

Axial dynamics during locomotion in vertebrates: lesson from the salamander

Jean-Marie Cabelguen^{†,*}, Auke Ijspeert[‡], Stéphanie Lamarque[†] and Dimitri Ryczko[§]

[†] Neurocentre Magendie, INSERM U 862, Université de Bordeaux, Bordeaux Cedex, France

[‡] Swiss Federal Institute of Technology, Lausanne (EPFL), Lausanne, Switzerland

[§] Groupe de Recherche sur le Système Nerveux Central, Département de physiologie, Université de Montréal, Montréal, Québec, Canada

Abstract: Much of what we know about the flexibility of the locomotor networks in vertebrates is derived from studies examining the adaptation of limb movements during stepping in various conditions. However, the body movements play important roles during locomotion: they produce the thrust during undulatory locomotion and they help to increase the stride length during legged locomotion. In this chapter, we review our current knowledge about the flexibility in the neuronal circuits controlling the body musculature during locomotion. We focus especially on salamander because, as an amphibian, this animal is able to display a rich repertoire of aquatic and terrestrial locomotor modes.

Keywords: Axial networks; Dynamical systems; Locomotion; Salamander.

Introduction

The function of the axial musculature during locomotion in vertebrates is of critical importance. In species using axial-based undulatory locomotion, animals (e.g., lampreys, most fish, and snakes) employ axial muscles in the production of lateral undulations of the trunk and tail to propel in aquatic and/or terrestrial medium (Grillner and

Kashin, 1976; Jayne, 1988; Lindsey, 1978). By contrast, in appendage-based modes of locomotion, the animals use primarily their limb muscles to propel themselves (Biewener, 2003; Orlovsky et al., 1999). However, the axial musculature serves two important roles in these animals: the production of trunk bending to increase the stride length and the stabilization of the trunk.

Much of what we know about axial muscle functions during locomotion is derived from studies examining animals moving within a single, homogeneous environment, at a constant speed

* Corresponding author.

Tel.: +33-5-57-57-40-52; Fax: +33-5-57-57-40-51

(or across a narrow range of speeds), and along a straight track. However, animals must be able to maneuver through complex and changing external environments at varying speeds, and using different modes of locomotion (dynamic conditions). As a result, the functions of the axial musculature during locomotion have remained relatively unexplored.

Among vertebrates, salamanders offer a remarkable opportunity to investigate the capacity of the neuronal circuits that control the body axis (“axial networks”) to adapt their output in response to alterations in external conditions, and to switches between locomotor modes. Indeed, adult salamanders are tetrapods capable of displaying a variety of aquatic and terrestrial locomotor modes. In water, they can both walk along the bottom and swim in the water column; while on land they can crawl, walk, or trot. Since aquatic and terrestrial environments pose different challenges for salamanders attempting to move, an analysis of the modifications of the activation patterns of the axial musculature associated with their different forms of locomotor behaviors should provide information about the flexibility of the axial locomotor networks.

The goal of this chapter is to review our current understanding of the adaptive processes that occur in axial networks during locomotion in vertebrates, with examples drawn mainly from salamanders. First, we review the current data about the changes in the axial locomotor pattern in response to changes in either external conditions or internal goals. Second, neurobiological data about the neural processes underlying the flexibility of the axial locomotor networks are presented.

Diversity and variability of axial locomotor patterns

Several studies have documented the patterns of activation of axial muscles during locomotion, but a few have documented their modification

in response to internal goals or external conditions. This part of the review focuses on such modifications, with examples drawn from appendage-based locomotion and axial-based locomotion.

Appendage-based locomotion

Mammals

Several studies have addressed the modifications of the axial locomotor patterns in mammals in relation to speed and types of gait. In cats and dogs, the transition from alternate stepping to galloping is associated with a switch from a synchronous bilateral activation of lumbar back muscles twice per cycle during alternate stepping, to once per cycle during galloping (Carlson et al., 1979; English, 1980; Tokuriki, 1974; Zomlefer et al., 1984). Moreover, in intact dogs trotting on a treadmill, the double activation pattern of epaxial muscles is more consistent at higher trotting speed than at lower trotting speed (Ritter et al., 2001).

