

# Sophisticated spinal contributions to motor control

Richard Poppele<sup>1</sup> and Gianfranco Bosco<sup>2</sup>

<sup>1</sup>Department of Neuroscience, University of Minnesota Minneapolis, MN 55455, USA

<sup>2</sup>Department of Neuroscience, Human Physiology Section, University of Rome at Tor Vergata, and Scientific Institute Santa Lucia, 00179 Rome, Italy

**The neural circuitry of the spinal cord is capable of solving some of the most complex problems in motor control. Therefore, spinal mechanisms are much more sophisticated than many neuroscientists give them credit for. A key issue in motor control is how sensory inputs direct and inform motor output, – that is, the sensorimotor process. Other major issues involve the actual control of the motor apparatus. In general, there are at least three basic requirements for motor control: the transformations that map information from sensory to motor coordinates, the specification of individual muscle activations to achieve a kinematic goal, and the control of multiple degrees of freedom. Here, we make the case that the vertebrate spinal cord has the capacity to solve each of these problems to a degree that is relevant for normal behavior.**

Neuroscientists have known for over a century that the intrinsic circuitry of the vertebrate spinal cord is sufficient to control many kinds of behaviorally important motor activities. Nevertheless, there is the dilemma that patients with spinal cord injury are often paralyzed. If the spinal cord does indeed contain the neural circuitry that can control locomotion then, for example, why can't Christopher Reeve walk?

Obviously, the answer to this question is complex – but not because the basic premise is false. The spinal cord circuitry is in fact capable of solving some of the most complex problems in motor control and, in that sense, spinal mechanisms are much more sophisticated than many neuroscientists give them credit for. Nevertheless, spinal cord function in motor control has been traditionally associated with reflex behaviors or with generating the basic rhythmic motor patterns associated with locomotion. These are deemed to be simple, automatic forms of motor behavior that do not require sophisticated neural control. Moreover, the proper operation of these systems seems to require a significant input from higher centers in the nervous system, and these can be interrupted by spinal cord injury.

Recent advances in the neural control of movement and the mechanisms of sensorimotor integration have led to a re-examination of some of ways in which spinal circuitry might contribute to motor control in general. A key issue in

understanding how the nervous system controls movement is how sensory inputs can direct and inform motor output – that is, the sensorimotor processes. Other major issues involve the actual control of the motor apparatus. In general, researchers have focused on at least three basic problems or questions regarding movement control.

One involves the kinds of transformation that map information from sensory coordinates to motor coordinates. This has been investigated by considering the respective sensory and motor reference frames [1]. For example, somatosensory input is organized within a reference frame consisting of the 2D array of receptors in the skin, whereas motor output seems to be organized in an entirely different reference frame, such as the 3D space of limb movement [2,3].

A second question arises from the fact that movement control must somehow be specified as muscle activation patterns through the activity of specific motoneurons. However, the equations of motion that specify the muscle forces required to move a multi-jointed limb to a particular location or through a particular trajectory can be very complex [4,5]. Thus, the solution to this 'inverse dynamics' problem is generally considered to require a considerable computational capacity, which is associated generally with nervous system structures such as the cortex or cerebellum [6–8].

There is also the degree-of-freedom (DOF) problem. Limb movements require a coordinated control of the limb joints to achieve an accurate movement of the limb endpoint (hand or foot). Theoretically however, there are infinitely many ways in which a multi-jointed limb can be manipulated to achieve any given endpoint position and, therefore, many possible solutions to the control problem [9–12]. Several kinds of control strategy have been proposed to deal with this problem [9,13–16], in addition to that proposed originally by the Russian physiologist Bernstein in the 1930s [17]. He suggested that the nervous system adopts strategies that reduce the effective number of DOFs to simplify the control problem.

Each of these problems raises complex issues that have been the subject of a large literature on motor control. The case we make here is that the vertebrate spinal cord has the capacity to solve each of these problems to some degree that is relevant for normal behavior. In fact, the solutions are required for even the simple, automatic forms of behavior attributed to spinal cord function.

Corresponding author: Richard Poppele (dick@umn.edu).

### Motor behavior organized by spinal circuits

We will examine two basic types of spinal motor behavior: target-directed limb movements and simple locomotion. Perhaps the simplest target-directed limb movements are reflexes. These are basically automatic motor responses to sensory stimuli and they are commonly associated with spinal circuits. One example is the wiping reflex, a form of scratching behavior found in many vertebrates. It consists of a well-directed foot swipe to remove an irritating stimulus from the surface of the body [18,19]. Experiments in spinalized frogs and turtles have demonstrated that the circuitry controlling this basic behavior is contained entirely within the spinal cord, and even within specific spinal segments [20,21].

Simple locomotion is another motor behavior that can be controlled largely by spinal circuits [22–26]. However, some essential elements of normal locomotion do require input from higher centers – namely, instructions about onset, speed and direction, as well as basic components of balance [27–30]. But, given the appropriate instruction (in whatever form that might take), spinal circuits can activate motoneurons to produce a typical kinematic pattern of locomotion, and this has now been confirmed in adult spinalized cats. Cats with a complete transection of the spinal cord at T11–T13 have been rehabilitated to walk on a treadmill with full weight support and normal kinematic gait patterns [31].

We will examine these behaviors further to illustrate the capabilities of spinal circuitry in solving some of the basic problems of motor control.

#### Sensorimotor processes

A major component of current motor-control research is focused on the mechanisms underlying goal-directed limb movements, which require a complex sensorimotor interaction [3]. The aforementioned wipe reflex is a goal-directed limb movement that clearly requires a precise mapping between a sensory input on the skin and the localization of the limb endpoint. Furthermore, in addition to the stimulus location on the body surface, this reflex also requires information about body geometry. For example, proprioceptive information about limb position must be combined with the somatosensory input that triggers the behavior. This is illustrated clearly by a variant of the wipe reflex, the frog heel wipe, in which the animal uses one leg to remove an irritant from the opposite leg. The target is reached even when the leg is placed in different positions [19].

