent effects of ramp-movements of the hip during 'fictive locomotion'. *Acta Physiologica Scandinavica* 113, 89–101.
- Andersson, O., Grillner, S., 1983. Peripheral control of the cat's step cycle. II. Entrainment of the central pattern generators for locomotion by sinusoidal hip movements during 'fictive locomotion'. *Acta Physiologica Scandinavica* 118, 229–239.
- Brown, T.G., 1911a. The intrinsic factors in the act of progression in the mammal. *Proceedings of the Royal Society of London, Series B* 84, 308–319.
- Brown, T.G., 1911b. The factors in rhythmic activity of the nervous system. *Proceedings of the Royal Society of London, Series B* 85, 278–289.
- Calancie, B., Needham-shropshire, B., Jacobs, P., Willer, K., Zych, G., Green, B.A., 1994. Involuntary stepping after chronic spinal cord injury. Evidence for a central rhythm generator for locomotion in man. *Brain* 117, 1143–1159.
- Capaday, C., 2000. Control of a 'simple' stretch reflex in humans. *Trends in Neuroscience* 23, 528–529.
- Clarac, F., 1991. How do sensory and motor signals interact during locomotion? In: Humphrey, D.R., Freund, H.J. (Eds.), *Motor control: concepts and issues*. Wiley, New York, pp. 199–221.
- Conway, B.A., Hultborn, H., Kiehn, O., 1987. Proprioceptive input resets central locomotor rhythm in the spinal cat. *Experimental Brain Research* 68, 643–656.
- Conway, B.A., Scott, D.T., Riddell, J.S., Hadian, M.R., 1994. Effects of plantar nerve stimulation on the transmission of late flexion reflexes in the decerebrate spinal cat. *Journal of Physiology* 155, 145P.
- Cruse, H., Bartling, Ch., Dreifert, M., Schmitz, J., 1995. Walking: A complex behavior controlled by simple networks. *Adaptive Behavior* 3, 385–418.
- De Visser, E., Pauwels, J., Duysens, J., Mulder, Th., Veth, R.P.H., 1998. Gait adaptations during walking under visual and cognitive constraints; a study of patients recovering from limb-sparing surgery of the lower limb. *American Journal of Physical Medicine and Rehabilitation* 77 (6), 503–509.
- Dietz, V., Discher, M., Faist, M., Trippel, M., 1990. Amplitude modulation of the human quadriceps tendon jerk reflex during gait. *Experimental Brain Research* 8, 211–213.
- Dietz, V., Colombo, G., Jensen, L., 1994. Locomotor activity in spinal man. *Lancet* 344, 1260–1263.
- Dietz, V., Colombo, G., Jensen, L., Baumgartner, L., 1995. Locomotor capacity of spinal cord in paraplegic patients. *Annals of Neurology* 37, 574–582.
- Dobkin, B.H., Harkema, S., Requejo, P., Edgerton, R., 1995. Modulation of locomotor-like EMG activity in subjects with complete and incomplete spinal cord injury. *Journal of Neurological Rehabilitation* 9, 183–190.
- Duysens, J., Pearson, K.G., 1976. The role of cutaneous afferents from the distal hindlimb in the regulation of the step cycle of thalamic cats. *Experimental Brain Research* 24, 245–255.
- Duysens, J., Pearson, K.G., 1980. Inhibition of flexor burst generation by loading ankle extensor muscles in walking cats. *Brain Research* 187, 321–332.
- Duysens, J., Stein, R.B., 1978. Reflexes induced by nerve stimulation in walking cats with implanted cuff electrodes. *Experimental Brain Research* 32, 213–224.
- Duysens, J., Van de Crommert, H.W.A.A., 1998. Neural control of locomotion; the central pattern generator from cats to humans. *Gait and Posture* 7, 131–141.
- Duysens, J., Trippel, M., Horstmann, G.A., Dietz, V., 1990. Gating and reversal of reflexes in ankle muscles during human walking. *Experimental Brain Research* 82, 351–358.