In human, the pattern of lumbar back muscle activity during both walking and running is phasic, with two bursts of activity per stride cycle on each side of the spine (Carlson et al., 1988; Cromwell et al., 2001; De Sèze et al., 2008; Saunders et al., 2005; Thorstensson et al., 1982; Waters and Morris, 1972). The two-burst pattern becomes more prominent during loading of the trunk, as also reported in the trotting dog (Ritter et al., 2001; Thorstensson, 1986).

Interestingly, a recent systematic study of the activation pattern of back muscles in humans provided evidence of waves of electromyography (EMG) activity traveling posteriorly along the vertebral column during forward or backward treadmill walking (De Sèze et al., 2008). Traveling waves of lateral bending have also been reported during free overground walking in the domestic ferret (Kafafi and Golani, 1998).

In human, the effects of locomotor mode and those of speed on the pattern of activation of paraspinal muscles can be further studied separately. A transition from walking to running at

the same speed produces substantial alterations in the pattern of activity of lumbar back muscles (Cappellini et al., 2006; Saunders et al., 2004, 2005; Thorstensson et al., 1982). Conversely, increases in speed during a given locomotor mode (walking or running) are associated with increases in the intensity and relative duration of muscle activations of paraspinal muscles, and only minor changes in their relative timings (Anders et al., 2007; Cappellini et al., 2006; Saunders et al., 2004, 2005; Thorstensson et al., 1982). Interestingly, interindividual variability is larger at low speeds than at high speeds of walking in humans (Ivanenko et al., 2009).

The amplitude and the activation pattern of back muscle during stepping in mammals are shaped by the direction of progression (De Sèze et al., 2008; Hase and Stein, 1999), the physical environment (Chevutschi et al., 2007; Masumoto et al., 2004, 2005; Wada et al., 2006a, 2006b), and during voluntary modifications of the locomotor task (Carlson et al., 1988; De Sèze et al., 2008).

Previous studies have demonstrated that some hypaxial muscles are phasically activated during locomotion in humans (Anders et al., 2007; Cappellini et al., 2006; Saunders et al., 2004; Waters and Morris, 1972) and dogs (Carrier, 1996; Deban and Carrier, 2002; Fife et al., 2001). However, the role of the hypaxial musculature during stepping in mammals remains poorly understood. The main reason is that this musculature performs simultaneously two functions (locomotion and lung ventilation) that are difficult to differentiate one from the other. However, hypaxial muscles with a pure or a primarily locomotor function (stabilization of the trunk against sagittal shearing torques) have been identified in dogs running on a treadmill (Deban and Carrier, 2002; Fife et al., 2001).

Lower vertebrates

While in mammals the pattern of activation of epaxial muscles is typically biphasic during alternated forms of stepping, lower legged

vertebrates (salamanders and lizards) show single bursting patterns per locomotor cycle (Delvolvé et al., 1997; Frolich and Biewener, 1992; Ritter, 1995, 1996). However, a comparison between salamanders and lizards reveals differences in epaxial muscle activation patterns during stepping.

In salamanders, the activity pattern of the main epaxial muscles (*dorsalis trunci*) during walking trot conforms to the one expected for the production of lateral bending of the trunk with fixed nodes close to the girdles (“standing wave”; Delvolvé et al., 1997; Frolich and Biewener, 1992; Fig. 1). Indeed, the myomeres located between the forelimb and hindlimb (mid-trunk myomeres) express single synchronous bursts of activity, contralateral to the hindlimb support during each step cycle. Conversely, in trotting lizards, the uniphasic activation of epaxial muscles occurs ipsilateral to the hindlimb support and contributes to the dynamic stabilization, and not to the lateral bending, of the trunk (Ritter, 1995, 1996). Similarly in mammals, the epaxial muscles stabilize the trunk and pelvis against inertial loadings, and the forces applied to it by the hindlimb muscles during stepping on a level surface (Carlson et al., 1979; English, 1980; Ritter et al., 2001; Schilling and Carrier, 2009; Thorstensson et al., 1982; Tokuriki, 1973a, 1973b).

It has been suggested that the difference in the activity pattern and function of the epaxial muscles may be associated with differences between vertebrate groups as to the anatomy of the epaxial musculature (i.e., myomeric vs. tripartite), the dorsoventral flexibility of the body axis, the limb position (parasagittal vs. lateral), and the locomotor habit (amphibious vs. fully terrestrial) (Ritter, 1995, 1996).

