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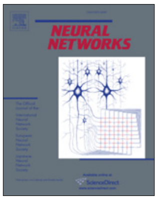

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Central pattern generators for locomotion control in animals and robots: A review

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ABSTRACT

The problem of controlling locomotion is an area in which neuroscience and robotics can fruitfully interact. In this article, I will review research carried out on locomotor central pattern generators (CPGs), i.e. neural circuits capable of producing coordinated patterns of high-dimensional rhythmic output signals while receiving only simple, low-dimensional, input signals. The review will first cover neurobiological observations concerning locomotor CPGs and their numerical modelling, with a special focus on vertebrates. It will then cover how CPG models implemented as neural networks or systems of coupled oscillators can be used in robotics for controlling the locomotion of articulated robots. The review also presents how robots can be used as scientific tools to obtain a better understanding of the functioning of biological CPGs. Finally, various methods for designing CPGs to control specific modes of locomotion will be briefly reviewed. In this process, I will discuss different types of CPG models, the pros and cons of using CPGs with robots, and the pros and cons of using robots as scientific tools. Open research topics both in biology and in robotics will also be discussed.

1. Introduction

The ability to efficiently move in complex environments is a key property of animals. It is central to their survival, i.e. to avoid predators, to look for food, and to find mates for reproduction. This capital property of animals means that many aspects of animal's morphologies and central nervous systems have been shaped by constraints related to locomotor skills. Similarly, providing good locomotor skills to robots is of primary importance in order to design robots that can carry out useful tasks in a variety of environments. This relevance of locomotion both for biology and for robotics has led to multiple interesting interactions between the two fields. The interactions have mainly been in one direction, with robotics taking inspiration from biology in terms of morphologies, modes of locomotion, and/or control mechanisms. In particular, many robot structures are directly inspired by animal morphologies, from snake robots, quadruped robots, to humanoid robots. Increasingly, robotics is now providing something back to biology, with robots being used as scientific tools to test biological hypotheses.

The focus of this article is on control aspects, in particular rhythm generation by central pattern generators. Central pattern generators (CPGs) are neural circuits found in both invertebrate and vertebrate animals that can produce rhythmic patterns of neural activity without receiving rhythmic inputs. The term *central* indicates that sensory feedback (from the *peripheral* nervous system) is not needed for generating the rhythms. CPGs underlie many fundamental rhythmic activities such as chewing, breathing, and digesting. They are also fundamental building blocks for the locomotor neural circuits both in invertebrate and vertebrate animals. As will be discussed in this article, they present several interesting properties including distributed control, the ability to deal with redundancies, fast control loops, and allowing modulation of locomotion by simple control signals. These properties, when transferred to mathematical models, make CPGs interesting building blocks for locomotion controllers in robots.

The article is structured as follows. I will first make a brief review of neurobiological findings concerning locomotor CPGs (Section 2), and present some of the mathematical models of biological CPGs that have been developed (Section 3). I will then review different CPG models developed for robotics and how they are being used for locomotion control (Section 4). In Section 5, I will focus on methodologies to design CPG models for a particular task. Finally, Section 6 will discuss a list of open research topics. When relevant, some notions will be illustrated with results from collaborators and myself. The review is not meant to be exhaustive, and interesting related reviews exist on the organization of animal locomotor systems (Bizzi, Tresch, Saltiel, & d'Avella, 2000; Dickinson et al., 2000; Grillner, 2006; Loeb, 2001), and the modelling of animal locomotion (Full & Koditscheck, 1999; Holmes, Full, Koditschek, & Guckenheimer, 2006). Also interesting collections of articles on biologically inspired robot locomotion can

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be found in Ayers, Davis, and Rudolph (2002), Beer, Chiel, Quinn, and Ritzmann (1998), Beer, Ritzmann, and McKenna (1993) and Kimura, Tsuchiya, Ishiguro, and Witte (2005).

2. Neurobiology of CPGs

Central pattern generators (CPGs) are neural networks capable of producing coordinated patterns of rhythmic activity without any rhythmic inputs from sensory feedback or from higher control centers. As reviewed in Delcomyn (1980), they underlie many rhythmic behaviors both in invertebrate and vertebrate animals. At the beginning of the last century, two different explanations were proposed for the creation of the rhythms underlying locomotion, see the discussion by Brown (1911). One explanation defended by C.S. Sherrington was that rhythms are the result of a chain of reflexes in which sensory feedback plays an important role in triggering switches between different parts of a locomotor cycle. The other explanation proposed by T.G. Brown was that rhythms were generated centrally, i.e. by neural networks that do not require input from the periphery (e.g. sensory neurons) for generating cyclic behavior. T.G. Brown for instance proposed a conceptual model called the *half-center* model in which two populations of neurons that are mutually coupled with inhibitory connections and that possess a fatigue mechanism produce alternating rhythmic activity (Brown, 1914).

There is now very clear evidence that rhythms are generated centrally without requiring sensory information. For instance, one can extract and isolate from the body the spinal cord of the lamprey (a primitive fish), and it will produce patterns of activity, called *fictive locomotion*, that are very similar to intact locomotion when activated by simple electrical or chemical stimulation (Cohen & Wallen, 1980; Grillner, 1985). Similar fictive locomotion has been reported in salamander (Delvolvé, Branchereau, Dubuc, & Cabelguen, 1999) and frog embryos (Soffe & Roberts, 1982). More generally CPGs have now been reported in many other animals, see Stein, Grillner, Selverston, and Stuart (1997) for a good review.

Similar experiments have also shown that CPGs are distributed networks made of multiple coupled oscillatory centers. Lamprey spinal cords have approx 100 segments, and small sections of the spinal cord (e.g. 1–2 segments) are capable of producing rhythmic activity. The same has been observed in salamanders (Delvolvé et al., 1999). This is in agreement with Grillner's proposition that CPGs are organized as coupled unit-burst elements with at least one unit per articulation (i.e. per degree of freedom) in the body (Grillner, 1985). Cheng et al. (1998) report experiments where these units can be divided even further with independent oscillatory centers for flexor and extensor muscles.[1]

While sensory feedback is not needed for generating the rhythms, it plays a very important role in shaping the rhythmic patterns. This is fundamental for keeping CPGs and body movements coordinated. Several experiments demonstrate the important influence of sensory feedback on CPG activity. Mechanically moving the tail of the lamprey will for instance induce CPG activity that is frequency-locked with the frequency of the mechanical movements, and this over a quite large frequency range (McClellan & Jang, 1993; Viana Di Prisco, Wallén, & Grillner, 1990; Williams, Sigvardt, Kopell, Ermentrout, & Rempler, 1990). Similarly, a mechanically driven treadmill can induce a normally looking walking gait in a decerebrated cat (Rossignol, 2000), and even induce gait transitions to trot and gallop when the treadmill is accelerated (unpublished work by Graham Brown, as described in Armstrong (1988)). These experiments show a tight coupling between CPG and sensory feedback. This coupling is also visible in the fact that many reflexes are phase-dependent, i.e. they have different effects depending on the timing within a locomotor cycle (Pearson, 1995; Pearson & Gordon, 2000; Rossignol, Dubuc, & Gossard, 2006). This is due to the fact that CPGs and reflex pathways often share interneurons (Pearson, 1995). See Rossignol et al. (2006) for an in-depth review of the interaction of CPGs and sensory feedback mechanisms.

Interestingly, simple signals are usually sufficient to induce activity in CPGs, as shown by the fictive locomotion experiments mentioned above. In many vertebrate animals, electrical stimulation of a specific region in the brain stem called Mesencephalic Locomotor Region (MLR) will induce locomotor behavior (Grillner, Georgopoulos, & Jordan, 1997). The MLR is an important locomotor region that has descending pathways to the spinal cord via the reticular formations. Typically low-level stimulation[2] leads to slow (low frequency) movements, and high-level stimulation to faster (higher frequency) movements. The level of stimulation can therefore modulate the speed of locomotion. Interestingly, MLR stimulation also induces automatic gait transition: in a decerebrated cat, increasing the stimulation leads to switches from walk to trot to gallop (Shik, Severin, & Orlovsky, 1966); in a decerebrated salamander increasing the stimulation leads to a switch from walk to swimming (Cabelguen, Bourcier-Lucas, & Dubuc, 2003). Similar gait transitions have been reported in other vertebrates (Grillner et al., 1997). This demonstrates that CPGs are sophisticated circuits that can generate complex locomotor behaviors and even switch between very different gaits while receiving only simple input signals.[3] From a control point of view, CPGs therefore implement some kind of internal model that "knows" which command signals need to be rhythmically produced to obtain a given speed of locomotion.

