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Steps Forward in Understanding Backward Gait: From Basic Circuits to Rehabilitation

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Abstract Backward locomotion is increasingly used in sports and rehabilitation. However, it is unclear whether training effects of backward walking/running (BW) can simply be transferred to forward walking/running (FW). This touches on the question whether the same neural substrate can generate FW and BW. The available evidence suggests that BW uses the same rhythm circuitry but additionally requires specialized control circuits.
Key words Central Pattern Generator; cortical; locomotion; running; sports; stability; walking

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Introduction

Backward walking and running (sometimes referred to as retro running, retro locomotion, reverse running) have been thought to be used already for several decennia in China and Japan not only to get a good physical work-out, but also to stay mentally fit. While running or walking backward, one has to rely more on other senses than the visual system (like the auditory and sensory system), since one does not have a complete view of the road and obstacles ahead. In the last decade interest in backward running and walking has risen in other parts of the world as well (e.g. United States, United Kingdom, Italy), as backward running races and championships are increasingly popular. Furthermore, backward walking and running are used as a preferred (rehabilitation) exercise under some conditions, in particular when the impact of heel strike needs to be avoided (35, 40). However, it is still unknown whether the effects of backward walking can be transferred to forward walking. This would be the case if the same neural structures are involved in both types of locomotion. It was indeed suggested that this is the case but it is not generally accepted. If one reverses a video from someone walking backward, one barely can notice any difference with the same subject walking forward (42). This apparent similarity has led some authors to propose that these two forms of locomotion are generated by the same basic neural mechanisms (10, 18, 23, 45). However, some findings, for example from adaptation studies (4), do not fit well into this framework. Hence this question needs reexamining, based on kinematic and kinetic studies as well as on experimental work with EMG. In addition, some studies on reflex modulation are also relevant for this issue. It is argued that both forms of gait can be largely controlled using the same basic neural generators. Furthermore, it is suggested that for both forms of locomotion, the basis is formed by a central structure that is generating a flexor synergy (flexor burst generator) that is periodically activated when unloading of the legs occurs.

Backward gait in exercise and rehabilitation

Backward walking (BW) and running (BR) are (increasingly) used in sports and in rehabilitation settings. Although several advantages for BW and BR have been advocated compared to forward walking (FW) and running (FR) (37), scientific evidence is rather scarce.

BW and BR have been used as part of specific training modalities in different athletic sports for different reasons. For instance in several sports, e.g. tennis and american football, at some point in a match players will need to run backwards, therefore, the implementation of BW and BR in their individual work-out allows for task-specific training. Conform to this line of reasoning Agbonlahor et al. (1) have studied BW at different slopes for tennis players, and suggested that this could be used as alternate training exercise to complement their sports training modality.

On the other hand, BW and BR are used as a training modality to improve general aspects of fitness (for instance endurance) that are related to other skills as well. Several studies have shown that BW and BR have a substantially increased cardiopulmonary load compared to FW and FR at similar speeds and elevation angles (for instance see (13)). This has led some coaches and trainers to believe that BW and BR are more appropriate to increase aerobic capacity than FW and FR (37). In this case, however, the question arises as to why one would start to train BW or BR at a specific speed and not just increase the speed for FW or FR to increase the cardiopulmonary requirements. The most frequently cited reason to start training BW or BR is that FW and FR are not possible or disadvantageous for an athlete. In that case BW and BR have been suggested to have the benefit of minimizing knee overload, since ground reaction, impact and patella-femoral joint compression forces are reduced compared to FW and FR (35, 40). This benefit of knee load reduction may help an athlete suffering from knee injury (e.g. anterior cruciate ligament injury, patella-femoral pain) to maintain, or even further improve cardio-respiratory fitness without increased knee joint stress when compared to FW or FR training techniques.