In salamanders, the lateral hypaxial musculature often exhibits a double bursting pattern during stepping, with one burst (main burst) present in every step cycle and one burst (facultative burst) of lower intensity and more variable in occurrence (Bennett et al., 2001). Furthermore, the timing of the bursts within the locomotor cycle supports the view that the hypaxial

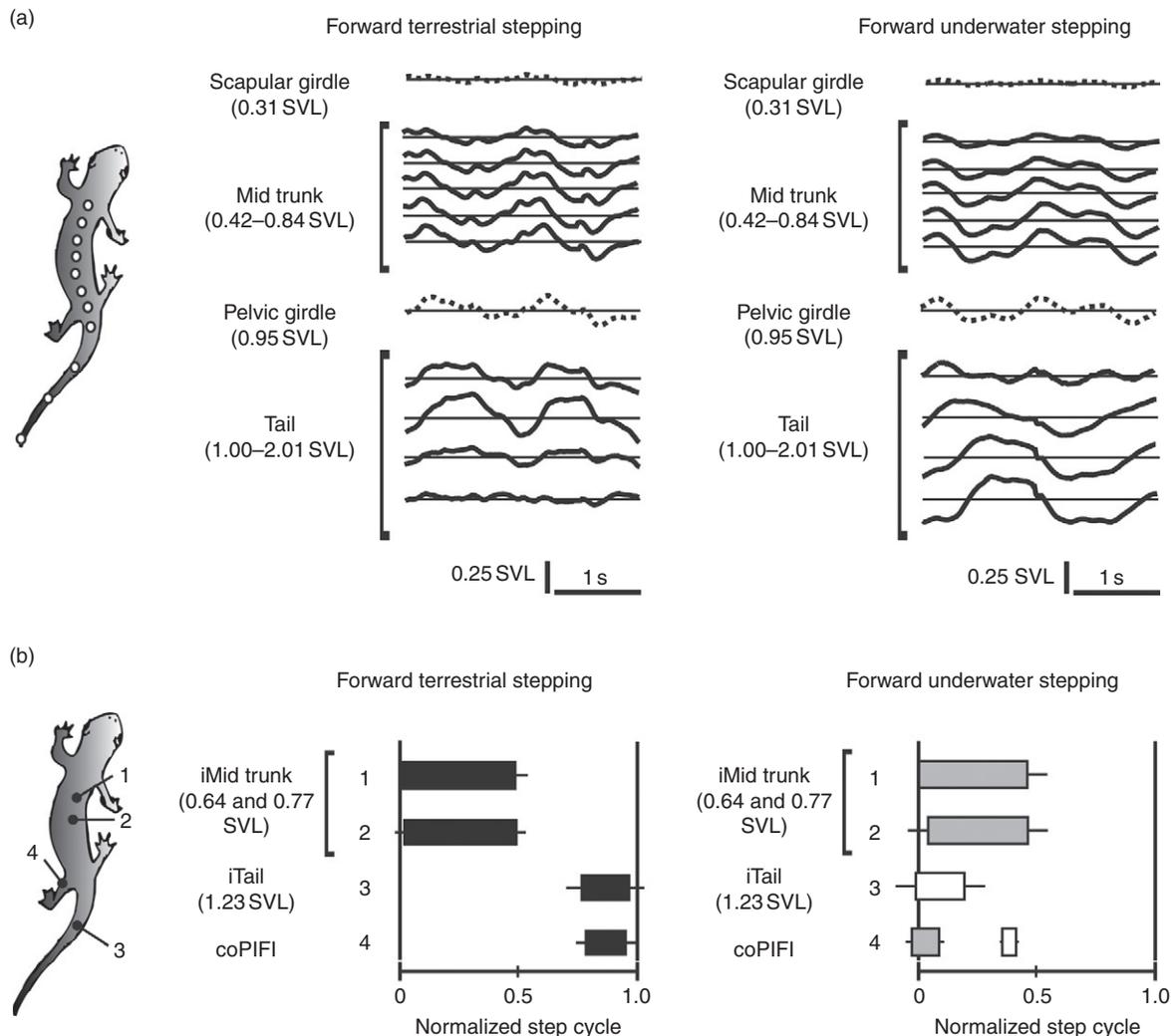


Fig. 1. Comparison between the locomotor patterns during terrestrial and underwater forward stepping in the same salamander. (a) Plots of lateral displacements versus time for 11 midline marker dots during a period of 2.5 s of terrestrial (*left*) and underwater (*right*) forward trotting. The locations (drawing at *left*) and the lateral displacement of the markers dots are expressed in percentage of snout vent length (SVL). In each plot, zero displacement is arbitrary, corresponding to the direction of travel (thin line). Upward deflections indicate movements toward one side and downward deflections movements toward the opposite side. Data are from the same *Pleurodeles waltlii* (SVL: 9.60 cm). (b) Relative timing of EMG activities of ipsilateral mid-trunk and tail myomeres, and of one protractor muscle (PIFI: *pubioischiofemoralis internus*) of the contralateral hindlimb during terrestrial (*left*) and underwater (*right*) forward stepping cycle. Anatomical positions of the recorded muscles are indicated in drawing at *left*. i, ipsilateral; co, contralateral. The step cycle (abscissa) is defined as the time interval between two successive onsets of activity in the 0.64 SVL myomere. For each longitudinal location (ordinate), bars illustrate the mean duration of the burst of activity expressed as a percentage of the step cycle. Error bars indicate SEM. Terrestrial stepping: average of 18 cycles. Underwater stepping, average of 55 cycles. Note that during underwater stepping, the EMG bursts have a low amplitude (gray-filled bars), or are absent in some strides (empty bars).

musculature plays a dual role during terrestrial locomotion in salamanders: (i) resisting torsional forces translated to the trunk by the limbs (main burst) and (ii) bending the trunk (facultative burst) (Bennett et al. 2001; Carrier, 1993; Deban and Schilling, 2009; O'Reilly et al., 2000). In lizards, some lateral hypaxial muscles are primarily involved in lateral bending of the trunk and not in long-axis stabilization of the trunk against torsional loads during terrestrial locomotion (Ritter, 1995, 1996).