In the lamprey, the direction of locomotion can, similarly to velocity, be modulated by simple variations of the stimulation applied to the MLR. Applying an asymmetric stimulation between the left and right MLRs leads to turning (Sirota, Viana Di Prisco, & Dubuc, 2000). This is in agreement with recordings in the reticular region during intact swimming in lamprey which shows significant higher activity of reticular neurons on one side, when the lamprey bends to the same side (Deliagina, Zelenin, Fagerstedt, Grillner, & Orlovsky, 2000).

To summarize, the (vertebrate) locomotor system is organized such that the spinal CPGs are responsible for producing the basic rhythmic patterns, and that higher-level centers (the motor cortex, cerebellum, and basal ganglia) are responsible for modulating these patterns according to environmental conditions. Such a distributed organization presents several interesting features: (i) It reduces time delays in the motor control loop (rhythms are coordinated with mechanical movements using short feedback loops through the spinal cord). (ii) It dramatically reduces the dimensionality of the descending control signals. Indeed the control signals in general do not need to specify muscle activity[4]

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[1] Note that, when there is extensive inter-oscillator coupling, the distinction of one oscillatory center from another is not always clear. The lamprey swimming CPG has for instance been modelled as a continuum (Wadden, Hellgren, Lansner, & Grillner, 1997) rather than distinct oscillatory centers that are coupled together.

[2] Stimulations are typically pulses of electric current. The level of stimulation can be changed by changing either the frequency of the pulses or their current. Increasing one or the other has usually the same effect.

[3] Note that CPGs can also accommodate more complex control signals, e.g. for the control of balance and visually-guided feet placement. This will be discussed further in Section 6.

[4] Mammals typically have more than 200 skeletal muscles, each composed on average of around one million muscle fibers, which would therefore require a huge number of different control pathways. Note that direct, e.g. cortico-spinal, pathways exist from the motor cortex to spinal motoneurons but only in some species for controlling some specific groups of muscles, for instance hand muscles in primates.

but only modulate CPG activity. (iii) It therefore significantly reduces the necessary bandwidth between the higher-level centers and the spinal cord.[5]

3. Neurobiological models of CPGs

In this section, I will review different types of mathematical models that have been developed to study biological CPGs, as well as the types of animal locomotion that have been modelled.

3.1. Different levels

Depending on the phenomena under study, CPG models have been designed at several levels of abstraction from detailed biophysical models, to connectionist models, to abstract systems of coupled oscillators. In some cases, the CPG models have been coupled to biomechanical simulation of a body, in which case they are called neuromechanical models.

Detailed biophysical models are constructed based on the Hodgkin–Huxley type of neuron models. That is, neuron models that compute how ion pumps and ion channels influence membrane potentials and the generation of action potentials. Examples of such CPG models include Hellgren, Grillner, and Lansner (1992) and Traven et al. (1993). Most biophysical models investigate the problem of rhythmogenesis, i.e. generation of rhythmic activity, in small neural circuits (Traven et al., 1993). In some cases, the pacemaker properties of single neurons are investigated. While most models concentrate on the detailed dynamics of small circuits, some models address the dynamics of larger populations of neurons, for instance the generation of travelling waves in the complete lamprey swimming CPG (Hellgren et al., 1992; Wadden et al., 1997).

Connectionist models use simplified neuron models such as leaky-integrator neurons or integrate-and-fire neurons (Buchanan, 1992; Ekeberg, 1993; Williams, 1992a, 1992b). The focus of these models is on how rhythmic activity is generated by network properties (e.g. half-center networks), and how different oscillatory neural circuits get synchronized via interneuron connections (e.g. for intra- or inter-limb coordination).

Oscillator models are based on mathematical models of coupled nonlinear oscillators to study population dynamics (Cohen, Holmes, & Rand, 1982; Collins & Richmond, 1994; Ijspeert, Crespi, Ryczko, & Cabelguen, 2007; Kopell, Ermentrout, & Williams, 1991; Matsuoka, 1987; Schoner, Jiang, & Kelso, 1990). In this case, an oscillator represents the activity of a complete oscillatory center (instead of a single neuron or a small circuit). The purpose of these models is not to explain rhythmogenesis (oscillatory mechanisms are assumed to exist) but to study how inter-oscillator couplings and differences of intrinsic frequencies affect the synchronization and the phase lags within a population of oscillatory centers. The motivation for this type of modelling comes from the fact that the dynamics of populations of oscillatory centers depend mainly on the type and topology of couplings rather than on the local mechanisms of rhythm generation, something that is well established in dynamical systems theory (Golubitsky & Stewart, 2002; Kuramoto, 2003).[6] See for instance the study by Collins and Richmond (1994) which obtains the same gait transitions in a given network topology with three different types of oscillators (van der Pol, Stein, and FitzHugh–Nagumo). Other extensively used oscillators include phase oscillators (Buchli & Ijspeert, 2004a; Cohen et al., 1982; Kopell et al., 1991; Schoner et al., 1990) and Matsuoka oscillators (Kimura, Akiyama, & Sakurama, 1999; Matsuoka, 1985; Taga, Yamaguchi, & Shimizu, 1991). Most of the oscillators have a fixed waveform for a given frequency, but in Righetti and Ijspeert (2006a) we developed a simple oscillator model that allows one to independently adjust the durations of the ascending and descending phases in the cycle (this is useful to independently adjust swing and stance phases, for instance). In some cases, closed-form solutions or specific regimes (e.g. phase-locked regimes) can be analytically derived (Cohen et al., 1982; Kopell, 1995), but most systems are solved using numerical integration.

Several neuromechanical models have been developed (Ekeberg, 1993; Ijspeert, 2001; Ijspeert, Crespi, & Cabelguen, 2005; Ijspeert, Hallam, & Willshaw, 1999; Taga et al., 1991; Williams, 1991). The addition of a biomechanical model of the body (and its interaction with the environment) offers the possibility to study the effect of sensory feedback on the CPG activity. Important phenomena such as mechanical entrainment can thus be studied. The pros and cons of using a biomechanical model versus a real robot will be discussed in Section 4.2.

3.2. Different animal models

Models of CPGs have mainly been made of insects and lower vertebrates. The vertebrate animal that has been most modelled is the lamprey, a primitive eel-like fish. It has been modelled with all the several types of models described above: biophysical (Ekeberg et al., 1991; Grillner, Wallén, & Brodin, 1991; Hellgren et al., 1992; Traven et al., 1993; Wadden et al., 1997), connectionist (Buchanan, 1992; Ekeberg, 1993; Ijspeert et al., 1999; Jung, Kiemel, & Cohen, 1996; Williams, 1992a, 1992b; Zhaoping, Lewis, & Scarpetta, 2004), system of coupled oscillators (Cohen et al., 1982; Kopell et al., 1991; Nishii, Uno, & Suzuki, 1994; Seo & Slotine, 2007; Sigvardt & Williams, 1996; Williams et al., 1990), and neuromechanical simulation (Ekeberg, 1993; Ijspeert et al., 1999; Williams, 1991). In the next section, we will also review work on CPG models in lamprey-like robots. These CPG models have been instrumental in validating conceptual models of the lamprey CPG, and in suggesting new experiments. In particular, the models have helped in clarifying different possible mechanisms which could explain the travelling waves of body undulations, i.e. the fact that segmental oscillatory networks in the lamprey oscillate with a positive phase lag between neighbor segments from head to tail, and that the phase lag between head and tail is usually maintained at a 100% of cycle duration even if the cycle duration is changed. Three possible mechanisms have been proposed: asymmetric coupling, different intrinsic frequencies along the spinal cord, and time delays due to axonal and synaptic conduction. The models have provided good evidence that the most likely explanation is asymmetric coupling, see Grillner et al. (1995), Sigvardt and Williams (1996) and Williams et al. (1990) for discussions. Another fish whose CPG has been modelled includes zebra fish (Kuo & Eliasmith, 2004).