This is not a simple one-to-one mapping of sensory to motor coordinates because the same sensory stimulus can engage completely different motor outputs. For example, an irritant on the lower back of the frog can elicit an ‘overhand’ toe wipe that sweeps the hind leg counter-clockwise, or it can, with nearly equal probability, elicit an ‘underhand’ heel wipe with a clockwise movement (Fig. 1). These behaviors, reminiscent of reaching an awkward itch on our own backs, could employ different sets of muscles, and they indicate the dynamic nature of the sensorimotor mapping [20].

A similar behavior is seen in the turtle. Three forms of scratching have been studied in this animal – a pocket scratch, a rostral scratch and a caudal scratch.

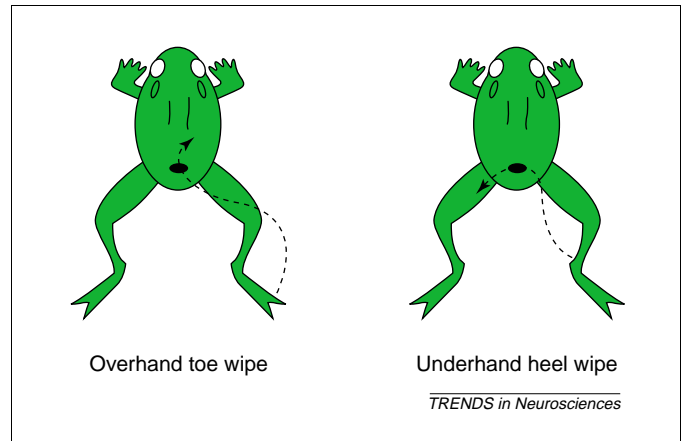


Fig. 1. Wiping reflex in the frog. An irritant on the lower back of a spinalized frog (black oval) evokes a well-directed wipe response to remove the offending stimulus. It can elicit one of two forms of wipe with approximately equal probability. A toe wipe begins with flexion at the hip and knee followed a general limb extension, moving the toe to the stimulus (dashed line). By contrast, a heel wipe begins with an extension of the hip and a foot trajectory in the opposite direction. Thus, two very different patterns of muscle activity are triggered by the same stimulus. Adapted from Refs [18,20].

Stimulation of sites within a transition zone between that of the pocket and rostral scratches, for example, can either produce one of the patterns or produce a motor pattern blend [32], suggesting that there is blending of modular motor programs [33].

There is little experimental evidence available on the detail of how these sensorimotor tasks are accomplished, although the turtle studies showed that broadly tuned propriospinal neurons with overlapping receptive fields are rhythmically activated during scratching [34]. The studies also provided evidence that discrete neuronal populations contributing to the behavior can be active or quiet in a coordinated manner during scratching. Thus, it seems that a few populations of neurons with overlapping influence might control a range of behaviors. Various combinations of these neural modules would correspond to different behaviors, such as the motor pattern blends observed in the turtle with transition behaviors. Transitions such as those observed in the frog wipe might be controlled in a similar way using a ‘winner-take-all’ strategy to determine the output. In that case, the module with the strongest representation would entirely control the motor output.

An important issue in understanding sensorimotor integration of the type observed in the wipe reflex is to understand how the nervous system maps sensory coordinates to motor coordinates. The goals of the wipe and scratch reflexes are defined in terms of kinematic parameters (i.e. locations and trajectories in space), yet the actual behavior is generated by muscle activation. A possible mechanism underlying this transformation was conceptualized by Bizzi, Giszter and colleagues with the notion of ‘motor primitives’ [35]. According to this idea, activity in distinct neuronal clusters in the spinal cord comprises a motor primitive that is responsible for controlling a specific sub-component of limb position and movement.

Giszter and colleagues found four stimulus locations in the frog spinal cord, each associated with a different

pattern of limb forces converging to a specific equilibrium limb position [35,36]. Stimulating more than one such location drove the foot towards an intermediate position, so it was possible to achieve many different limb positions by activating one or more of these discrete areas, regardless of the starting position of the limb. The attractiveness of this type of neural organization is its simplicity. Modular activity can be combined with different weightings to produce a behaviorally relevant motor output.

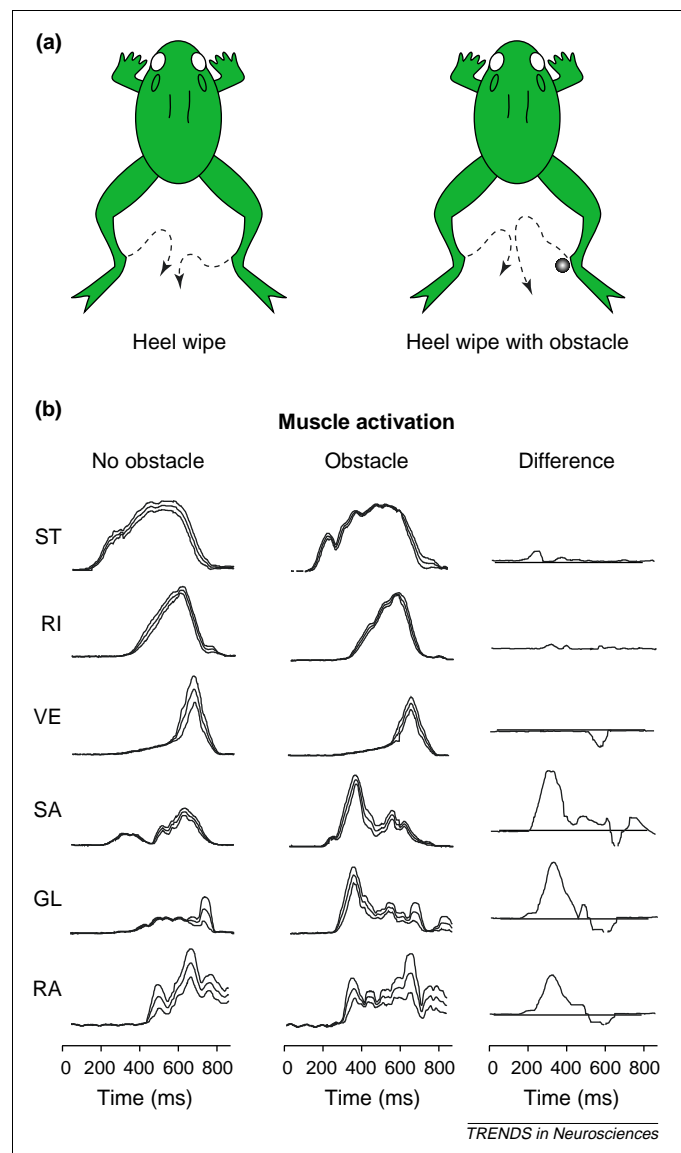
The initial evidence in support of this notion was controversial because it was based on the results of electrical microstimulation [36]. However, later findings showed that motor primitives could be also identified using more natural means of activating the spinal circuitry [37,38]. For example, Kargo and Giszter [39,40] showed that a sensory stimulus applied to a frog limb during a wipe can evoke a muscle activation pattern that looks like a motor primitive (Fig. 2). Such data suggest that motor primitives can also be activated together in chains to achieve movements. Through this mechanism, kinematic sensory information (in this case, the location of a sensory stimulus) engages motor elements that can be combined to produce behaviorally appropriate movements that might also be contingent on the interaction of proprioceptive feedback with central motor programs.