Several studies have provided evidence of a high degree of variability in the axial locomotor pattern in salamanders, depending on gait and physical environment (e.g., aquatic vs. terrestrial; dry vs. slippery surface). During forward stepping on land, combinations of standing and traveling mechanical waves have been reported in salamanders depending on the speed of locomotion or type of gait (Ashley-Ross, 1994a; Edwards, 1977). It has further been suggested that the more reduced the limbs are, the slower the speed at which the traveling waves appear, that is, salamanders with very reduced limbs rely more on traveling waves on ground, while those with stronger limbs mainly use standing waves (Ashley-Ross, 1994a). Interestingly, salamanders with reduced forelimbs and no hindlimbs (e.g., the aquatic *Siren lacertina*) combine alternating use of the forelimbs with traveling undulatory waves during aquatic walking (Azizi and Horton, 2004). Similar observations have been previously reported in lizards (Daan and Belterman, 1968; Ritter, 1992, 1996).

Salamanders use either standing or head-to-tail traveling waves of axial undulation and epaxial muscle activity during straightforward stepping performed along a submerged trackway (i.e., during reduced gravity and increased viscosity; Fig. 1; Lamarque et al., 2009; see also Deban and Schilling, 2009). Interestingly, the variability in the mid-trunk pattern (Lamarque et al., 2009) and in limb kinematics (Ashley-Ross et al., 2009) is greater during aquatic than during terrestrial stepping. The higher variability of the motor

pattern during aquatic stepping likely results from reduced constraints on the underlying substratum because of buoyancy.

Furthermore, the tail EMG activity is absent or very weak during underwater forward stepping in a straight line, although the concomitant tail movements are large (Fig. 1). This suggests that the tail movements during aquatic straightforward stepping mainly result from a passive transmission of the active mid-trunk movements to the tail. This further supports the view that the part of the axial network generating the tail movements can be functionally decoupled from that controlling the mid-trunk movements (Delvolvé et al., 1997).

In contrast, during straightforward stepping on a wet surface, tail myomeres typically display an additional burst of activity in phase with every ipsilateral mid-trunk burst (Delvolvé et al., 1997). This double bursting pattern can help the animal to maintain the tail as much as possible aligned to the direction of movement during straightforward stepping (Ashley-Ross, 1994a, 1994b; Roos, 1964). A similar stabilizing function of the head has been attributed to the myomeres located rostrally to the scapular girdle (Ashley-Ross, 1994a, 1994b; Roos, 1964).