- Duysens, J., Clarac, F., Cruse, H., 2000. Load-regulating mechanisms in gait and posture: Comparative aspects. *Physiological Reviews* 80, 83–133.
- Faist, M., Blahak, C., Duysens, J., Berger, W., 1999. Modulation of the biceps femoris tendon jerk reflex during human locomotion. *Experimental Brain Research* 125 (3), 265–270.
- Forssberg, H., Grillner, S., Rossignol, S., 1975. Phase dependent reflex reversal during walking in chronic spinal cats. *Brain Research* 85, 103–107.
- Grillner, S., 1985. Neurobiological bases on rhythmic motor acts in vertebrates. *Science* 228, 143–149.
- Grillner, S., Wallen, P., 1985. Central pattern generators for locomotion, with special reference to vertebrates. *Annual Review of Neuroscience* 8, 233–261.
- Grillner, S., Zanger, P., 1984. The effect of dorsal root transection on the efferent motor pattern in the cat's hindlimb during locomotion. *Acta Physiologica Scandinavica* 120, 393–405.
- Harkema, S.J., Hurley, S.L., Patel, U.K., Requejo, P.S., Dobkin, B.K., Edgerton, V.R., 1997. Human lumbosacral spinal cord interprets loading during stepping. *Journal of Neurophysiology* 77, 797–811.
- Hiebert, G.W., Whelan, P.J., Prochazka, A., Pearson, K.G., 1996. Contribution of hind limb flexor muscle afferents to the timing of phase transitions in the cat step cycle. *Journal of Neurophysiology* 75 (3), 1126–1137.
- Hirai, K., Hirose, M., Haikawa, Y., Takenaka, T., 1998. The development of Honda humanoid robot. In: *Proceedings of the IEEE International Conference on Robotics and Automation*, pp. 1321–1326.

- Kimura, H., Fukuoka, Y., 2000. Adaptive dynamic walking of the quadruped on irregular terrain—autonomous adaptation using neural system model. *Proceedings of the 2000 IEEE*, pp. 436–442.
- Kriellaars, D.I., Brownstone, R.M., Noga, B.R., Jordan, L.M., 1994. Mechanical entrainment of fictive locomotion in the decerebrate cat. *Journal of Neurophysiology* 71, 2074–2086.
- Loeb, G.E., Duysens, J., 1979. Activity patterns in individual hindlimb primary and secondary muscle spindle afferents during normal movements in unrestrained cats. *Journal of Neurophysiology* 42, 420–440.
- Loeb, G.E., Bak, M.J., Duysens, J., 1977. Long-term unit recording from somato-sensory neurons in the spinal ganglia of the freely walking cat. *Science* 197, 1192–1194.
- Lundberg, A., Malmgren, K., Schomburg, E.D., 1975. Convergence from Ib, cutaneous and joint afferents in reflex pathways to motoneurons. *Brain Research* 87, 81–84.
- Lundin-Olsson, L., Nyberg, L., Gustafson, Y., 1997. Stops walking when talking. *Lancet* 349, 617.
- McGeer, T., 1990. Passive dynamic walking. *International Journal of Robotic Research* 9 (2), 62–82.
- Pearson, K.G., 1995. Proprioceptive regulation of locomotion. *Current Opinions in Neurobiology* 5, 786–791.
- Pearson, K.G., Collins, D.F., 1993. Reversal of the influence of group Ib afferents from plantaris on activity in medial gastrocnemius muscle during locomotor activity. *Journal of Neurophysiology* 70, 1009–1017.
- Pearson, K.G., Duysens, J., 1976. Function of segmental reflexes in the control of stepping in cockroaches and cats. In: Herman, R.E., Grillner, S., Stuart, D., Stein, P. (Eds.), *Neural Control in Locomotion*. Plenum Press, New York.
- Pearson, K.G., Ramirez, J.M., Jiang, W., 1992. Entrainment of the locomotor rhythm by group Ib afferents from ankle extensor muscles in spinal cats. *Experimental Brain Research* 90, 557–566.