Proprioceptive feedback originates within muscles and joints and, therefore, it operates within a reference frame that is more like that of the muscles and joints than that of the skin receptors. Thus, any combination of proprioception and somatoreception must somehow deal with the coordinate frame difference. Recent studies of spinal proprioception in the cat have suggested that one way this difference might be resolved is by adopting a common reference frame for both kinds of information [41]. For example, spinocerebellar neurons receive sensory input from proprioceptors and cutaneous receptors in the cat hindlimb. The activity of these cells during passive postures and movements encodes global parameters of the limb kinematics – namely, the orientation and length of the limb axis rather than specific local information about muscles or joints [42,43].

#### The problem of inverse dynamics

Spinal reflex behaviors also imply that spinal mechanisms can solve the inverse-dynamics problem in some way. However, the potential complexity of this problem has led many investigators to propose that higher neural centers are also necessary for solving the problem [44–49]. Such considerations underlie a controversy about whether the CNS controls (or specifies) movement kinematics or movement kinetics [50–53]. Obviously it does both, but several lines of evidence suggest a hierarchical organization in which kinematic goals are specified mainly at higher levels in the hierarchy and are translated into kinetic motor commands mostly at lower hierarchical levels.

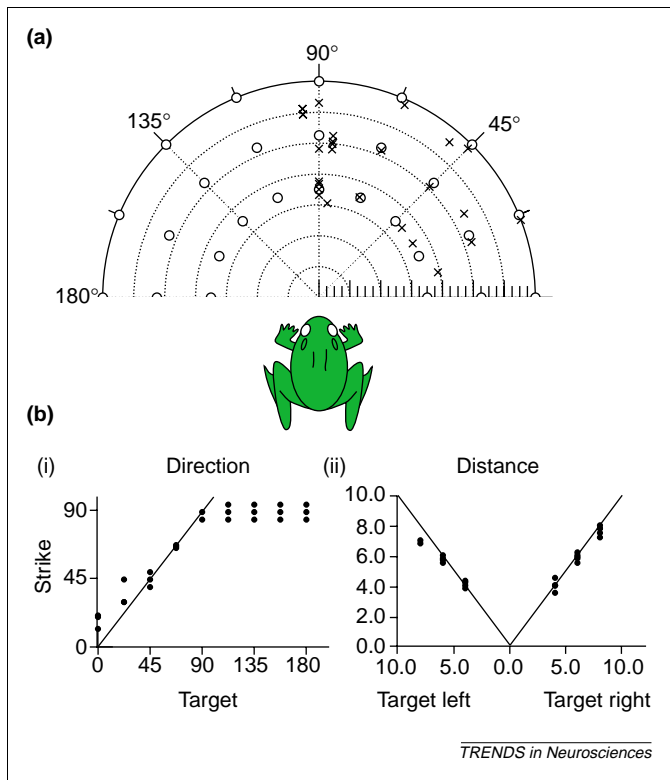
This idea also recognizes the fact that at least goal-directed movements are planned in terms of a kinematics framework. However, the hierarchy is not necessarily an anatomical one and the specific roles played by the spinal circuitry are basically unknown. Nevertheless, several



**Fig. 2.** Overcoming an obstacle. (a) A spinalized frog removes an irritant on one leg using a heel wipe with the opposite leg. An obstacle in the path of the wipe is overcome by changing the foot trajectory (dashed lines) around the obstacle. (b) Electromyography (EMG) activity in six leg muscles reveals a difference pattern corresponding to a motor primitive triggered early in the response. Abbreviations: GL, gluteus; RA, rectus anterior; RI, rectus internus; SA, sartorius; ST, semitendinosus; VE, vastus externus. Reproduced, with permission, from Ref. [40], © (2000) the Society for Neuroscience.

lines of experimental evidence suggest that control signals directed at the spinal circuitry could be encoded in a basically kinematic framework. One such example is the orienting of head and/or body toward a visual or auditory stimulus. Studies, again in the frog, have shown that this behavior has at least two components: one that involves the direction of the stimulus and one involving its distance from the animal [54] (Fig. 3).

Information about these two stimulus attributes is derived from the visual and auditory inputs, which are combined in the optic tectum. Tectal neurons relay this information to brainstem and spinal circuits via specific pathways, and interrupting one of these pathways can remove a specific component of the behavior. For example, a normal orientation behavior for a frog confronted with a live cricket can be to turn its head and body towards the



**Fig. 3.** Orienting behavior in the frog. (a) Frogs presented with a live cricket (represented by circles in the figure) will orient their head and/or body towards the morsel and then hop towards it to strike (denoted by x). Tectal efferent pathways were lesioned unilaterally on the right side. Because tectal representations of space are contralateral, the frog does not orient toward crickets on the left but it does respond by hopping the appropriate distance. (b) Target direction versus strike direction (i) and target distance (in the right or left directions) versus strike distance (ii). Orientation is appropriate for angles between 0° and 90° and remains directed forward (90°) for targets between 90° and 180°. However, strike distance is appropriate for both right and left targets. Note that orienting movements to the right are normal even though they involve muscles on both sides of the body, so the failure to orient to the left cannot be attributed to a right-side paralysis, for example. These results show that motor commands to the brainstem and spinal cord do not specify muscle activation but, rather, more global commands, such as direction and distance. Based on data presented in Ref. [55].