Salamanders can spontaneously exhibit short episodes of backward stepping during maneuvering on land. Thereafter, they switch to a more efficient forward stepping. Much longer episodes of backward stepping can be induced by training the animal to walk backward on a motorized treadmill. In these conditions, backward walking involves a very different and more variable hindlimb motor pattern than that observed during forward walking (Ashley-Ross and Lauder, 1997). Unfortunately, the precise bending pattern of the trunk (i.e., the presence of traveling or standing waves) and the EMG pattern of axial muscles have not been investigated.

The flexibility of the spinal pattern-generating networks can also be revealed by comparing the axial motor pattern in restrained and free-stepping salamanders. When grasped by the pelvic girdle during ongoing overground stepping,

salamanders respond with slow, strong rhythmic trunk movements characterized by waves of undulations and epaxial muscle activity traveling from tail to head (Lamarque et al., 2009). This motor behavior is quite similar to that exhibited during struggling behavior in the tadpole (Kahn and Roberts, 1982) and zebrafish (Liao and Fetcho, 2008).

In conclusion, the studies of pattern of activity of axial muscles during stepping in various limbed vertebrates have demonstrated some aspects of the dynamics of the stepping networks which allows organisms to adapt to the various demands of a particular situation, such as speed and physical environment.

Axial-based locomotion

In lampreys (Davis et al., 1993; Williams, 1986), eels (Gillis, 1998a; Grillner and Kashin, 1976), larval zebrafish (Budick and O'Malley, 2000), *Xenopus* tadpoles (Kahn et al., 1982; Soffe et al., 1983), and in some snakes (Jayne, 1988), steady undulatory swimming in water is characterized by waves of lateral displacement traveling from head to tail. The waves of lateral bending are produced by epaxial muscle activations which alternate between the two sides of the body, and travels caudally with a constant speed (Gillis, 1998b; Grillner and Kashin, 1976; Hoff and Wasserburg, 2000; Wallén and Williams 1984). The speed of swimming is mainly modulated by the frequency and the amplitude of the body undulations which are controlled by both recruitment of new motor units and increase in their firing frequency (Gillis 1998b; Grillner and Kashin, 1976; McLean et al., 2007).

In water, salamanders are capable of rapidly switching from forward stepping to forward swimming. The swimming mode is similar to that of lampreys and eels, with axial undulations being propagated as traveling waves from head to tail (Carrier, 1993; D'Août and Aerts, 1997; Daan and Belterman, 1968; Deban and Schilling, 2009;

Frolich and Biewener, 1992; Gillis, 1997; Roos, 1964). The amplitude of these axial undulations typically increases along the body of the salamander. Such a swimming mode is called anguilliform swimming and does not involve limb movements: limbs are folded backward along the body. As in the lamprey, the average wavelength usually corresponds to the length of the body (i.e., the body produces one complete wave per cycle) and does not vary with the frequency of oscillation (D'Août and Aerts, 1997; Frolich and Biewener, 1992).

An interesting difference between the two locomotor modes of the salamander (forward swimming and forward stepping) is that the frequency of the swimming movements is generally two to three times higher than that of the trotting movements (Bennett et al., 2001; Deban and Schilling, 2009; Delvolvé et al., 1997; Frolich and Biewener, 1992). There is generally no overlap of frequencies between the two locomotor modes (i.e., no slow frequency swimming or high-frequency trotting).

Previous EMG data are consistent with the hypothesis that the *dorsalis trunci* muscles and hypaxial muscles act synergistically to produce lateral bending of the body during salamander swimming (Bennett et al., 2001; Carrier, 1993; Deban and Schilling, 2009; Delvolvé et al., 1997; Frolich and Biewener, 1992). The EMG recordings from the *dorsalis trunci* muscles further revealed that nonuniformities in both the intersegmental coordination pattern and the speed propagation of the EMG traveling waves occur at two specific trunk positions, one located caudal to the pectoral girdle and the other close to the pelvic girdle (Delvolvé et al., 1997; Frolich and Biewener, 1992). These nonuniformities have been related to the presence of the limbs (Delvolvé et al., 1997), since they have not been observed in anguilliform swimmers without paired fins (lamprey) or with reduced pectoral fins and no pelvic fins (eel) (Gillis, 2000; Grillner and Kashin, 1976; Williams et al., 1989).