In addition to reducing knee joint stress, BR training may also improve anterior cruciate ligament stability (and anterior lateral rotator stability) in people with knee injury (30). This study, however, did not include a FR control group. The authors suggested that an overstretching of the anterior cruciate ligament was prevented by excessive quadriceps muscle action during the BR training. This is an observation that is supported by some researchers who found that BR has increased power and torque demands on the knee extensors (for instance see (40)). Flynn & Soutas-Little (14) studied the muscle firing patterns in FR and BR in detail. Their results indicated that muscle action of the knee extensors was largely eccentric and concentric during FR, while they were isometric and concentric during BR, which could be beneficial for the rehabilitation of patellar tendinitis (i.e. decreased eccentric loading of the extensors which is implicated in these patients). A combination of BW and moving up an inclination has been suggested to further enhance the positive effects of BW on rehabilitation of knee injury, since uphill BW requires increased activation of the lower limb muscles in combination with an increased knee flexion and ankle dorsiflexion (5).

One of the reasons that BW and BR are advocated for athletes (e.g. long distance runners) is that it would be one of the few natural ways of strengthening the quadriceps (37). This claim is actually supported by previously mentioned findings that BR requires increased knee extensor activations. It is also suggested that this way the imbalance between the knee extensors and flexors (i.e. quadriceps/hamstring strength ratio) can be realigned towards the ideal 60/40 (37). In that case, maintaining this muscle balance would prevent possible knee injuries. However, it is unclear why one would start a training paradigm with BW or BR, since we have found no evidence that BW would result in a faster strengthening of the quadriceps muscle than other (conventional or analytic) strength exercises.

Related to the prevention of injury are the results described by Whitley and Dufek (44). They reported that hamstring flexibility increased (measured with the sit-and-reach test) after a four week BW intervention, which could further explain the possible preventive effect of BW or BR on knee injuries (44). However, no control group was included that received a FW intervention to be able to determine whether the positive effect on hamstring flexibility is due to BW specifically. The authors measured the effect of BW training on both hamstring flexibility and low back range of motion, because it is suggested that BW or BR training could have a positive effect on low back pain (7). A 10-15 minutes BW training program during three days per week for three weeks significantly decreased low back pain and increased low back range of motion (ROM) in 5 athletes (that experienced low back pain) (7). Low back ROM was also increased in 5 control (non-athletic, pain-free) subjects. The study by White and Dufek (44), however, could not duplicate the low back ROM results in ten normal control subjects after a similar training paradigm. None of these studies included a control group that received FW or FR training. Hence it is still not possible to conclude unequivocally that BW or BR are responsible for these effects rather than walking or running as such.

The combination of possible preventive benefits, the increased cardiopulmonary requirements and its relatively novel character, have made BW and BR a source of inspiration for research in normal (non-athlete) adults (38), children (21) and elderly (16, 29). In adult women, BW and BR training had a positive effect on cardio-respiratory fitness and body composition compared to a control group that had no training. Even though again no FW and FR training control group was included in this study, this study has indicated that a BW and BR training program does have a positive effect on oxygen consumption during a FR test as well (38). The growing interest in the use of BW and BR for rehabilitation, have led some researchers to focus on its advantages on a population that might benefit even more than young adults, i.e. the elderly. Several studies have suggested that BW and BR could be used in an elderly population, however, caution is warranted since some of the elderly have been found to experience difficulties during BW (29). These difficulties could be related to instability during BW, since it was found that BW measures were even more sensitive than FW measures to differentiate elderly that are prone to fall from those not prone to fall (16). The proposition that BW is related to instability, has resulted in a study that examined whether balance would improve after BW training in school-aged children (21). After eight weeks of BW training (twice per week), balance was significantly improved compared to a control group that received a normal physical education class. A suggested possible explanation for this effect of BW on balance was that children could not use visual input during BW and, therefore, learned to rely more on other sources of sensory input (cutaneous, proprioceptive and vestibular senses).