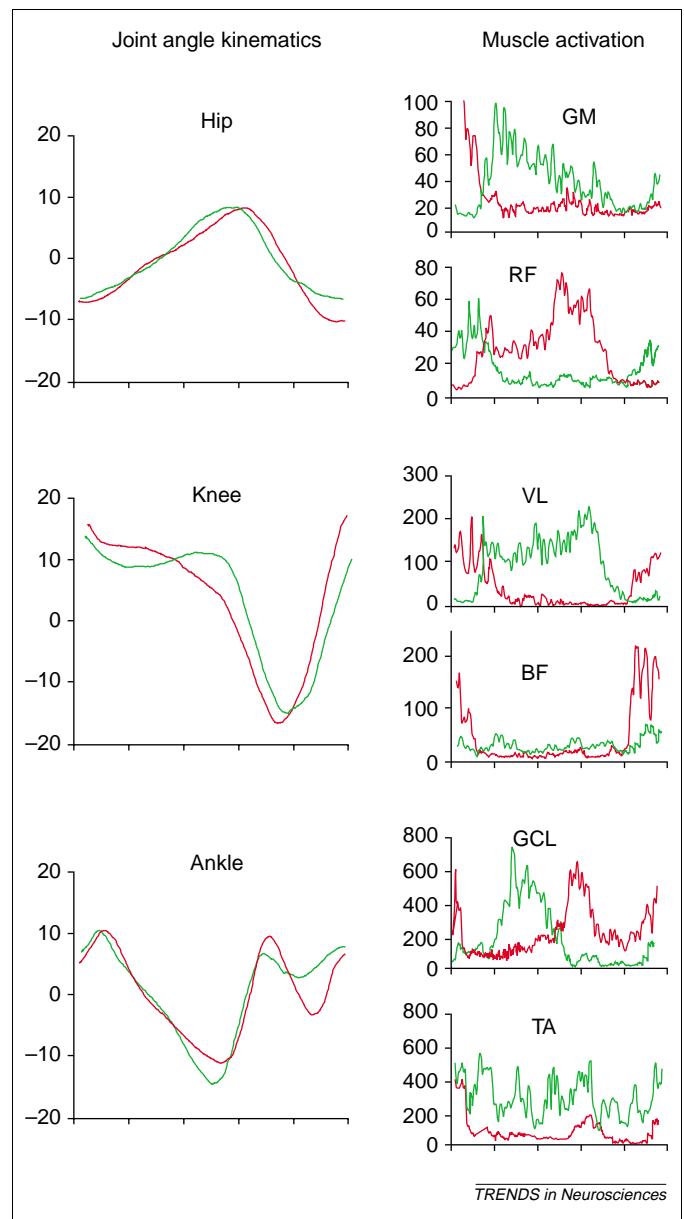
cricket and then to hop towards it. After a lesion of the 'direction' pathway, the animal still responds to the cricket but the response consists of hopping an appropriate distance without re-orientation [55] (Fig. 3).

Observations such as these suggest that the information relayed to spinal centers can have a global context, relating in this case to directions and distances in extra-personal space. This implies that the spinal circuitry could carry out the inverse-dynamics transformation required to generate the appropriate motor behavior, although the observations do not suggest how that might be done. Additional clues might be found in the studies of locomotion – another form of motor behavior that is controlled or directed by supraspinal pathways [27,28] but largely elaborated by the spinal circuitry.

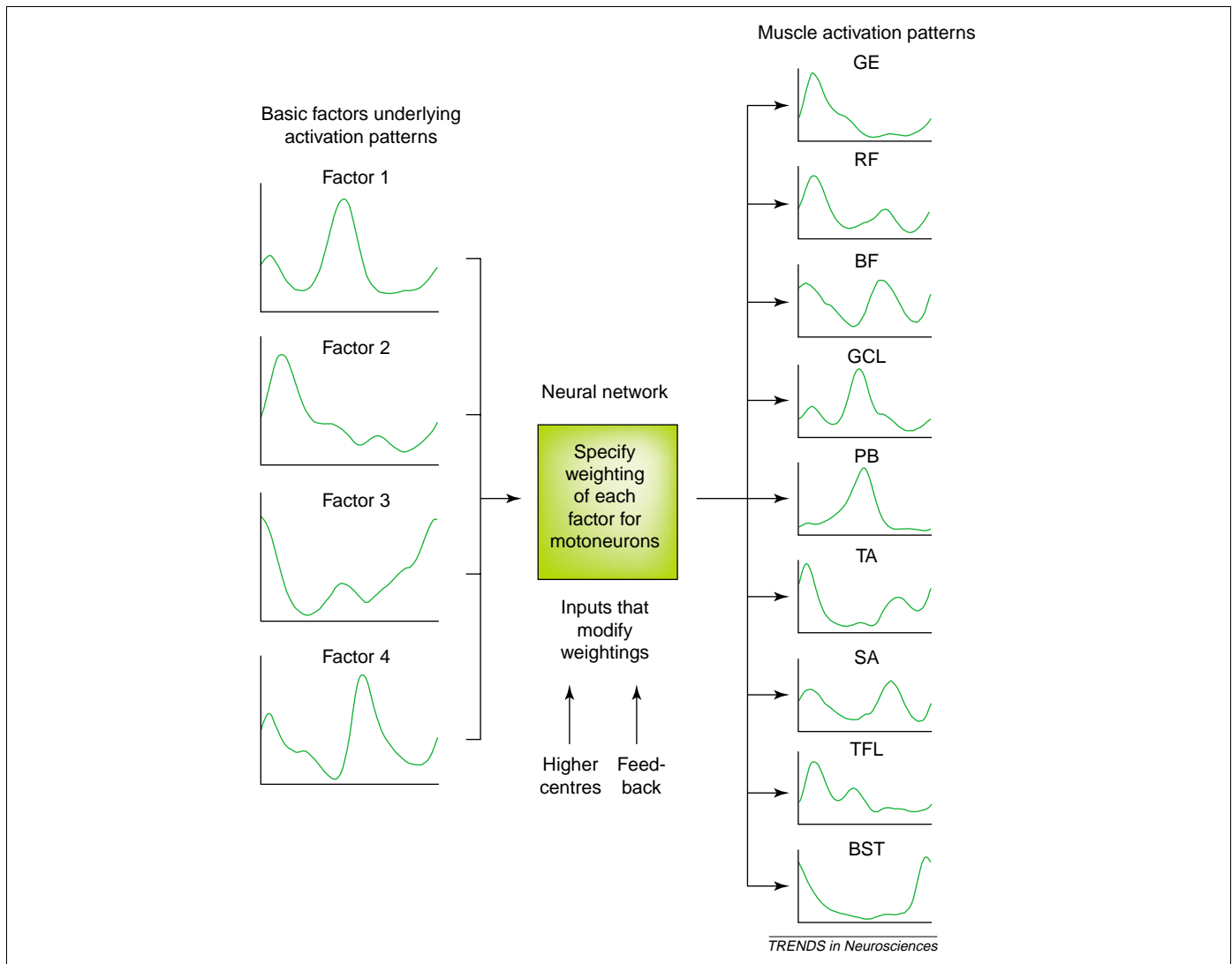
Spinal 'pattern generator' circuits that produce the typical rhythmicity of locomotion have been known about and studied for many decades in invertebrate nervous systems and lower vertebrate (e.g. fish) spinal cords [22,24]. Such circuits are known to be largely sufficient and necessary for the rhythmic movements of the limbs in mammalian locomotion. The seminal work of Shik, Severin and Orlovsky in the 1960s also