Although the EMG waves have a nonuniform propagation speed along the body, the propagation speed of lateral bending appeared to be constant along the entire length of the salamander

(D'Août and Aerts, 1997; Frolich and Biewener, 1992). This suggests that the locomotor command is well matched to the mechanical properties of the body and to hydrodynamical forces applied along the body, in order to provide mechanical waves with constant propagation speed during swimming.

In salamanders (D'Août et al., 1996; Frolich and Biewener, 1992), lampreys (Williams et al., 1989), and eels (Gillis and Blob, 2001; Grillner and Kashin, 1976), the waves of EMG activity travel down the body faster than the mechanical waves of body curvature. As a consequence, a progressive, posteriorly increasing delay occurs between the timing of muscle activity and lateral bending (or muscle strain). It has been suggested that axial musculature earlier in its muscle strain cycle can provide a mechanism for increasing power production or stiffening the tail for improving transmission of propulsive forces (see, e.g., Altringham and Ellerby, 1999; D'Août et al., 1996; Ellerby et al., 2001; Williams, 1986).

Some studies in eels and lampreys have shown that the timing between EMG activity and lateral bending depends on the external environment (aquatic vs. terrestrial). Indeed, similar to swimming, eels use waves of lateral bending traveling from head to tail to produce propulsive thrust during undulatory locomotion on land (crawling) (Gillis, 1998a). However, the epaxial muscles are activated much more strongly and later in their strain cycle during crawling than during swimming (Gillis, 2000; Gillis and Blob, 2001). Furthermore, when a lamprey is taken out of the water and placed on a wet bench, it tends to make undulations which look almost like standing waves because the lateral displacement does not increase along the body but forms quasi-nodes (i.e., points with very little lateral displacements) at specific points along the body (Bowtell and Williams, 1994).

These data support the view that the sensory feedback plays a key role in the operating mode of the axial locomotor networks in order to adjust the stiffness of the animal body relative to the

compliance of the environment (Biewener and Gillis, 1999; Gillis and Blob, 2001).

Salamanders sometimes use a terrestrial crawling resembling swimming movements performed on the ground (i.e., with limbs folded against the body; Edwards, 1977). However, it is not known whether these “terrestrial swimming movements” are generated by caudally directed waves of EMG activity, as previously reported during terrestrial locomotion in the eel (Gillis and Blob, 2001). The study of swimming in an aquatic medium of increased viscosity and in water stream should also provide further insight on how the environment affects the neuromuscular control of aquatic locomotion in salamanders.

Lampreys (Islam et al., 2006; McClellan, 1989) and eels (D'Août and Aerts, 1999) can display brief episodes of backward undulatory swimming (e.g., when encountering an obstacle). By contrast, as in most vertebrates, backward undulatory swimming has never been observed in salamanders. Backward swimming in the lamprey is characterized by waves of epaxial muscle activations which propagate rostrally along the body, with a speed higher than that of the associated kinematic waves (Islam et al., 2006). Therefore, backward swimming seems to result from a functional reversal of the operating mode of the axial locomotor network generating forward swimming (Matsushima and Grillner, 1992). Backward swimming, however, shows important kinematic differences from forward swimming. The snout shows considerable lateral deflections during backward, but not during forward swimming, and the cycle duration during backward swimming is much longer than during forward swimming (D'Août and Aerts, 1999; Islam et al., 2006). These kinematic differences likely reflect the asymmetry of the body mechanics (e.g., heavy head/light tail) which contribute to the translation of the locomotor drive into effective movements.

Salamanders can use other specialized forms of aquatic locomotion such as paddling behavior (Ashley-Ross, 1994a, 1994b; Delvolvé et al., 1997; Frolich and Biewener, 1992) and steering

behavior in three-dimensional space which have received much less attention. It would be interesting to investigate the axial motor patterns underlying these locomotor behaviors since this may help us to get a deeper insight into the flexibility of the axial networks in salamanders.