The salamander, an amphibian capable of swimming and walking, offers an interesting link between research on the lamprey and research on tetrapods. Different models related to salamander locomotion have been developed (Bem, Cabelguen, Ekeberg, & Grillner, 2003; Ermentrout & Kopell, 1994; Ijspeert, 2001; Ijspeert et al., 2005, 2007; Seo & Slotine, 2007). Our latest model (Ijspeert et al., 2007) explores how a lamprey-like swimming circuit can be extended to control both swimming

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[5] To illustrate the importance and general role played by spinal cord, G.E. Loeb proposes the nice analogy to a marionette puppet, in which the puppeteer (the brain) has to control the puppet, a highly-redundant system, by using a limited set of strings (the descending commands sent to the spinal cord circuits), see Loeb (2001).

[6] This importance of the topology also means that, for robotic applications, there is not much to gain from using too complicated oscillators as building blocks of a CPG model. See a discussion in Buchli, Righetti, and Ijspeert (2006).

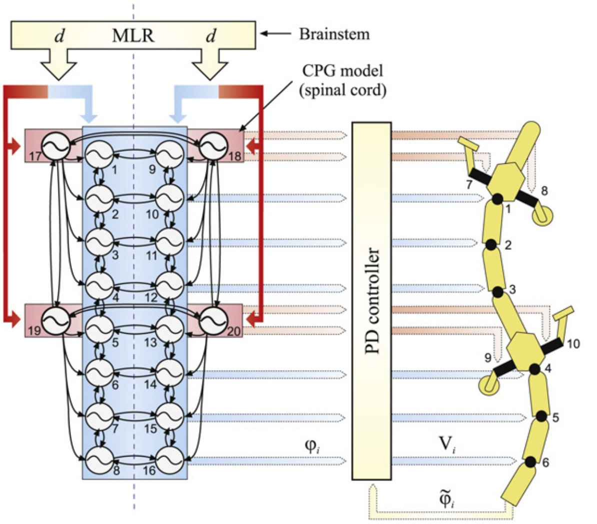

Fig. 1. Salamander CPG model tested with a amphibious salamander-like robot (Ijspeert et al., 2007). The model is composed of 20 amplitude-controlled phase oscillators. The oscillators receive a drive d signal representing the descending stimulation from the Mesencephalic Locomotor Region (MLR) in the brain stem. The outputs of the CPG are desired joint angle positions φ_i that are used by a Proportional-Derivative (PD) feedback controller (V_i are the voltages applied to the motors and $\tilde{\varphi}_i$ are the actual joint angles measured from incremental encoders). For details see the text and (Ijspeert et al., 2007).

and walking, and provides potential mechanisms explaining the automatic transition from walking to swimming by modulating the electrical stimulation of the MLR (Figs. 1 and 2). The central idea behind the model is that salamander bi-modal locomotion can be explained by adding limb oscillatory centers with lower intrinsic frequencies and lower saturation frequencies to a lamprey swimming circuit. The model provides a potential explanation of (i) how the body undulations switch between standing waves during walking and travelling waves during swimming, (ii) why salamanders walk at low frequencies and swim at high frequencies, and (iii) why there is a rapid increase of frequencies as soon at the animal switches to swimming. Another amphibian that has been modelled is the frog embryo (Roberts & Tunstall, 1990; Wolf & Roberts, 1995). More generally other animals whose locomotor CPGs have been numerically modelled include the leech (Lockery & Sejnowski, 1993), the cockroach (Ghigliazza & Holmes, 2004; Ritzmann, Quinn, & Fischer, 2004) and the cat (Ekeberg & Pearson, 2005; Ito, Yuasa, Luo, Ito, & Yanagihara, 1998; Kaske, Winberg, & Cöster, 2003; Pribe, Grossberg, & Cohen, 1997; Rybak, Shevtsova, Lafreniere-Roula, & McCrea, 2006; Rybak, Stecina, Shevtsova, & McCrea, 2006; Yakovenko, McCrea, Stecina, & Prochazka, 2005). Other related models are models that focus on quadruped gait transitions at a more abstract level (Buchli & Ijspeert, 2004a; Buono, 2001; Buono & Golubitsky, 2001; Canavier et al., 1997; Collins & Richmond, 1994; Golubitsky, Stewart, Buono, & Collins, 1999; Kaske et al., 2003; Pribe et al., 1997; Schoner et al., 1990; Schoner & Kelso, 1988).

For all these studies, the numerical models have proven to be very useful tools to test hypotheses concerning the functioning of CPGs. Since rhythm generation and locomotion are intrinsically dynamical phenomena, numerical simulations allow one to test whether a conceptual model of a locomotor circuit can actually reproduce recorded animal locomotor patterns, and to explore what needs to be modified in case the match to biological data is poor. Numerical models are also useful to suggest new experiments and predict their outcomes. Examples of experiments whose outcomes were predicted by a model include (1) the effect of mechanically moving the tail of the lamprey on the CPG rhythms (Williams et al., 1990), (2) the effect of manipulating intrinsic frequencies of the lamprey CPG by baths of different concentrations (Sigvardt & Williams, 1996), and (3) the effect of transecting inter-CPG couplings on the oscillation frequencies of body and limb CPGs in the salamander (Ijspeert et al., 2007).

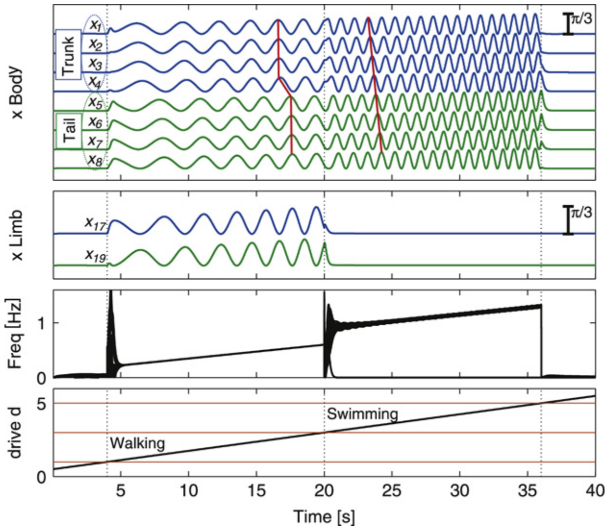

Fig. 2. Gait transition from walking to swimming with the salamander CPG model (Ijspeert et al., 2007). (A) output signals from the left body CPG oscillators (oscillators on the right side are exactly in anti-phase). The numbering corresponds to that of Fig. 1. Units are in radians (scale bar on the top right). The red lines illustrate the transition from standing waves (with synchrony in the trunk, synchrony in the tail, and an anti-phase relation between the two) to travelling waves. (B) output signals from the left limb CPG oscillators. Ipsilateral fore and hindlimbs are in anti-phase. (C) Instantaneous frequencies measured as in cycles/s. (D) Linear increase of the drive signal applied to all oscillators. The horizontal red lines correspond to the lower and upper oscillation thresholds for limb and body oscillators in arbitrary drive units. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

4. CPGs in robotics

In this section, I will now review how CPG models have been used to control the locomotion of robots. The first part of this section will be devoted to CPG models as a new control technology, while the second part will focus on how robots can be used as scientific tools for testing hypotheses on biological CPGs, and the pros and cons of such an approach.

4.1. CPGs for robot locomotion

As illustrated by Fig. 3, CPG models are increasingly used in the robotics community. The types of CPG models implemented in robots include connectionist models (Arena, 2000; Lu, Ma, Li, & Wang, 2005), vector maps (Okada, Tatani, & Nakamura, 2002), and systems of coupled oscillators (Crespi & Ijspeert, 2006; Ijspeert et al., 2007; Kimura et al., 1999; Williamson, 1998). In some rare cases spiking neural network models have been used (Lewis, Tenore, & Etienne-Cummings, 2005). Virtually all implementations involve sets of coupled differential equations that are numerically integrated (on a microcontroller or a processor). Probably the only exceptions are CPGs that are directly realized in hardware, i.e. on a chip (DeWeerth, Patel, Simoni, Schimmel, & Calabrese, 1997; Lewis et al., 2005; Nakada, Asai, & Amemiya, 2003; Simoni & DeWeerth, 2007) or with analog electronics (Still & Tilden, 1998). Also to some extent related to CPG research are quasi-periodic motions generated by chaotic maps (Kuniyoshi & Suzuki, 2004).