revealed the nature of the supraspinal control of locomotion in the cat [27]. They identified a mesencephalic locomotor region (MLR) that could trigger the onset of locomotion and vary its speed. This MLR control, like the tectospinal control in the frog, does not specify muscle activity directly. This point is dramatically illustrated by the gait changes, from walk to trot to gallop, that are induced by simply increasing MLR stimulus intensity.

Recently, the relationship between the kinematics of locomotion and the corresponding muscle activation was



**Fig. 4.** Forward and backward walking. The kinematic trajectories of the joint angles and limb-segment angles are basically the same (but time-reversed) for forward (green curves) and backward (red curves) walking. However, the muscle activation patterns are entirely different in the two types of behavior, reflecting the different force and torque demands on the limbs. The basic invariance of the kinematics in locomotion has led to the suggestion that the kinematics are what the nervous system controls. The x-axes represent a single cycle, from 0% to 100% of the cycle for the forward records and from 100% to 0% for the backward records. Abbreviations: BF, biceps femoris; GCL, gastrocnemius lateralis; GM, gluteus maximus; RF, rectus femoris; TA, tibialis anterior; VL, vastus lateralis. Reproduced, with permission, from Ref. [56].



**Fig. 5.** Transforming a simple set of activation patterns into specific muscle activations. A factor analysis carried out on the activation patterns of 16 lower-limb muscles recorded during normal locomotion showed that the activation can be fully accounted for by a few underlying factors. These basic factors can be combined in various ways and with various weightings to produce any individual muscle activation. This suggests the existence of a neural network to transform a few simple patterns that represent global aspects of an intended movement into the individual muscle activations required to actually perform the movement. To account for the different patterns of muscle activation for different forms of locomotion, for example, the weights set by the network might also be modulated by proprioceptive feedback and by descending pathways. Abbreviations: BF, biceps femoris; BST, biceps semitendinosus; GCL, gastrocnemius lateralis; GE, gluteus medius; PB, peronius brevis; RF, rectus femoris; SA, sartorius; TA, tibialis anterior; TFL, tensor fasciae latae. Adapted from Refs [59,60].

the subject of several studies of human locomotion [56–58]. Typical human gait is characterized by stereotypical kinematics and muscle activation pattern, as revealed by muscle electromyography (EMG) [59]. However, a recent examination of various forms of walking has shown that the kinematics and muscle activation can be specified separately. The kinematics were found to be basically invariant in various conditions, such as backwards or bent-over walking or walking with various levels of weight support, whereas muscle activation was different in each case. The results suggested that perhaps the kinematics of gait is somehow primarily controlled by the system (Fig. 4).

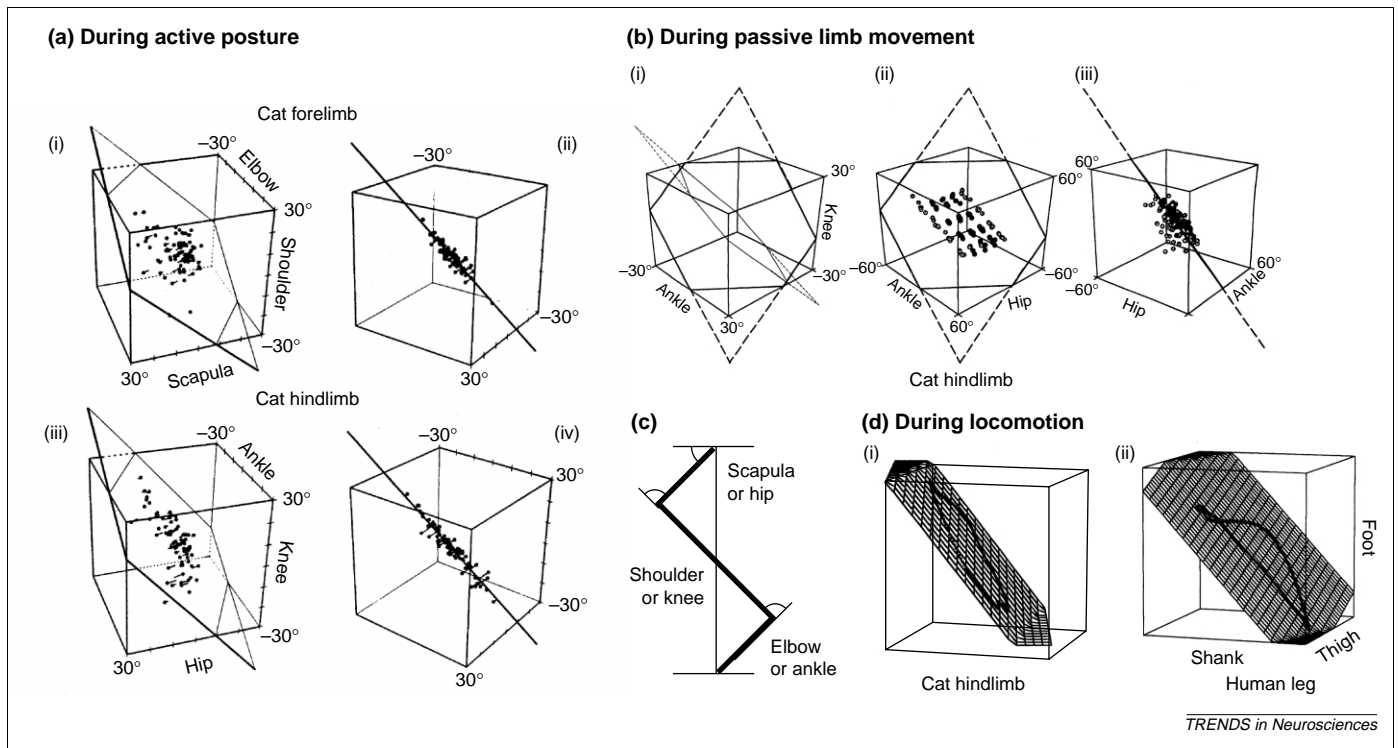
In fact, a given muscle can be activated differently in each of these different kinds of walking, and activation patterns can differ significantly across muscles. Nevertheless, it has been shown that as few as four or five basic activation patterns can account for all the variety of