Due to this reduced ability to rely on vision during BW or BR, caution is warranted when implementing BW or BR into training. This is of specific importance in rehabilitation settings, where patients have less balance control and are more vulnerable to fall. Nonetheless, training with BW or BR has found its place in neuro-rehabilitation as well. In several populations with neurological impairments, BW has been implemented in the gait rehabilitation program. For several decades, physiotherapists have been treating patients with neurological disorders (e.g. stroke or cerebral palsy) using BW to improve specific components of FW required to develop an independent gait pattern (3). In these rehabilitation concepts BW is used to increase the motor control of the patient, and to reduce the use of aberrant movement patterns. For instance, some children with cerebral palsy present with a crouched gait pattern (i.e. the ankle in a dorsiflexion and the hip and knee are in a flexed position). Gait rehabilitation with BW puts emphasis on positioning the foot behind the body, and, thus, facilitates hip extension while performing a knee flexion (rather than using the crouched pattern). To the best of our knowledge, however, no studies have investigated this mechanism and whether there is an actual transfer from practicing BW to improving FW.

Two studies have examined the effects of BW training combined with conventional training in post-stroke patients (43, 47). Yang et al. (47) compared a control group, which received conventional rehabilitation training, to an experimental group, which additionally received a BW training program. The patients in the experimental group showed superior improvement in several gait characteristics (e.g. walking speed, stride-length, and symmetry) compared to the control group. The improvement in the experimental group, however, could simply be due to the increased amount of training they received. Weng et al. (43) performed a similar training study. However, their control group received the same amount of conventional training as the experimental group received BW training. Their results also indicated that walking speed was significantly more improved in the experimental group. Furthermore, they found that balance function and the motor function of the lower limbs were significantly increased in the BW group compared to the control group. Only one study was found that investigated BW training in children with cerebral palsy (25). This study was aimed at examining whether a BW training program would improve the gait characteristics in children with cerebral palsy. After 8 weeks of training, significant improvements were found for several gait parameters (such as walking speed, weight-bearing symmetry, stride and step length). Since this study did not include a control group, we question whether any of the observed improvements would also be present in children that did not receive BW training.

Several researchers have indicated a beneficial effect of BW (or BR) training on FW, however, the underlying mechanisms of the transfer of these improvements are poorly understood. It is important to point out that transfer characteristics may be either related to common gains in cardiovascular fitness (or in musculoskeletal properties) or due to common neural structures. Training that results in cardiovascular (e.g. aerobic fitness) or musculoskeletal (e.g. strength, flexibility) gains may be expected to transfer to other tasks that place similar demands on these systems. Thus, it might be possible that the BR training places similar demands on the cardiovascular and musculoskeletal systems as FR, and therefore transfer of gains in these systems may be expected (e.g. aerobic fitness, strength, flexibility). In contrast, for less physically demanding tasks it is thought that common neural structures could explain transfer. In particular, walking is less demanding than running and therefore the transfer of FW and BW could rely more on the use of common neural structures. For podokinetic adaptation (walking on a circular treadmill) some transfer was observed from FW to BW (originating from changes in trunk rotation) (12). In contrast, using a different paradigm (moving platform), Reynolds and Bronstein (34) showed a lack of transfer from forward to backward walking. The transfer data of Choi and Bastian (4) go in the same direction. In intact subjects they failed to find transfer of FW split-belt adaptation on BW. This was taken as evidence that FW and BW are generated by networks for each leg which are largely non-overlapping. At first sight this seems to contradict the suggestion that FW and BW are generated by the same circuitry (10, 18, 23, 27, 28, 45). Hence it is worthwhile to briefly review the evidence for and against this proposal.

Neural control of FW and BW

The idea that the same neural control structures are involved in both FW and BW stems from the observation that there are many similarities in kinematics and kinetics. If one reverses a video from someone walking backward, one can barely notice any difference with the same subject walking forward (42). Not surprisingly, this apparent similarity has led some authors to believe that these two forms of locomotion are generated by the same basic neural mechanisms (10, 18, 23, 24, 27, 28, 39, 45).