Models of CPGs have been used to control a variety of different types of robots and different modes of locomotion. For instance

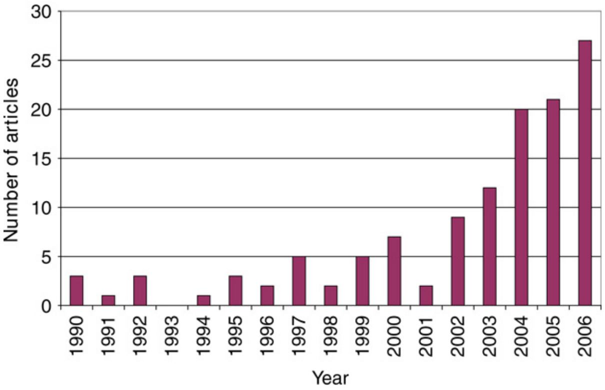

Fig. 3. Number of articles per year whose abstract contains the terms "robot" and "central pattern generator OR CPG" in the IEEE Explore database, from 1990 to 2006.

CPG models have been used with hexapod and octopod robots inspired by insect locomotion (Arena, Fortuna, Frasca, & Sicurella, 2004; Inagaki, Yuasa, & Arai, 2003; Inagaki, Yuasa, Suzuki, & Arai, 2006; Klaassen, Linnemann, Spenneberg, & Kirchner, 2002). See also Delcomyn (1999) for a summary of aspects of locomotor control in insects that are useful for controlling hexapod robots. Related work in simulation was realized by Randall Beer and his colleagues in the early 1990s (Beer, Chiel, Quinn, Espenshied, & Larsson, 1992; Beer & Gallagher, 1992). The work of Holk Cruse on the Stick insect is also relevant here to show that reflexive controllers (i.e. based on reflexes without CPGs) can also lead to robust insect locomotion (Cruse et al., 1995).

CPGs have also been used for controlling swimming robots. Examples include anguilliform swimming of lamprey/eel robots (Arena, 2001; Crespi & Ijspeert, 2008; Ijspeert & Crespi, 2007; Stefanini, Orlandi, Menciassi, Ravier, Spina, & Grillner, 2006; Wilbur, Vorus, Cao, & Currie, 2002). Anguilliform swimming implies that forward motion is obtained by a travelling undulation of the elongated body from head to tail. The CPG models are usually inspired by the lamprey swimming circuit (see also the next section), and have been implemented using finite-state machines (Wilbur et al., 2002), cellular networks (Arena, 2001), and systems of coupled oscillators (Ijspeert & Crespi, 2007). Related to lamprey/eel robots, terrestrial snake robots have also been driven by CPG models (Conradt & Varshavskaya, 2003; Ijspeert & Crespi, 2007; Inoue, Ma, & Jin, 2004; Lu, Ma, Li, & Wang, 2006; Tsakiris, Sfakiotakis, Menciassi, La Spina, & Dario, 2005). Other types of swimming have been less studied with CPGs. One example is a CPG for ostraciform swimming that we implemented as a system of coupled oscillators in a box-fish-like robot (Lachat, Crespi, & Ijspeert, 2006). See also Zhao, Yu, Fang, and Wang (2006) for a similar approach.

Quadruped walking control using CPGs has been extensively explored by Hiroshi Kimura and his colleagues (Fukuoka, Kimura, & Cohen, 2003; Kimura et al., 1999; Kimura, Fukuoka, & Cohen, 2007). Among other things, they have explored different means of integrating sensory feedback in the locomotion control and found that sensory feedback that modulates CPG activity tends to lead to the most stable locomotion in complex terrain (as opposed to feedback that is independent of the CPG activity). Other work on CPGs in quadruped robots can be found in Billard and Ijspeert (2000), Brambilla, Buchli, and Ijspeert (2006), Buchli, Iida, and Ijspeert (2006), Manoonpong, Pasemann, and Roth (2007), Tsujita, Toui, and Tsuchiya (2004), Tsujita, Tsuchiya, and Onat (2001a) and Tsujita, Tsuchiya, and Onat (2001b). We also developed a salamander robot to study the transition between (anguilliform) swimming and walking (Ijspeert et al., 2007), this work will be further described in the next section.

Models of CPG are also increasingly used for the control of biped locomotion in humanoid robots, often inspired by Gentaro Taga's seminal work on neuromechanical simulations (Taga, 1998; Taga et al., 1991). Examples of CPG-controlled biped locomotion include Aoi and Tsuchiya (2005), Aoi and Tsuchiya (2006), Endo, Nakanishi, Morimoto, and Cheng (2005), Héliot and Espiau (2008), Komatsu and Usui (2005), Matsubara, Morimoto, Nakanishi, Sato, and Doya (2006), Miyakoshi, Taga, Kuniyoshi, and Nagakubo (1998), Morimoto, Endo, Nakanishi, Hyon, Cheng, and Bentivegna (2006), Nakanishi et al. (2004), Righetti and Ijspeert (2006b) and Shan and Nagashima (2002). Note that interesting biologically inspired locomotion controllers for biped locomotion can also be constructed based on reflexes rather than on CPGs (Collins, Ruina, Tedrake, & Wisse, 2005; Geng, Porr, & Wörgötter, 2006; Geyer, Seyfarth, & Blickhan, 2003).

There are several interesting properties that make CPG models useful for the control of locomotion in robots as an alternative to methods based on finite-state machines, sine-generators, prerecorded reference trajectories, e.g. ZMP-based (Vukobratovic & Borovac, 2004), or heuristic control laws, e.g. Virtual Model control (Pratt, Chew, Torres, Dilworth, & Pratt, 2001). I identified at least five interesting properties: (i) The purpose of CPG models is to exhibit limit cycle behavior, i.e. to produce stable rhythmic patterns. When this is the case, the system rapidly returns to its normal rhythmic behavior after transient perturbations of the state variables. See an example in Fig. 4. This provides robustness against perturbations. (ii) CPGs are well suited for distributed implementation, which might be interesting for modular robots, i.e. see snake robot (Conradt & Varshavskaya, 2003) and reconfigurable robots (Kamimura et al., 2003, 2004; Marbach & Ijspeert, 2005). (iii) CPG models typically have a few control parameters (e.g. drive signals) that allow modulation of the locomotion, for instance the speed and direction or even the type of gait (Ijspeert et al., 2007). A properly implemented CPG model therefore reduces the dimensionality of the control problem such that higher-level controllers (or learning algorithms) do not need to directly produce multidimensional motor commands but only higher-level control signals. As discussed in Section 2, this is one of the most interesting features of biological CPGs. Related to this, CPG models typically produce smooth modulations of the produced trajectories even when the control parameters are abruptly changed (because the differential equations typically act as first or second order filters). See an example in Fig. 5. This property is useful for doing online trajectory generation that avoids possible damage in motors and gearboxes due to abrupt changes of motor commands.[7] (iv) CPGs are ideally suited to integrate sensory feedback signals (which can be added as coupling terms in the differential equations). This provides the opportunity to obtain mutual entrainment between the CPG and the mechanical body (Kimura et al., 1999; Taga, 1998; Taga et al., 1991; Verdaasdonk, Koopman, & van der Helm, 2006). (v) CPG models usually offer a good substrate for learning and optimization algorithms. This will be further discussed in Section 5.

CPG-based approaches also present disadvantages/challenges. I see two main challenges to be overcome: First a sound design methodology is yet missing for designing CPGs to solve a particular locomotor problem. We will come back to this in Section 5. A second, related, challenge is that a solid theoretical foundation for describing CPGs is yet missing. For instance, it is very difficult to prove the stability of the complete CPG-robot system.

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[7] Note however, that too smooth/slow changes might not be adequate when rapid responses are required, e.g. for producing a corrective step to keep balance after a perturbation. Such fast movements require reflex-like responses that act in addition to the CPGs.