- Perret, C., Cabelguen, J.M., 1980. Main characteristics of the hindlimb locomotor cycle in the decorticate cat with special reference to bifunctional muscles. *Brain Research* 187, 333–352.
- Prochazka, A., Westerman, R.A., Ziccone, S., 1976. Discharges of single hindlimb afferents in the freely moving cat. *Journal of Neurophysiology* 39, 1090–1104.
- Prochazka, A., Western, R.A., Ziccone, S., 1977. Ia afferent activity during a variety of voluntary movements in cat. *Journal of Physiology* 268, 423–448.
- Prochazka, A., Stephens, J.A., Wand, P., 1979. Muscle spindle discharge in normal and obstructed movements. *Journal of Physiology* 287, 57–66.
- Prochazka, A., Gillard, D., Bennett, D.J., 1997a. Positive force feedback control of muscles. *Journal of Neurophysiology* 77, 3226–3236.
- Prochazka, A., Gillard, D., Bennett, D.J., 1997b. Indications of positive feedback in the control of movement. *Journal of Neurophysiology* 77, 3237–3251.
- Roby-Brami, A., Bussel, B., 1987. Long-latency spinal reflex in man after flexor reflex afferent stimulation. *Brain* 110, 707–725.
- Schomburg, E.D., Behrends, H.B., 1978. The possibility of phase-dependent monosynaptic and polysynaptic Ia excitation to homonymous motoneurons during fictive locomotion. *Brain Research* 143, 533–537.
- Sherrington, C.S., 1910. Flexor reflex of the limb, crossed extension reflex, and reflex stepping and standing. *Journal of Physiology* 40, 28–121.
- Shik, M.L., Orlovsky, G.N., 1965. Coordination of the limbs during running of the dog. *Biophysics* 10, 1148–1159.
- Smith, J.L., 1986. Hindlimb locomotion of the spinal cat: synergistic patterns, limb dynamics and novel blends. In: Gurfinkel, V.S., Ioffe, M.E., Massion, J., Roll, J.P. (Eds.), *Stance and Motion*. Plenum Press, London, pp. 185–197.
- Taga, G., 1995. A model of the neuro-musculoskeletal system for human locomotion: I emergence of basic gait. *Biological Cybernetics* 73, 97–111.
- Van de Crommert, H.W.A.A., Faist, M., Berger, W., Duysens, J., 1996. Biceps femoris tendon jerk reflexes are enhanced at the end of the swing phase. *Brain Research* 734, 341–344.
- Van der Helm, F.C.T., Schouten, A.C., De Vlugt, E., Brouwn, G.G., 2001. Identification of intrinsic and reflexive components of human arm dynamics during postural control. *Journal of Neurophysiology* (submitted for publication).
- Wernig, A., Müller, S., Nanassy, A., Cagol, E., 1995. Laufband therapy based on ‘rules of spinal locomotion’ is effective in spinal cord injured persons. *European Journal of Neurosciences* 7 (4), 823–829.
- Wernig, A., Nanassy, A., Muller, S., 1999. Laufband (treadmill) therapy in incomplete paraplegia and tetraplegia. *Journal of Neurotrauma* 16, 719–726.
- Whelan, P.J., Hiebert, G.W., Pearson, K.G., 1995. Stimulation of the group I extensor afferents prolongs the stance phase in walking cats. *Experimental Brain Research* 103, 20–30.
- Winter, D.A., Yack, H.J., 1987. EMG profiles during normal human walking: stride-to-stride and inter-subject variability. *Electroencephalography and Clinical Neurophysiology* 67, 401–411.
- Wisleder, D., Zernicke, R.F., Smith, J.L., 1990. Speed-related changes in hindlimb intersegmental dynamics during the swing phase of cat locomotion. *Experimental Brain Research* 79, 651–660.
- Wisse, M., Schwab, A.L., van de Linde, R.Q., 2001. A 3D passive biped with jaw and roll compensation. *Robotica* 19, 275–284.
- Yang, J.F., Stein, R.B., 1990. Phase-dependent reflex reversal in human leg muscles during walking. *Journal of Neurophysiology* 63, 1109–1117.