Kinetics, Kinematics and Muscle Activity

To further explore this hypothesis it is essential to first examine the similarities and differences between BW and FW, for the various aspects of gait (kinetics, kinematics and muscle activity). Since the classic work of Thorstensson (39) on this topic, many studies have compared kinematics and kinetics during FW and BW (18, 24, 32, 45). For example, Winter et al. (45) compared joint angles, moments and powers for the ankle, knee and hip. They observed similar knee and hip angle patterns, but different ankle angle patterns. Hip and ankle moment patterns were similar, but a difference in knee moment during the stance phase was noted. For all joints, the power curves of FW and BW were almost exact mirror images. These findings in the sagittal plane have been confirmed for the anatomical joint angles (18, 24). Meyns et al. (32) compared elevation angles of several lower and upper limb segments during FW and BW. Their results indicated that also the upper limb kinematics of FW correlated highly to reversed BW kinematics. The findings appeared to be consistent with the proposal that control of FW and BW may be similar for the upper and lower limbs (both in adults and children).

For muscle activity, the similarity between FW and BW has also been investigated in multiple studies (10, 18, 22-24, 39, 45). After analyzing tibialis anterior (TA), rectus femoris (RF), hamstrings, lateral gastrocnemius (LG), vastus lateralis (VL) and gluteus maximus (GM) muscle activity, Thorstensson (39) concluded that drastic changes occur between FW and BW. Winter et al. (45) compared activity in the same first three muscles, together with the medial gastrocnemius, vastus medialis and soleus muscles. They attributed differences in the amplitude of the muscle activation between FW and BW to changes between concentric and eccentric tasks and they concluded that somewhat similar, but time reversed, muscle activation patterns could be used in both modes. Grasso et al. (18) used cross-correlation and principal component analysis to address the similarities between muscle activation patterns in FW and BW. They analyzed TA, RF, LG, VL, GM and biceps femoris (BF) muscle activity. The activity of all these muscles in BW was strikingly different from that during FW with r2 coefficients below 0.2 for all muscles. Additionally, for all muscles but the BF, it was impossible to predict BW waveforms starting from FW waveforms, despite using all 10 principle components. The differences in muscle activity patterns between FW and BW were again confirmed by Ivanenko et al. (23) in a study on the spatiotemporal organization of -motoneuron activity in the human spinal cord during gait. The different muscle activity patterns resulted in different spatiotemporal spinal activity maps, with a more intense rostrocaudal banding in BW. However, the temporal structure of the motor output was observed to be similar between FW and BW, meaning that both gaits can be constructed from the same collection of patterns. The shape of those patterns does not change between FW and BW but the timing and weight of the patterns may change considerably (27). Note that the method of pattern extraction was different from Grasso et al. (18), who failed to predict BW patterns starting from FW patterns.

Central Pattern Generators coordinating FW and BW

Overall, these data listed above gave rise to the proposition that BW could be mostly the reverse of FW as far as neural control is concerned. What is the basis of this control? In cats it is well-established that the core control units for walking consists of spinal circuitry labeled central pattern generators (CPGs), but in humans there is only indirect evidence for CPGs (11). Nevertheless, as gait is usually quite automated, it is reasonable to expect that the same spinal automatisms are used for FW and BW (as also proposed by Earhart et al. (12) and Ivanenko et al. (23)). The best evidence for a role of spinal CPGs comes from infant stepping, where BW can be generated, despite the absence of mature corticospinal projections (28). Infants, when held under their arms with their feet touching a moving treadmill belt display stepping movements. This behavior has been observed in the majority of 52 infants (2-11 months old) in forward, sideways and backward direction. Opposed to adults, the FW kinematic patterns were not similar to the time reversed BW patterns. However, differences in muscle activity between FW and BW were similar to those in adults. Furthermore, it was observed that children can make transitions between forward and sideways stepping in a continuous way. The authors argued that those findings are consistent with the concept of a common locomotor network controlling walking in different directions (28). More supportive data came from work by Selionov et al. (36), who studied induced air-stepping movements in humans. When such movements were performed unilaterally it was found that there were spontaneous transitions between forward and backward stepping movements. The authors explained their data by assuming that spinal CPGs could generate both types of movements.

While parts of the CPG possibly may be used in common for FW and BW, it is too simplistic to expect that there would be a simple reversal of the pattern (as we and others originally proposed, see (10, 49)). FW and BW have very different constraints; hence a simple reversal is out of the question. The point is however, that there is no need for a completely different circuitry either. Basic features of the CPG can be used in FW and BW.