muscle activation seen in locomotion [60]. These results suggest that motoneuron activation is synthesized by combining a simple set of basic activation patterns (Fig. 5).

Although it is tempting to relate such basic activation patterns to the motor primitives observed in the frog, we are still far from understanding the underlying mechanisms that might be involved. However, recent studies of posture and locomotion in experimental animals have begun to elaborate some of the complexities in terms of these more basic issues [23,61–64]. For example, the motor apparatus itself, with its complex array of muscles and their connections between joints, might play an important role in solving the control problem [65].

#### *The DOF Problem*

Given that the muscles, joints and limb segments, and the neural circuitry that controls them, have evolved in parallel, it seems reasonable to assume that the peripheral



**Fig. 6.** Co-variation of limb joint and segment angles. The interdependence of joint angles during posture and movement is illustrated by these joint-angle plots. For each limb position or increment of movement, three principle angles are plotted along the three angle coordinates. (a) A similar behavior is observed for the cat forelimb (i,ii) and hindlimb (iii,iv) while the animal actively maintains balance on a tilting platform. The plots in (ii) and (iv) show the same data edge-on, to illustrate that the data points fall on a plane in this 3D coordinate system. (b) Joint-angle co-variation is also 2D in the anaesthetized cat hindlimb during passive foot placements by a robot (ii,iii). A comparison between the passive and active co-variance planes in (i) shows that the passive plane is rotated with respect to the active plane. The rotation is due to a reversed relationship between hip and ankle angles in the passive and active states. (c) The joint angles of the forelimb (scapula, shoulder and elbow) and hindlimb (hip, knee and ankle), as referred to in panels (a) and (b). (d) During locomotion, the cat hindlimb (i) and human leg (ii) also show a similar 2D constraint of the elevation angles of the limb segments. Reproduced, with permission, from Refs [42,63,67].

apparatus also plays a role in the motor control strategy. One way in which the limb itself might contribute is to reduce the number of DOFs, through the arrangement of single- and multi-joint muscles in the limb. A typical limb has three primary DOFs for movement in a plane, so that the 2D position of the endpoint in the plane can be achieved by an infinite number of limb geometries – even taking into account the mechanical constraints of the bony articulations at some of the joints. However, experimentally one finds that generally only one limb configuration is used for each endpoint position – that is, there are effectively two DOFs instead of three. This suggests that the joint angles are not determined independently (Fig. 6).

This phenomenon has been investigated most thoroughly by recording limb joint angles during posture and locomotion. Joint angles do, indeed, co-vary during both active and passive postures, and during locomotion in the limbs of both animals and humans [42,63,66,67]. Although the joint angle co-variation is very similar during both active posture and locomotion in the cat hindlimb, for example, it differs systematically from the co-variation found in the passive hindlimb. The difference displays a negative rather than a positive correlation between hip and ankle angles. Observations such as this suggest that neural controllers could somehow manipulate the joint angle co-variance instead of individual joint angles, perhaps through reflex pathways.

### Concluding remarks

The evidence from the animal studies cited here is that the basic circuitry required to produce the coordinated movements of locomotion, for example, are contained within the spinal cord. This brings us back to patients such as Christopher Reeve and why they cannot walk. One major issue is whether these animal models are adequate to apply to human spinal cord function. This is still a matter of uncertainty because of the greater complexity of the primate motor system. However, recent clinical evidence has shown that a complex pattern of descending neural input to the spinal cord might not be required for basic locomotion [68]. Spinal cord injury patients can recover locomotion function through intensive training on a treadmill with body-weight support, in much the same way as has been demonstrated for the spinalized cat [31]. Even hemiplegic patients who were confined to a wheelchair and unable to support their body weight have been able to recover weight support and walking abilities [68,69].

These studies and others combining training with functional electrical stimulation and pharmacological approaches comprise an exciting new approach for patients with spinal cord injury and other neurological impairments leading to spinal dysfunction [70–72]. Additional fundamental investigations of the inherent capabilities of the spinal circuitry should be directed at understanding the spinal mechanisms that transform basic instructions into complex patterns of muscle

activation. Such research might also help us to understand better how to revive spinal capabilities when they have been compromised by injury or disease.