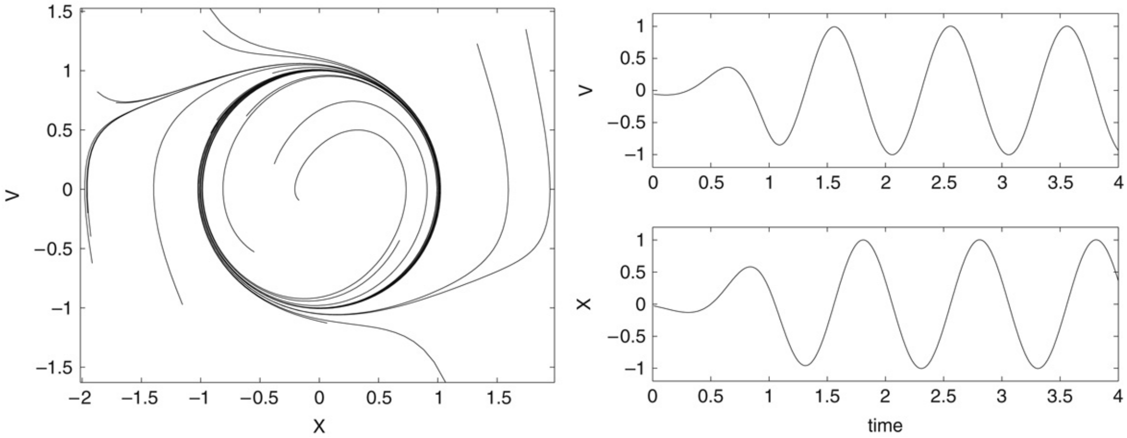

Fig. 4. Limit cycle behavior of an energy-controlled nonlinear oscillator (Ijspeert et al., 2005). The oscillator is governed by the following differential equations $\tau\dot{v} = -\alpha\frac{x^2+v^2-E}{E}v - x$ and $\tau\dot{x} = v$, where τ, α, and E are positive constants. Left: phase plot of the time evolution of the nonlinear oscillator with different random initial conditions. Right: particular example of the time evolution of two state variables x and v.

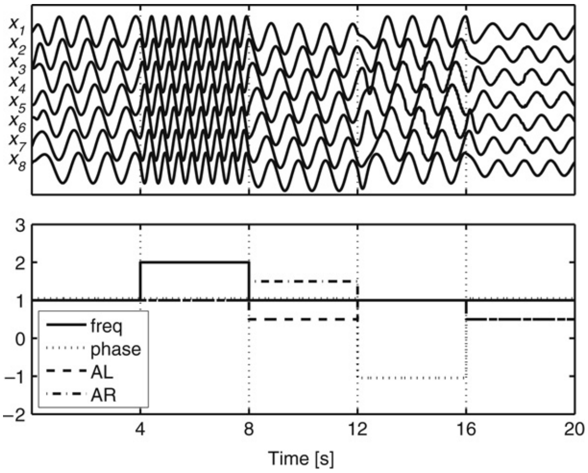

Fig. 5. Smooth changes of locomotor patterns when changing the parameters of a swimming CPG constructed as a chain of coupled amplitude-controlled phase oscillators, see Ijspeert and Crespi (2007). Top: setpoint signals, Bottom: control parameters. Initial parameters are left and right amplitudes $A_L = A_R = 1$, frequency $\nu = 1$ Hz and phase bias $N \cdot \Delta\phi = 1$. At $t = 4s$, the frequency is temporarily changed to 2.0 Hz, at $t = 8$ s, amplitudes A_L and A_R are temporarily changed to 0.5 and 1.5 respectively which leads to a negative offset of the setpoint oscillations. At $t = 12$ s, the phase bias $N \cdot \Delta\phi$ is temporarily set to −1.0 which leads to a reversal of the direction of the travelling wave. At $t = 16$ s, A_L and A_R are changed to 0.5 which leads to reduced amplitude in the oscillations.

4.2. Robots for neurobiological research

While most interactions between biology and robotics are mainly in one direction, with robotics benefiting from biological inspiration, an increasing number of projects try to provide something back, i.e. to specifically use robots as scientific tools to test biological models. Here I will present a few illustrative examples, and then discuss the pros and cons of using robots for neurobiological research. Part of this discussion comes from Ijspeert et al. (2005). For a more general discussion of the topic of using robots in biological research see Webb (2001, 2002).

Projects which contribute to test hypotheses concerning CPGs using robots include the lobster robot project (Ayers & Crisman, 1993; Ayers & Witting, 2007), the lamprey robot projects (Stefanini et al., 2006; Wilbur et al., 2002), the Polychaete-like undulatory robot (La Spina, Sfakiotakis, Tsakiris, Menciassi, & Dario, 2007; Tsakiris et al., 2005), to name a few. Other projects that are not directly related to CPGs but also use robots to test hypotheses about animal locomotion include Altendorfer et al. (2001), Long, Schumacher, Livingston, and Kemp (2006) and Ritzmann et al. (2004).

In our own work on CPG models of salamander locomotion (Ijspeert et al., 2007), the robot was very useful for validating various aspects of the mathematical model. In particular, the robot allowed us (i) to show that our CPG model can generate forward motion with variable speed and heading (i.e., aspects that need a "body" for validation and cannot be studied at a neuronal level alone), and (ii) to qualitatively compare the gaits generated to those of the real salamander. It also allowed us to demonstrate that the coordination between body undulation and limb movements during walking allows the salamander to optimize its walking velocity. In the future, we plan to use the robot to test the hypothesis that sensory feedback plays a role in explaining the transition from travelling waves (in water) to standing waves (on ground) in body undulations. See Ijspeert et al. (2005) for preliminary tests in simulation.

An interesting aspect of using robots in computational neuroscience is that they allow computational models to be tested as they are coupled to a real body and embedded in a real environment. In particular, this means that models can be tested within a complete sensing to acting loop. This is important since some aspects of locomotion might depend critically on the interaction with the environment. For instance, the potential role of interaction forces and sensory feedback in gait transitions discussed above for the salamander CPG would be difficult to study in isolated neural network models.

Dynamic simulators can be used to simulate the physics of the body and the environment, but one should realize they only provide a first approximation. Some interaction forces such as contact forces, frictional forces, and hydrodynamic forces are extremely difficult to simulate correctly, especially for articulated bodies that move and change shape. Using a robot means that the physical laws do not need to be simulated, and reduces the risk of numerical artifacts. In our case, the amphibious salamander robot was a key tool for testing swimming gaits, and for validating the simulation results. The same holds for perception: the use of real sensors (e.g. cameras, etc.) in a real environment eliminates the need to simulate the richness (in terms of noise, variations, energy spectrum, etc.) of sensory inputs due to the real world.

Another interesting aspect of using robots, is that they allow one to evaluate a computational model by comparing its results with biological data at multiple levels: from neuronal activity, to EMG recordings, to kinematic studies, and up to behavioral studies.

Finally, using robots forces one to aim at a comprehensive understanding of the functioning of a system. Failure is very visible with a robot (e.g. it will fall over, get stuck, etc.), and all the components of the control system have to be in place for the robot to work properly. For example, in the case of locomotion this requires correctly solving the problems of rhythm generation, coordination between degrees of freedom, control of balance, and modulation of speed and direction. This requirement to be comprehensive reduces the risks of wrongly assuming that some key computation is performed by another component than the one under study.

One should however not underestimate the difficulties in using robots for computational neuroscience. First of all, it is very difficult, if not impossible, to correctly replicate the biomechanical properties of animal bodies, in particular their numbers of degrees of freedom, their mass distribution, and their visco-elastic properties. The benefits of not needing to simulate the physics is therefore counterbalanced by the fact that the robot might present an intrinsic dynamics which is significantly different from that of the modelled animal. Similarly, while some sensor modalities can correctly approximate biological ones, like vision and sound processing, others, like touch and proprioception, are yet far from being correctly replicated by current sensor technologies. Compared to simulations, robots present several additional constraints including (1) being less adjustable (i.e. only few parameters/quantities can be easily changed, most require designing and constructing a new robot), (2) requiring a large overhead for construction and maintenance, and (3) being less amenable to extensive experiments.

5. Design methodologies for CPGs

We have so far reviewed different CPG models used in neurobiology and in robotics, but we have not yet discussed how these models are created. Here I will briefly review what needs to be designed as well as different methodologies for designing CPGs to control a particular type of locomotion. As mentioned above, there is not yet a well-established design method, and people have explored different approaches including hand-coding, designs based on dynamical systems theory, and learning/optimization algorithms. This is related to the fact that a sound methodology does not exist yet for learning arbitrary limit cycles in dynamical systems, see a discussion in Buchli et al. (2006).