Neural mechanisms underlying the flexibility of axial networks

During locomotion in vertebrates, the rhythmic and coordinated activations of axial and limb muscles are generated by neural networks located in the spinal cord and called central pattern generators (CPGs) (Grillner, 1981). It is convenient to distinguish the network controlling axial motion (axial locomotor CPG) from those controlling limb motions (limb locomotor CPGs; Ijspeert, 2008).

Architecture of the axial locomotor CPG

The axial locomotor CPGs have been extensively investigated in limbless, swimming vertebrates. A combination of neurobiological and modeling work in the lamprey (Grillner, 2006) and the *Xenopus laevis* embryo (Roberts et al., 1997) has demonstrated the segmental structure for the axial CPG for swimming, with a double chain of reciprocally coupled identical oscillators (pools of neurons that exhibit a rhythmic activity) distributed all along the spinal cord, and mutually coupled by local and long distance intersegmental coordinating systems. These data further suggest that each hemisegmental oscillator is a pool of excitatory (glutamatergic) neurons generating recurrent bursting, coupled with a pool of inhibitory (glycinergic) neurons to ensure inhibition of the contralateral hemisegment, and generate left–right alternation (Cangiano and Grillner, 2005; Roberts et al., 2008). The left–right inhibitory connections also lower the burst frequency of the axial network and make the oscillations more robust.

By contrast, there is little information about the organization of the axial locomotor CPGs in limbed vertebrates.

Recent experiments on surgically isolated segments or hemisegments from the axial spinal cord of adult salamanders provide direct evidence of a strong similarity of the global architecture, and operating mode of the axial CPG of the salamander with that of the swimming CPG of the lamprey (Ryczko et al., 2010). Our previous modeling studies also support this proposition (Bem et al., 2003; Ijspeert et al., 2007). However, some differences between salamanders and lampreys as to the intrinsic neuronal properties underlying the bursting of spinal segments have been observed. For example, the mechanism for terminating each burst does not involve the Ca^{2+} -activated K^+ channels in salamanders (Ryczko et al., 2010), while it does in lampreys (El Manira et al., 1994).

Taken together, these results support the hypothesis that the basic design of the axial locomotor CPG has been conserved during evolution, albeit with different neural mechanisms for bursting (Falgairolle et al., 2006; Grillner, 2006; Ryczko et al., 2010).

Adaptive mechanisms in the axial locomotor CPG

Propagated waves of motor activity along the spinal cord have been observed during chemically induced locomotor-like activity in isolated spinal cords of adult lampreys, adult salamanders, and newborn rodents (Bonnot et al., 2002; Delvolvé et al., 1999; Falgairolle and Cazalets, 2007; Wallén and Williams, 1984; see also Cuellar et al., 2009).

A systematic investigation of the different patterns of ventral root activity produced by the *in vitro* isolated spinal cord of salamander has revealed a high degree of flexibility in the intersegmental coordination pattern, that is, in the operating mode of the axial networks (Ryczko et al., 2009). Intersegmental phase lags range from positive values (i.e., backward propagating waves) to

negative values (i.e., forward propagating waves), including all the values which can be observed *in vivo* (Ryczko et al., 2009). A similar flexibility in the operating mode of the axial networks has previously been observed in the lamprey (Matsushima and Grillner, 1992), and to a lesser extent, in the tadpole (Green and Soffe, 1996).

The flexibility in the intersegmental phase lag value has been related to the diversity of the locomotor behaviors observed *in vivo* (Green and Soffe, 1996; Matsushima and Grillner, 1992; Ryczko et al., 2009). Interestingly, during pharmacologically induced fictive locomotion in the high spinal cat, the muscle nerves innervating the lumbar back muscles also display a variety of rhythmic patterns corresponding to the different gaits observed in freely moving animals (Koehler et al., 1984).

The neuronal mechanisms underlying the flexibility in the axial locomotor CPG are not fully understood, although several biological and modeling studies suggest that the descending and movement-related sensory inputs play a critical role by regulating the coupling between segmental bursting units (Friesen and Cang, 2001; Grillner and Wallén, 2002).

Coupling of axial and limb locomotor CPGs

During locomotion, the axial and limb networks are working together to increase the propulsive efficiency.