This is perhaps most elegantly shown in the above mentioned work in which the muscle activation patterns are analyzed with respect to basic underlying synergies (23, 27). While the muscle activity patterns of FW and BW differ they still can be reconstructed using just a few of these synergies.

Reflex Studies

Further insights on the control of BW come from reflex studies. It was proposed that reflexes are modulated during the step cycle and that there may be similarities in this modulation during FW and BW if there are common elements in the control of these two modes of locomotion (48, 50). A series of studies by the group of Charles Capaday (for overview: see (41)) explored the soleus H-reflex during BW. In FW, the soleus H-reflex followed the classic pattern of reciprocal inhibition between antagonistic muscles, but in BW the modulation pattern was different. In BW, the soleus H-reflex was markedly increased during the swing phase. At first sight this could be taken as evidence that BW was controlled differently, but it soon appeared that the differences were to be explained differently. After training of the BW task, or when participants held on to handrails, the marked reflex increase in swing was no longer present. This suggested to the authors that the reflex increase in BW was related to elements of instability (the unfamiliarity and reduced balance in BW). This explanation was supported by the observation that after training the marked reflex increase re-appears when subjects close their eyes during BW. As changes in H-reflex were not due to changes in motor activity or kinematics, they are likely part of the motor program controlling BW. It was initially hypothesized that the motor cortex would be involved in the control of the H-reflex during BW through the corticospinal tract (41). However, so far this hypothesis could not be confirmed since transcranial magnetic stimulation (TMS) did not result in high motor evoked potentials in the soleus in the same period as the high H-reflex was observed (41).

For cutaneous reflexes the phase-dependent modulation is more pronounced and, therefore, an obvious target to compare FW and BW (50). Duysens et al. (10) compared the reflex activity after cutaneous nerve (sural) stimulation during BW and FW. Based on their observations of similar phase-dependent modulation of reflex activity in the muscles of the stimulated leg during FW and BW, the authors suggested that the reflex modulation could largely rely on a common locomotor network for FW and BW. This was supported by findings from cutaneous reflex studies on backwards (arm) cycling (48, 49). For arm cycling, it was observed that reflex patterns at equivalent positions were similar between forward and backward motion (48). Along the same line, for leg cycling, reflex patterns were similar at equivalent functional phases (49). More insights came from observations on the phase-dependent reflex modulation during BW in the contralateral leg muscles (22). Selective reflex activity was observed in the TA of the contralateral leg during stance phase. This reflex activity was mostly independent of background muscle activity. The selective TA reflex activity during stance was suggested to be related to the reduced stability in BW. However, reflex activity and gait stability measures were uncorrelated. More likely, the increased reflex activity was related to the TAs decelerating function during the stance phase in BW (24). The low correlation between the reflex activity and the background muscle activity, suggested again some pre-motoneuronal modulation but the source remains unclear. The modulation patterns of BW in reverse showed some similarities with FW modulations, but with major deviations. Hence, overall these data are only partly compatible with a possible common source for FW and BW. These differences in modulation patterns between FW and BW could reflect cortical input in gait control (for overview: see (22)).

Cortical Control

There are many indications that, in addition to basic locomotor patterns generated by spinal CPGs, some features of gait are strongly controlled by the cortex. This is particularly true for the control of muscles such as TA and VL, which are important in the control of touchdown (which depends heavily on vision in the case of FW). This cortical control of gait has recently been studied intensively by TMS and by electroencephalography (EEG) (for overview: see (9)). This cortical input is not evenly distributed but preferentially focuses on some muscles. Dietz (6) suggested that the corticospinal tract is most closely linked with the segmental circuits controlling the flexors such as TA. Studies using TMS have confirmed this. TA receives strong facilitatory input from fast corticospinal connections, while the soleus and gastrocnemius muscles receive a less developed corticomotorneuron drive, at least when the size of the contributing cortical surface is measured (2). In the context of the present review the question arises whether FW and BW have different cortical representations. The few data available indicate that this is not the case. The same areas seem to be involved but to a different degree. For example, using imagery tasks, Godde and Voelcker-Rehage (17) showed that BW as compared to FW required larger activations in the primary motor cortex, supplementary motor area, parietal cortex, thalamus, putamen, and caudatum, but less activation in the cerebellum and brainstem. Similarly, using fNIRS and real walking, Kurz et al. (26) showed that oxyHb was greater in the supplementary motor area, pre-central gyrus, and superior parietal lobule when participants walked backwards rather than forwards. This was suggested to show that BW presents more of a stability challenge than FW. Indeed, in human bipedal gait the motor cortex is especially important because of the added need for control of stability (46).