When constructing a CPG model, one has to define the following items: (1) The general architecture of the CPG. This includes the type and number of oscillators or neurons. In a robot, it also involves choosing between position control (i.e. the outputs of the CPG are the desired joint angles provided to a feedback controller) or torque control (i.e. the outputs of the CPG directly control the torque produced by the motors). (2) The type and topology of couplings. These will determine the conditions for synchronization between oscillators and the resulting gaits, i.e the stable phase relations between oscillators. (3) The waveforms. These will determine what trajectories will actually be performed by each joint angle during a cycle. The waveforms are clearly dependent on the shape of the limit cycle produced by the chosen (neural) oscillator, but can be transformed by the addition of filters. (4) The effect of input signals, i.e. how control parameters can modulate important quantities such as the frequency, amplitude, phase lags (for gait transition), or waveforms (e.g. for independently adjusting swing and stance phases). (5) The effect of feedback signals, i.e. how feedback from the body will affect the activity of the CPG (for instance accelerating or decelerating it depending on environmental conditions). A major difficulty in designing CPGs is that these five design axes are all strongly interconnected.

The theory of dynamical systems can help in designing CPGs. For instance, the theory can help in identifying when synchronization occurs in a system of coupled oscillators depending on parameters such as coupling weights and intrinsic frequencies (Buchli et al., 2006; Cohen et al., 1982; Ermentrout & Kopell, 1991; Golubitsky & Stewart, 2002; Kopell, 1995; Pham & Slotine, 2007; Pikovsky, Rosenblum, & Kurths, 2001; Schoner et al., 1990; Seo & Slotine, 2007; Stan & Sepulchre, 2007; Wang & Slotine, 2005). In particular, it can determine which phase differences are stable and unstable, and this knowledge can be used to design systems of coupled oscillators that evolve towards specific phase-locked regimes (e.g specific gaits). Symmetry considerations are particularly useful to determine the number of oscillators and the topology of the couplings necessary to obtain particular gaits (Buono, 2001; Buono & Golubitsky, 2001; Golubitsky & Stewart, 2002; Golubitsky et al., 1999; Pham & Slotine, 2007; Righetti & Ijspeert, 2008; Schoner et al., 1990).

Learning and optimization algorithms can be used in different ways. The approaches can be split into two categories: supervised learning and unsupervised learning. Supervised learning techniques can be applied when the desired rhythmic pattern that the CPG should produce is known. The desired pattern can then be used to define an explicit error function to be minimized. Such techniques can sometimes be used for designing CPGs, but they are restricted to situations where suitable patterns are available (e.g. they are obtained from kinematic measurements of animals). Examples of techniques include gradient-descent learning algorithms for recurrent neural networks (Pearlmutter, 1995; Prentice, Patla, & Stacey, 1998), learning for vector fields (Okada et al., 2002), and statistical learning algorithms (e.g. locally weighted regression) for dynamical systems (Ijspeert, Nakanishi, & Schaal, 2003; Nakanishi et al., 2004). We also explored the notion of programmable central pattern generators that use pools of frequency adaptive oscillators to learn a specific rhythmic pattern (Righetti & Ijspeert, 2006b). An interesting aspect here is that learning is embedded into the dynamical system (as opposed to being implemented by an external algorithm), see Buchli and Ijspeert (2004b) and Righetti, Buchli, and Ijspeert (2006).

Unsupervised learning techniques are used when the desired behavior of the CPG is not defined by a specific desired pattern (as in supervised learning), but by a high-level performance criterion, for instance, moving as fast as possible. Among unsupervised learning techniques, stochastic population-based optimization algorithms such as evolutionary algorithms have extensively been used to design CPG-like models (Beer & Gallagher, 1992; Gruau & Quatramaran, 1997; Ijspeert, 2001; Ijspeert & Kodjabachian, 1999; Kamimura et al., 2003; Lewis, Fagg, & Bekey, 1993; Paul & Bongard, 2001; Sims, 1994). An interesting property of these algorithms is that they can optimize a large class of cost functions (for instance, the cost functions do not need to be continuous as required for gradient-descent algorithms) and that they do not require knowing the gradient of the cost functions (which is usually not available). That makes them well suited to optimize performance measurements of a robot, for instance, the forward speed of locomotion. The parameters that are optimized are usually synaptic weights in fixed neural network architectures and coupling weights in systems of coupled oscillators. In some cases, the architecture of the CPGs themselves are evolved using developmental encoding (Gruau & Quatramaran, 1997; Ijspeert & Kodjabachian, 1999). Two drawbacks of evolutionary approaches are that they are slow, and they usually require extensive use of simulators which might make the transfer of the CPG model to the real robot difficult. See Nolfi and Floreano (2001) for a discussion. Other unsupervised approaches include reinforcement learning algorithms[8] (Matsubara et al., 2006; Nakamura, Mori, Sato, & Ishii, 2007; Ogino, Katoh, Aono, Asada, & Hosoda, 2004; Sato, Nakamura, & Ishii, 2002) and heuristic optimization algorithms such as Powell's method (Crespi & Ijspeert, 2008; Marbach & Ijspeert, 2005; Sproewitz, Moeckel, Maye, & Ijspeert, 2008).

Note that while the above design methodologies have mainly been used for engineering purposes, they might also be usable as scientific tools for designing and evaluating biological CPG models. In particular, most learning and optimization algorithms described above can be used to instantiate open parameters in biological models, and to explore what parameters are found depending on the criteria that are optimized. For instance, a variant of the backpropagation algorithm has been applied to define synaptic weights of a connectionist model representing the escape reflex in a leech (Lockery & Sejnowski, 1993). See Ijspeert et al. (1999) for an example in which a genetic algorithm is used to set synaptic weights in a circuit corresponding to the lamprey segmental network.

6. Open research topics

Here I will review a list of questions which in my opinion remain open research topics. These questions are related to various aspects of CPGs both from a biological and/or a robotic perspective, namely the evolution of CPGs, their modification through development, their coupling to a mechanical body, the ability to produce multiple gaits, the link between CPGs and rich motor skills, and finally the theoretical foundations of CPGs.

An important question which remains to be studied in more detail is the evolutionary transition between different modes of locomotion and different ecological niches. In vertebrates, for instance, one would like to know how CPGs have changed from lamprey-like primitive swimming circuits up to the various types of locomotion seen in terrestrial animals (walking, flying, running, crawling, etc.). Interestingly it seems that morphologies of vertebrates have changed more than the underlying motor control circuits (Cohen, 1988; ten Donkelaar, 2001). Comparative studies and numerical modelling can be used to study what might have been the chain of changes that have occurred to switch from one type of locomotion to the other. In Ijspeert et al. (2007), we have explored such a question for the evolutionary transition from lamprey swimming to salamander swimming and walking. One would like to see similar studies linking different locomotor circuits up to mammal circuits, including human locomotion. Related to this study, it would also be interesting to explore links between locomotion control and higher cognition. For instance, an article by Yuste, MacLean, Smith, and Lansner (2005) presents intriguing similarities between CPG mechanisms and microcircuits in the cortex, hinting that some mechanisms evolved for locomotion control might also play a role in cognition.

Another important question concerns developmental mechanisms, that is what are the mechanisms that underlie how a CPG constructs itself. Apart from a few exceptions (e.g. human infants), animals need to be capable of efficiently moving at all stages of their lives from newborns to adults. That often involves adapting to body properties that vary over several orders of magnitude (in dimensions and mass). In many cases, the modes of locomotion are quite different for different stages in life, especially in animals that undergo metamorphosis (e.g. frogs and butterflies). Furthermore there is good evidence that biological CPGs are capable of some plasticity (i.e. some learning with locomotor training) see Rossignol (2000). These are fascinating adaptation capabilities from a robotics point of view, and it would be very interesting and useful to understand the underlying organizational principles.

The notion of mutual entrainment between a CPG and a mechanical body is of great importance in robotics. Most robots have several resonant frequencies due to pendulum and/or (in compliant robots) spring–mass phenomena. It is typically useful to adapt gaits to these frequencies such as to minimize energy consumption. See for instance the work on passive or dynamic walkers (Collins et al., 2005). In many cases, a CPG with mutual coupling will synchronize with a frequency close to those resonant frequencies, if the coupling from body to CPG is strong enough compared to the difference between the resonant frequency and the intrinsic frequency of the CPG (Taga, 1998; Verdaasdonk et al., 2006). In more general cases, it might be worth adding frequency adaptation to the CPGs, that is, mechanisms that go beyond mere synchronization and that can change the intrinsic frequencies of CPGs according to feedback signals from the body. We have developed such a method in Buchli et al. (2006) using adaptive frequency oscillators (Righetti et al., 2006), and related work can be found in Nishii (1998, 1999). It is likely that biological CPGs have similar adaptation mechanisms in order to adapt to changing body properties during growth (as discussed above).