## References

- 1 Soechting, J. and Flanders, M. (1992) Moving in three-dimensional space: frames of reference, vectors and coordinate systems. *Annu. Rev. Neurosci.* 15, 167–191
- 2 Levinsson, A. *et al.* (2002) Spinal sensorimotor transformation: relation between cutaneous somatotopy and a reflex network. *J. Neurosci.* 22, 8170–8182
- 3 Jeannerod, M. *et al.* (1995) Grasping objects: the cortical mechanisms of visuomotor transformation. *Trends Neurosci.* 18, 314–320
- 4 Atkeson, C.G. (1989) Learning arm kinematics and dynamics. *Annu. Rev. Neurosci.* 12, 157–183
- 5 McIntyre, J. and Bizzi, E. (1993) Servo hypothesis for the biological control of movement. *J. Motor Behav.* 25, 193–202
- 6 Schweighofer, N. *et al.* (1998) Role of the cerebellum in reaching movements in humans I Distributed inverse dynamics control. *Eur. J. Neurosci.* 10, 86–94
- 7 Kawato, M. (1999) Internal models for motor control and trajectory planning. *Curr. Opin. Neurobiol.* 9, 718–727
- 8 Darlot, C. *et al.* (1996) Computation of inverse dynamics for the control of movements. *Biol. Cybern.* 75, 173–186
- 9 Wada, Y. *et al.* (2001) Quantitative examinations for multi joint arm trajectory planning—using a robust calculation algorithm of the minimum commanded torque change trajectory. *Neural Netw.* 14, 381–393
- 10 Hogan, N. *et al.* (1987) Controlling multijoint motor behavior. *Exerc. Sport Sci. Rev.* 15, 153–190
- 11 Todorov, E. and Jordan, M.I. (2002) Optimal feedback control as a theory of motor coordination. *Nat. Neurosci.* 5, 1226–1235
- 12 Gielen, C.C. *et al.* (1997) Principles for the control of kinematically redundant limbs. In *Three-Dimensional Kinematic Principles of Eye-, Head- and Limb-Movements* (Fetter, M. *et al.*, eds), pp. 285–297, Harwood
- 13 Buchanan, J.J. and Horak, F.B. (2001) Transitions in a postural task: do the recruitment and suppression of degrees of freedom stabilize posture? *Exp. Brain Res.* 139, 482–494
- 14 Gielen, C.C. and van Bolhuis, B.M. (1998) Task-dependent reduction of the number of degrees of freedom in sensorimotor systems. *Brain Res. Brain Res. Rev.* 28, 136–142
- 15 Soechting, J.F. *et al.* (1995) Moving effortlessly in three dimensions: does Donders' law apply to arm movement? *J. Neurosci.* 15, 6271–6280
- 16 Gottlieb, G.L. *et al.* (1996) Coordinating movement at two joints: a principle of linear covariance. *J. Neurophysiol.* 75, 1760–1764
- 17 Bernstein, N.A. (1967) *The Co-ordination and Regulation of Movements*, Oxford Press
- 18 Giszter, S.F. *et al.* (1989) Kinematic strategies and sensorimotor transformations in the wiping movements of frogs. *J. Neurophysiol.* 62, 750–767
- 19 Fukson, O.I. *et al.* (1980) The spinal frog takes into account the scheme of its body during the wiping reflex. *Science* 209, 1261–1263
- 20 Berkinblit, M.B. *et al.* (1984) Adaptability of innate motor patterns and motor control mechanisms. *Behav. Brain Sci.* 9, 585–638
- 21 Mortin, L.I. and Stein, P.S. (1989) Spinal cord segments containing key elements of the central pattern generators for three forms of scratch reflex in the turtle. *J. Neurosci.* 9, 2285–2296
- 22 Grillner, S. and Wallen, P. (1985) Central pattern generators for locomotion, with special reference to vertebrates. *Annu. Rev. Neurosci.* 8, 233–261
- 23 Pearson, K.G. (1995) Proprioceptive regulation of locomotion. *Curr. Opin. Neurobiol.* 5, 786–791
- 24 Arshavsky, Y.I. *et al.* (1997) Pattern generation. *Curr. Opin. Neurobiol.* 7, 781–789
- 25 Hiebert, G.W. and Pearson, K.G. (1999) Contribution of sensory feedback to the generation of extensor activity during walking in the decerebrate cat. *J. Neurophysiol.* 81, 758–770
- 26 Pearson, K.G. *et al.* (1998) Enhancement and resetting of locomotor activity by muscle afferents. *Ann. New York Acad. Sci.* 860, 203–215
- 27 Shik, M.L. *et al.* (1969) Control of walking and running by means of electrical stimulation of the mesencephalon. *Electromyogr. Clin. Neurophysiol.* 26, 549
- 28 Mori, S. *et al.* (1999) Stimulation of a restricted region in the midline cerebellar white matter evokes coordinated quadrupedal locomotion in the decerebrate cat. *J. Neurophysiol.* 82, 290–300
- 29 Dietz, V. (2002) Proprioception and locomotor disorders. *Nat. Rev. Neurosci.* 3, 781–790
- 30 Pearson, K.G. (2000) Neural adaptation in the generation of rhythmic behavior. *Annu. Rev. Physiol.* 62, 723–753
- 31 Rossignol, S. *et al.* (1999) Locomotor performance and adaptation after partial or complete spinal cord lesions in the cat. *Prog. Brain Res.* 123, 349–365
- 32 Mortin, L.I. *et al.* (1985) Three forms of scratch reflex in the turtle: Movement analysis. *J. Neurophysiol.* 53, 1501–1516
- 33 Stein, P.S. and Daniels-McQueen, S. (2002) Modular organization of turtle spinal interneurons during normal and deletion fictive rostral scratching. *J. Neurosci.* 22, 6800–6809
- 34 Berkowitz, A. and Stein, P.S. (1994) Activity of descending propriospinal axons in the turtle hindlimb enlargement during two forms of fictive scratching: broad tuning to regions of the body surface. *J. Neurosci.* 14, 5089–5104
- 35 Bizzi, E. *et al.* (1995) Modular organization of motor behavior in the frog's spinal cord. *Trends Neurosci.* 18, 442–446
- 36 Giszter, S.F. *et al.* (1993) Convergent force fields organized in the frog's spinal cord. *J. Neurosci.* 13, 467–491
- 37 Bizzi, E. *et al.* (2000) A new perspectives on spinal motor systems. *Nat. Rev. Neurosci.* 1, 101–108
- 38 Tresch, M.C. *et al.* (1999) The construction of movement by the spinal cord. *Nat. Neurosci.* 2, 162–167
- 39 Kargo, W.J. and Giszter, S.F. (2000) Afferent roles in hindlimb wipe-reflex trajectories: free-limb kinematics and motor patterns. *J. Neurophysiol.* 83, 1480–1501
- 40 Kargo, W.J. and Giszter, S.F. (2000) Rapid correction of aimed movements by summation of force-field primitives. *J. Neurosci.* 20, 409–426
- 41 Bosco, G. and Poppele, R.E. (2001) Proprioception from a spinocerebellar perspective. *Physiol. Rev.* 81, 539–568
- 42 Bosco, G. *et al.* (1996) Representation of passive hindlimb postures in cat spinocerebellar activity. *J. Neurophysiol.* 76, 715–726
- 43 Poppele, R.E. *et al.* (2002) Independent representations of limb axis length and orientation in spinocerebellar response components. *J. Neurophysiol.* 87, 409–422
- 44 Johnson, M.T. *et al.* (2001) Central processes for the multiparametric control of arm movements in primates. *Curr. Opin. Neurobiol.* 11, 684–688
- 45 Kalaska, J.F. *et al.* (1997) Cortical control of reaching movements. *Curr. Opin. Neurobiol.* 7, 849–859
- 46 Schwartz, A.B. (1994) Distributed motor processing in cerebral cortex. *Curr. Opin. Neurobiol.* 4, 840–846
- 47 Ghez, C. *et al.* (1991) Organization of voluntary movement. *Curr. Opin. Neurobiol.* 1, 664–671
- 48 Georgopoulos, A.P. (1995) Current issues in directional motor control. *Trends Neurosci.* 18, 506–510
- 49 Todorov, E. (2000) Direct cortical control of muscle activation in voluntary arm movements: a model. *Nat. Neurosci.* 3, 391–398
- 50 Scott, S.H. (2000) Reply to 'One motor cortex, two different views'. *Nat. Neurosci.* 3, 964–965
- 51 Georgopoulos, A.P. and Ashe, J. (2000) One motor cortex, two different views. *Nat. Neurosci.* 3, 963
- 52 Moran, D.W. and Schwartz, A.B. (2000) One motor cortex, two different views. *Nat. Neurosci.* 3, 963
- 53 Todorov, E. (2000) Reply to 'One motor cortex, two different views'. *Nat. Neurosci.* 3, 3963–3964
- 54 Grobstein, P. (1988) Between the retinotectal projection and directed movement: topography of a sensorimotor interface. *Brain Behav. Evol.* 31, 34–48
- 55 Kostyuk, S.K. and Grobstein, P. (1987) Neuronal organization underlying visually elicited prey orienting in the frog—I. Effects of various unilateral lesions. *Neuroscience* 21, 41–55
- 56 Grasso, R. *et al.* (1998) Motor patterns for human gait: backward versus forward locomotion. *J. Neurophysiol.* 80, 1868–1885
- 57 Ivanenko, Y.P. *et al.* (2002) Control of foot trajectory in human