This added need is likely to be higher in BW than in FW as BW is often reported to be more variable than FW (20, 22, 26). Specifically, stride time, stride length, knee and hip range of motion and relative stance phase have been reported to be more variable during BW (20, 26). In addition to being more variable, BW is observed to have lower local dynamic stability than FW (22). This lower local dynamic stability makes BW a more demanding task from the perspective of control. However, it is important to note that, in the majority of studies, the familiarization time for the BW task was limited. Whether differences in variability and stability are still apparent when participants are more accustomed to BW after repetitive training of the task is still an important open question. A second notable point is that it is important to have matched speeds to compare FW and BW variability and stability. Self selected walking velocity is commonly observed to be reduced in BW (20). When BW and FW at equal speed are compared, cadence is higher in BW (18, 39).

Kurz et al. (26) have addressed the variability and cortical activation in FW and BW simultaneously, and have indeed found an increase in sensorimotor cortical activation measured (using fNIRS) and a greater stride-time variability during BW. However, they were not able to find a relationship between the amount of stride-time variability during BW and the amount of cortical activation of the sensorimotor cortex. The lack of correlation suggests that another gait parameter would be related to the increased cortical processing during BW. However, it should be noted that all participants in this study were required to hold on to handrails during the walking trials. Holding on to the handrails has most probably improved the balance of BW, which likely could have artificially decoupled the relationship between stride-time variability and changes in the cortical activations.

Further insights on the role of the cortex in BW come from a study by Meyns et al. (31). They have compared the gait and coordination patterns during FW and BW in children with cerebral palsy and age-matched healthy control subjects, to examine to what extent cortical deficits influenced the kinematic reversal from FW to BW. Both groups presented with the same basic type of interlimb coordination pattern during FW and BW. However, compared to the control subjects, the children with cerebral palsy showed a significant decrease in coordination between the legs and significantly worse coordinative stability between the legs. These results indicate that, in persons with a cortical deficit, the reversal to BW elicits greater coordinative problems in the lower limbs.

Conceptual Framework

How can the same circuitry be used in FW and BW? In the cat, the experiments of Musienko et al. (33) convincingly show that afferent input is likely to be a main contributor. However, in the intact animal or human there probably is also an important contribution from supraspinal sources. In adults with spinal cord injury, BW can be induced but there is no transfer of learning (19). Learning to walk FW had no effect on the performance of (untrained) BW indicating again that BW may require a higher level of supraspinal control for this type of learning (see also (41)). Contributions of supraspinal structures in gait control have also been observed in brain imaging studies using motor im-

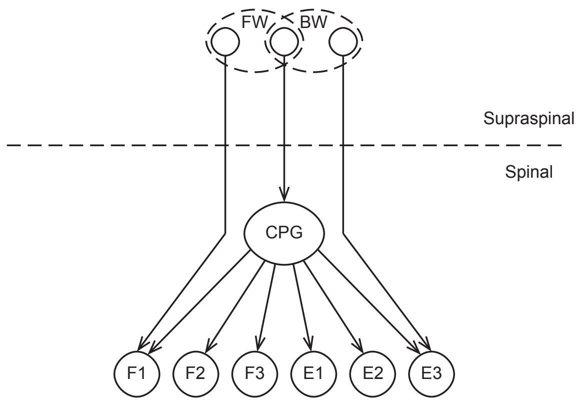

Figure 1: Basic organization of FW and BW. Some basic features of the CPG (such as the rhythm generator part) can be used in FW and BW, while parts of the spinal pattern generators may be more specific for FW and BW. Hence the CPG can work in different configurations. The choice of the configurations and the fine tuning is made by separate supraspinal networks (that may be located at specialized separate areas). The F1-F3 refer to different flexors and E1-E3 to different extensors. The scheme indicates that some motoneuron pools get input from both the CPG and from supraspinal sources but this input could go either to flexors or extensors, irrespective of the direction of gait (hence no direction specific bias for F or E is implied). For simplicity the feedback from afferent sources to the various levels is not depicted.