In vertebrates, the limb locomotor networks are located within the cervical segments for the forelimbs (Ballion et al., 2001) and within the lower thoracic-upper lumbar segments for the hindlimbs (for review see Kiehn, 2006). Spinal sections and pharmacological manipulations further show that these regions can be separated into left and right neural networks, which independently coordinate each limb, and are connected by reciprocal (inhibitory and excitatory) connections (for review, see Butt et al., 2002). The reciprocal excitatory connections have been proposed to be functionally important for in-phase

gaits. In salamander, they might be involved during the synchronous tonic activation of a pair of limbs during swimming or for in-phase paddling.

The bursting frequency of the surgically isolated two sides of the spinal cord is higher than that of the intact spinal cord in salamanders (Ryczko et al., 2009), lampreys (Cangiano and Grillner, 2003), and *Xenopus* embryos (Soffe, 1989). In contrast, the bursting frequency of surgically or pharmacologically uncoupled two halves of the lumbosacral spinal cord is lower than that of the intact spinal cord in neonatal rodents (Bracci et al., 1996; Kjaerulff and Kiehn, 1997; Kudo and Yamada, 1987; Whelan et al., 2000; see however Kremer and Lev-Tov, 1997) and turtles (Samara and Currie, 2007). This difference may reflect a species difference and/or a difference in the left-right coupling mechanisms within axial and limb oscillatory networks. However, more experiments are needed to determine the contribution of developmental changes to the left-right coordinating mechanisms in rodents (Nakayama et al., 2002).

Studies on surgically isolated spinal segments in salamander provide evidence that the intrinsic frequency of the segmental networks controlling the limb musculature is lower than that of the segmental network controlling the axial musculature (Ijspeert et al., 2007).

The axial and the hindlimb locomotor CPGs can be coupled in different ways and the mode of coupling can be changed by peripheral inputs in high decerebrate cats (Koehler et al., 1984). It is reasonable to postulate a similar flexibility for the coupling between axial and forelimb locomotor CPGs. A flexibility of the coupling of limb CPGs has also been revealed in several vertebrates, depending on descending and peripheral inputs (reviewed in Pearson, 2000). The flexibility of the couplings (axial/limb and limb/limb) not only enables a spinal adaptation of locomotion to different external conditions but may also serve as a basis for the use of these spinal facilities by higher centers for the performance of complex goal-directed movements (Grillner et al., 2008).

As an example, the mesencephalic locomotor region (MLR) can activate (via reticulospinal neurons), depending on strength, specific spinal networks to produce motor synergies underlying specific locomotor modes (Cabelguen et al., 2003; Steeves et al., 1987). In salamanders, walking occurs during electrical microstimulation of the MLR at low intensity, whereas swimming requires higher intensities (Cabelguen et al., 2003). Our previous numerical simulations (Ijspeert et al., 2007) suggest that the limb oscillators are recruited at low intensity and drive the axial network at a low frequency (walking). At higher intensity, the limb oscillators become silent (saturate), and release the faster swimming rhythms due to the higher intrinsic frequencies of the body oscillators. This is consistent with swimming being the fastest mode of locomotion and also explain why salamander stepping and swimming frequencies do not overlap (Delvolvé et al., 1997; Frolich and Biewener, 1992), but have distinct ranges with a gap between them. The exact mechanism underlying this induced gait transition is still unknown. One possible explanation is that the saturation of the limb oscillator is a spinal mechanism (i.e., it is an intrinsic property of the oscillator), another possible explanation is a gating mechanism in the reticular formation and/or the MLR (i.e., the descending drive is not transmitted to the limb oscillator when it exceeds some threshold).

Conclusion

This review provides a brief survey of data from various vertebrates which emphasize the importance of considering locomotion as a complex motor task involving not only the limbs but also the body axis. These data also support the view that the axial locomotor networks are dynamical systems. The dynamics of the axial networks, in combination with that of the limb networks, allows the generation of robust and stable muscle synergies appropriate for locomotion in a continuously varying environment.

One important goal for future research is to investigate the mechanisms that enable flexibility in the axial motor output depending on the locomotor task. This should be evaluated by considering the complex interplay between the central nervous system, the sensory receptors, the body dynamics, and the environment. A promising approach is to combine neurobiological experiments, modeling, and robotics, as we have previously done in the salamander (Ijspeert et al., 2007).

Acknowledgment

The support from European Community (LAMPETRA Grant: FP7-ICT-2007-1-216100) and ANR (ImNet Grant: ANR-07-NEURO-015-01) is gratefully acknowledged.

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