- locomotion: role of ground contact forces in simulated reduced gravity. *J. Neurophysiol.* 87, 3070–3089
- 58 Grasso, R. *et al.* (2000) Interactions between posture and locomotion: motor patterns in humans walking with bent posture versus erect posture. *J. Neurophysiol.* 83, 288–300
- 59 Winter, D.A. and Yack, H.J. (1987) EMG profiles during normal human walking: stride-to-stride and inter-subject variability. *Electromyogr. Clin. Neurophysiol.* 67, 402–411
- 60 Davis, B.L. and Vaughan, C.L. (1993) Phasic behavior of EMG signals during gait: Use of multivariate statistics. *J. Electromyogr. Kinesiol.* 3, 51–60
- 61 McCrea, D.A. (2001) Spinal circuitry of sensorimotor control of locomotion. *J. Physiol. (Lond.)* 533, 41–50
- 62 Prochazka, A. (1996) The fuzzy logic of visuomotor control. *Can J. Physiol. Pharmacol.* 74, 456–462
- 63 Lacquaniti, F. *et al.* (1999) Motor patterns in walking. *News Physiol. Sci.* 14, 168–174
- 64 Yakovenko, S. *et al.* (2002) Spatiotemporal activation of lumbosacral motoneurons in the locomotor step cycle. *J. Neurophysiol.* 87, 1542–1553
- 65 Nichols, T.R. (1994) A biomechanical perspective on spinal mechanisms of coordinated muscular action: an architecture principle. *Acta Anat. (Basel)* 151, 1–13
- 66 Shen, L. and Poppele, R.E. (1995) Kinematic analysis of cat hindlimb stepping. *J. Neurophysiol.* 74, 2266–2280
- 67 Lacquaniti, F. and Maioli, C. (1994) Independent control of limb position and contact forces in cat posture. *J. Neurophysiol.* 72, 1476–1495
- 68 Dietz, V. (2002) Do human bipeds use quadrupedal coordination? *Trends Neurosci.* 25, 462–467
- 69 Dietz, V. (2001) Spinal cord lesion: effects of and perspectives for treatment. *Neural Plast.* 8, 83–90
- 70 de Leon, R.D. *et al.* (2001) Is the recovery of stepping following spinal cord injury mediated by modifying existing neural pathways or by generating new pathways? A perspective. *Phys. Ther.* 81, 1904–1911
- 71 Barbeau, H. *et al.* (1999) Tapping into spinal circuits to restore motor function. *Brain Res. Brain Res. Rev.* 30, 27–51
- 72 Pearson, K.G. (2001) Could enhanced reflex function contribute to improving locomotion after spinal cord repair? *J. Physiol. (Lond.)* 533, 75–81

## Trends Editorial Policy

*Trends journals* are indispensable reading for anyone interested in the life-sciences. At the heart of the journal there are authoritative Reviews and Opinions written in an accessible style by leading authors, which summarize exciting developments in your field. The majority of Reviews and Opinions are commissioned by the editor, but some originate from proposals. All of them are thoroughly peer reviewed.

- **Review** articles provide clear, concise, well illustrated and balanced views of recent advances, citing the primary literature and identifying important trends and key questions for on-going research.
- **Opinion** articles are special reviews designed to stimulate debate and cover controversial and emerging areas of research, and to present new models and hypotheses relating to a particular viewpoint.
- **Research Focus** articles provide detailed commentary and analysis in relation to recent primary research papers, and are restricted to 1500 words plus figures.