agery of gait (for overview: see (17)). Specifically, imagery of BW required larger activation of cortical areas, e.g., for visual-spatial processing and sensorimotor control, and less activation in the brainstem and cerebellum, as compared to imagery FW (17). Hence BW seems to be less automated than FW. The cerebellum and brainstem may be needed for fine tuning and learning. At that level there may be separate circuits supporting either type of gait (Fig. 1). This notion is also supported by the cat experiments of Musienko et al (33). They compared locomotion evoked from the brainstem (by stimulation of the mesencephalic locomotor region (MLR)) with locomotion evoked by epidural stimulation of the spinal cord. They found that MLR stimulation evoked well-coordinated stepping movements only if the treadmill was moving in the front-to-rear direction. They concluded that supraspinal commands select one of the numerous forms of operation of the spinal limb controllers, namely, the forward walking. Presumably there are other supraspinal networks where BW is fine tuned.

This conceptual framework could also explain why there is a lack of transfer in FW and BW adaptations (see above). The lack of transfer is not necessarily in conflict with the idea that there may be common generator parts being involved in both FW and BW. Choi and Bastian propose that independently adaptable locomotor networks exist for each leg in humans. The basic locomotor networks are configured and modulated by feedforward commands from descending brain signals as well as via sensory feedback from afferent input (4). Hence CPGs may provide basic rhythms but the details of the pattern are dictated both by spinal and supraspinal circuits, some of which are specialized for FW, others for BW. Hence the idea arises of generators which have elements that can be reconfigured so that they can be used for different locomotion modes (15). On the basis of such models one can predict that some muscles show a simple reversal of the activity patterns but that others would show quite different patterns for FW and BW.

This concept has been confirmed and expanded on by a recent modeling study of our group (24), using forward simulations to study the effects of muscles on the acceleration of the center of mass in FW and BW (24). It was observed that there was a reversal in function in the muscle control of the horizontal movement of the center of mass (e.g. TA and gastrocnemius). However, in the control of the vertical movement some muscles showed direction-specific contributions (dorsiflexors, including TA). It was concluded that the changes in muscle contributions imply that a simple time-reversal would be insufficient to produce BW from FW and that BW utilizes extra elements, presumably supraspinal, in addition to a common spinal drive. These additions are needed for propulsion and to meet the specific constraints of BW, in particular those related to the ankle joint. This requires that supraspinal sources can give rise to a partial reconfiguration of lower level common networks. Other parts of the spinal generator could be easily used in both types of gait. Control of antigravity muscles is likely through activation of circuits sensitive to load receptors, hence there is no functional reversal needed in the circuits controlling basic extension (as confirmed by (24)). Similarly, in both types of gait there is a need to flex the limb at the different joints and this function could be achieved by a flexor synergy, based on flexor reflex circuitry (8).

Future Perspectives

In recent years, BW and BR are increasingly used in sports and rehabilitation settings. Backward gait is observed to have biomechanical and cardiopulmonary benefits over forward gait under specific conditions. Training that results in cardiovascular (e.g. aerobic fitness) or musculoskeletal (e.g. strength, flexibility) gains may be expected to transfer to other tasks that place similar demands on these systems. From studies evaluating the neural control of gait it is known that FW and BW can be controlled largely by the same basic neural mechanisms but with the addition of circuits that are more specialized for FW or BW. Transfer of any functional outcomes, motor learning or adaptation from backward gait to forward gait has not been observed convincingly, indicating that BW is also at least partly controlled by specialized circuits.

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