Many animals are capable of using multiple gaits. As discussed in Section 2, often simple electrical stimulation of a particular region of the brain stem in vertebrate animals can induce dramatic gait changes, for instance from walk to trot to gallop in cat. The underlying neural mechanisms are not yet fully understood, and mathematical modelling and robotic implementations can help in exploring them. Several computational studies of gait transitions exist, for instance by modelling gait transitions as bifurcation phenomena (Buchli & Ijspeert, 2004a; Buono, 2001; Buono & Golubitsky, 2001; Canavier et al., 1997; Collins & Richmond, 1994; Golubitsky et al., 1999; Kaske et al., 2003; Pribe et al., 1997; Schoner et al., 1990; Schoner & Kelso, 1988), but few have been applied to robotics. CPG-based gait transitions in robots have been explored in Ijspeert et al. (2007). It would be interesting to have more studies in that direction, in particular, to study (1) how different gaits are produced, e.g. the role of central versus peripheral mechanisms, and (2) to relate this to the usefulness of gait transitions, e.g. in terms of equilibrium, speed, and energy efficiency (Full & Koditscheck, 1999; Hoyt & Taylor, 1981; Kimura, Shimoyama, & Miura, 1990).

Animals rarely perform steady-state locomotion for long, and tend to superpose, and switch between, multiple motor behaviors. A remaining open challenge is therefore to design control architectures capable of exhibiting such richness of motor skills. For a long time, central pattern generators were falsely perceived (by neurobiologists and roboticists) to produce only stereotyped fixed patterns. As reviewed in this article, neurophysiological experiments and CPG models have now clearly shown that CPGs can produce very rich behavior, being for instance capable of modulating speed, direction, and types of gaits depending on descending control signals. But the link with other motor behaviors such as scratching, standing up, kicking, sitting down, laying down, reaching, manipulation, etc. remains, to a large extent, to be decoded in animals and implemented in robots. To take one example, the problem of visually-guided feet placement is an interesting topic since it involves the superposition of discrete and rhythmic movements. For instance, when specific feet placements are required during walking (e.g. when a cat walks over a branch or when we cross a river walking on stones), rhythmic signals from the CPGs need to be modulated such that the feet reach specific end positions. Examples of CPG-based models capable of superposing discrete and rhythmic movements can be found

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[8] See also Collins et al. (2005) and Geng et al. (2006) for two interesting examples of the application of reinforcement learning to biped locomotion control without CPGs.

in Degallier, Santos, Righetti, and Ijspeert (2006), Lewis (2002) and Taga (1998). More generally, the problem of how to design controllers capable of producing rich motor skills is still an open research question. Many researchers now propose that animal motor control is based on the combination of motor primitives, i.e. complex movements are generated by combining a finite set of simpler elementary movements (Flash & Hochner, 2005; Thoroughman & Shadmehr, 2000; Todorov, 2004; Tresch, Saltiel, d'Avella, & Bizzi, 2002). Motor primitives (and related concepts such as muscle synergies, force fields, and motor schemas) are seen like elementary controllers that produce specific movements under the control of a few open control parameters. Experiments on decerebrated and spinalized animals indicate that, like CPGs, many of these motor primitives are implemented at a low level in the vertebrate central nervous system, namely in the brainstem and the spinal cord (Bizzi et al., 2000; Grillner, 2006; Stein & Smith, 1997; Tresch et al., 2002; Whelan, 1996). The interesting features of CPGs discussed in Section 2, e.g. in terms of the dimensionality of the control signals, can indeed also be found in discrete pattern generators, see the force field concept identified by Bizzi et al. (2000). CPGs should therefore be seen as particular movement primitives that can be activated together with others. From a robotics point of view, the idea of using motor primitives for constructing controllers for complex motor skills is appealing and is attracting a growing number of researchers (Ijspeert et al., 2003; Mussa-Ivaldi, 1997; Schaal & Schweighofer, 2005; Todorov, Li, & Pan, 2005).

Finally, one of the most important open research topics is the development of a solid methodology and theoretical foundation for designing CPGs. Excellent theoretical approaches have been developed for analyzing systems of coupled oscillators (Ermentrout & Kopell, 1991; Golubitsky & Stewart, 2002; Kopell, 1995; Pham & Slotine, 2007; Pikovsky et al., 2001; Slotine & Li, 1991; Wang & Slotine, 2005), but many of these tools are not yet sufficient to completely design CPGs for a particular task, namely the five design items listed in Section 5. While good progress is being made, the development of mathematical tools to help in synthesizing CPG-based controllers that exhibit particular desired characteristics for a particular robot structure is still needed.

7. Conclusion

In this article, I have reviewed research on locomotor CPGs both in animals and in robots. It is a field of research in which there are very exciting interactions between mathematics, biology, and robotics. As illustrated by several examples in this review, each of these three fields has something to gain from the other two. I hope that the discussion presented here will stimulate young researchers to join this type of research and to contribute to the development of new mathematical tools, new biological hypotheses and experiments, as well as new technologies for robotics. Advances in the fundamental understanding of the functioning of CPGs will not only help biology and robotics, but hopefully also have an impact in medicine, with possible contributions in the long run to the design of therapies (e.g. using electrical stimulation) for patients with spinal cord injuries (Loeb, 2001).

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References

Altendorfer, A., Moore, N., Komsuoglu, H., Buehler, M., Brown, H. B., Jr., McMordie, D., et al. (2001). Rhex: A biologically inspired hexapod runner. *Autonomous Robots*, *11*, 207–213.

Aoi, S., & Tsuchiya, K. (2005). Locomotion control of a biped robot using nonlinear oscillators. *Autonomous Robots*, *19*, 219–232.

Aoi, S., & Tsuchiya, K. (2006). Stability analysis of a simple walking model driven by an oscillator with a phase reset using sensory feedback. *IEEE Transactions on Robotics*, *22*(2), 391–397.

Arena, P. (2000). The central pattern generator: A paradigm for artificial locomotion. *Soft Computing*, *4*(4), 251–266.

Arena, P. (2001). A mechatronic lamprey controlled by analog circuits. In *Proceedings of the 9th IEEE mediterannean conference on control and automation*.

Arena, P., Fortuna, L., Frasca, M., & Sicurella, G. (2004). An adaptive, self-organizing dynamical system for hierarchical control of bio-inspired locomotion. *IEEE Transactions on Systems, Man and Cybernetics, Part B*, *34*(4), 1823–1837.

Armstrong, D. M. (1988). Review lecture: The supraspinal control of mammalian locomotion. *Journal of Physiology*, *405*, 1–37.

Ayers, J., & Crisman, J. (1993). The lobster as a model for an omnidirectional robotic ambulation control architecture. In R. D. Beer, R. E. Ritzmann, & T. M. McKenna (Eds.), *Biological neural networks in invertebrate neuroethology and robotics* (pp. 287–316). Academic Press.

Ayers, J., Davis, J. L., & Rudolph, A. (2002). *Neurotechnology for biomimetic robots*. MIT Press.

Ayers, J., & Witting, J. (2007). Biomimetic approaches to the control of underwater walking machines. *Philosophical Transactions: Mathematical, Physical and Engineering Sciences (Series A)*, *365*(1850), 273–295.

Beer, R. D., Chiel, H. J., Quinn, R. D., Espenshied, K. S., & Larsson, P. (1992). A distributed neural network architecture for hexapod robot locomotion. *Neural Computation*, *4*, 356–365.

Beer, R. D., Chiel, H. J., Quinn, R. D., & Ritzmann, R. E. (1998). Biorobotic approaches to the study of motor systems. *Current Opinion in Neurobiology*, *8*, 777–782.

Beer, R. D., & Gallagher, J. C. (1992). Evolving dynamical neural networks for adaptive behavior. *Adaptive Behavior*, *1*(1), 91–122.

Beer, R. D., Ritzmann, R. E., & McKenna, T. M. (1993). *Biological neural networks in invertebrate neuroethology and robotics*. Academic Press.

Bem, T., Cabelguen, J. M., Ekeberg, O., & Grillner, S. (2003). From swimming to walking: A single basic network for two different behaviors. *Biological Cybernetics*, *88*, 79–90.

Billard, A., & Ijspeert, A. J. (2000). Biologically inspired neural controllers for motor control in a quadruped robot. In *Proceedings of the IEEE-INNS-ENNS international joint conference on neural networks – IJCNN2000*: *Vol. VI* (pp. 637–641). IEEE Computer Society.

Bizzi, E., Tresch, M. C., Saltiel, P., & d'Avella, A. (2000). New perspectives on spinal motor systems. *Nature Reviews Neuroscience*, *1*, 101–108.

Brambilla, G., Buchli, J., & Ijspeert, A. J. (2006). Adaptive four legged locomotion control based on nonlinear dynamical systems. In *SAB'06*: *Vol. 4095. From animals to animats 9. Proceedings of the ninth international conference on the simulation of adaptive behavior*. Springer Verlag.

Brown, T. G. (1911). The intrinsic factors in the act of progression in the mammal. *Proceedings of the Royal Society of London. Series B*, *84*(572), 308–319.

Brown, T. G. (1914). On the nature of the fundamental activity of the nervous centres; together with an analysis of the conditioning of rhythmic activity in progression, and a theory of the evolution of function in the nervous system.. *Journal of Physiology - London*, *48*, 18–46.

Buchanan, J. T. (1992). Neural network simulations of coupled locomotor oscillators in the lamprey spinal cord. *Biological Cybernetics*, *66*, 367–374.

Buchli, J., Iida, F., & Ijspeert, A. J. (2006). Finding resonance: Adaptive frequency oscillators for dynamic legged locomotion. In *Proceedings of the IEEE/RSJ international conference on intelligent robots and systems* (pp. 3903–3909). IEEE.

Buchli, J., & Ijspeert, A. J. (2004a). Distributed central pattern generator model for robotics application based on phase sensitivity analysis. In A. J. Ijspeert, M. Murata, & N. Wakamiya (Eds.), *BioADIT 2004*: *Vol. 3141. Biologically inspired approaches to advanced information technology: First international workshop* (pp. 333–349). Springer Verlag Berlin Heidelberg.

Buchli, J., & Ijspeert, A. J. (2004b). A simple, adaptive locomotion toy-system. In S. Schaal, A. J. Ijspeert, A. Billard, S. Vijayakumar, J. Hallam, & J. A. Meyer (Eds.), *From animals to animats 8. Proceedings of the eighth international conference on the simulation of adaptive behavior* (pp. 153–162). MIT Press.

Buchli, J., Righetti, L., & Ijspeert, A. J. (2006). Engineering entrainment and adaptation in limit cycle systems — from biological inspiration to applications in robotics. *Biological Cybernetics*, *95*(6), 645–664.

Buono, P. L. (2001). Models of central pattern generators for quadruped locomotion. ii. Secondary gaits. *Journal of Mathematical Biology*, *42*(4), 327–346.

Buono, P. L., & Golubitsky, M. (2001). Models of central pattern generators for quadruped locomotion. i. Primary gaits. *Journal of Mathematical Biology*, *42*(4), 291–326.

Cabelguen, J. M., Bourcier-Lucas, C., & Dubuc, R. (2003). Bimodal locomotion elicited by electrical stimulation of the midbrain in the salamander notophthalmus viridesecens. *The Journal of Neuroscience*, *23*(6), 2434–2439.

Canavier, C. C., Butera, R. J., Dror, R. O., Baxter, D. A., Clark, J. W., & Byrne, J. H. (1997). Phase response characteristics of model neurons determine which patterns are expressed in a ring circuit model of gait generation. *Biological Cybernetics*, *77*, 367–380.

Cheng, J., Stein, R. B., Jovanovic, K., Yoshida, K., Bennett, D. J., & Han, Y. (1998). Identification, localization, and modulation of neural networks for walking in the mudpuppy (necturus maculatus) spinal cord. *The Journal of Neuroscience*, *18*(11), 4295–4304.

Cohen, A. H. (1988). Evolution of the vertebrate central pattern generator for locomotion. In A. H. Cohen, S. Rossignol, & S. Grillner (Eds.), *Neural control of rhythmic movements in vertebrates*. Jon Wiley & Sons.

Cohen, A. H., Holmes, P. J., & Rand, R. (1982). The nature of coupling between segmented oscillations and the lamprey spinal generator for locomotion: A mathematical model. *Journal of Mathematical Biology*, *13*, 345–369.

Cohen, A. H., & Wallen, P. (1980). The neural correlate of locomotion in fish. fictive swimming "induced in a in vitro preparation of the lamprey spinal cord". *Experimental Brain Research*, *41*, 11–18.

Collins, J., & Richmond, S. (1994). Hard-wired central pattern generators for quadrupedal locomotion. *Biological Cybernetics*, *71*, 375–385.

Collins, S., Ruina, A., Tedrake, R., & Wisse, M. (2005). Efficient bipedal robots based on passive-dynamic walkers. *Science*, *307*(5712), 1082–1085.

Conradt, J., & Varshavskaya, P. (2003). Distributed central pattern generator control for a serpentine robot. In *International conference on artificial neural networks*.

Crespi, A., & Ijspeert, A. (2008). Online optimization of swimming and crawling in an amphibious snake robot. *IEEE Transactions on Robotics*, *24*(1), 75–87.

Crespi, A., & Ijspeert, A. J. (2006). AmphiBot II: An amphibious snake robot that crawls and swims using a central pattern generator. In *Proceedings of the 9th international conference on climbing and walking robots* (pp. 19–27).

Cruse, H., Brunn, D. E., Bartling, C., Dean, J., Dreifert, M., Kindermann, T., et al. (1995). Walking: A complex behavior controlled by simple networks. *Adaptive Behavior*, *3*(4), 385–418.

Degallier, S., Santos, C. P., Righetti, L., & Ijspeert, A. J. (2006). Movement generation using dynamical systems: A humanoid robot performing a drumming task. In *IEEE-RAS international conference on humanoid robots*.

Delcomyn, F. (1980). Neural basis for rhythmic behaviour in animals. *Science*, *210*, 492–498.

Delcomyn, F. (1999). Walking robots and the central and peripheral control of locomotion in insects. *Autonomous Robots*, *7*, 259–270.

Deliagina, T. G., Zelenin, P. V., Fagerstedt, P., Grillner, S., & Orlovsky, G. N. (2000). Activity of the reticulospinal neurons during locomotion in freely behaving lamprey. *Journal of Neurophysiology*, *83*, 853–863.

Delvolvé, I., Branchereau, P., Dubuc, R., & Cabelguen, J. M. (1999). Fictive rhythmic motor patterns induced by NMDA in an in vitro brain stem-spinal cord preparation from an adult urodele. *Journal of Neurophysiology*, *82*, 1074–1077.

DeWeerth, S. P., Patel, G. N., Simoni, M. F., Schimmel, D. E., & Calabrese, R. L. (1997). A VLSI architecture for modeling intersegmental coordination. In R. Brown, & A. Ishii (Eds.), *17th conference on advanced research in VLSI* (pp. 182–200). IEEE Computer Society.

Dickinson, M. H., Farley, C. T., Full, R. J., Koehl, M. A. R., Kram, R., & Lehman, S. (2000). How animals move: An integrative view. *Science*, *288*(5463), 100–106.

Ekeberg, Ö. (1993). A combined neuronal and mechanical model of fish swimming. *Biological Cybernetics*, *69*, 363–374.

Ekeberg, Ö., & Pearson, K. (2005). Computer simulation of stepping in the hind legs of the cat: An examination of mechanisms regulating the stance-to-swing transition. *Journal of Neurophysiology*, *94*, 4256–4268.

Ekeberg, Ö., Wallén, P., Lansner, A., Traven, H., Brodin, L., & Grillner, S. (1991). A computer-based model for realistic simulations of neural networks i: The single neuron and synaptic interaction. *Biological Cybernetics*, *65*, 81–90.

Endo, G., Nakanishi, J., Morimoto, J., & Cheng, G. (2005). Experimental studies of a neural oscillator for biped locomotion with Q RIO. In *Proceedings of the 2005 IEEE international conference on robotics and automation* (pp. 598–604)..

Ermentrout, B., & Kopell, N. (1991). Multiple pulse interactions and averaging in systems of coupled neural oscillators. *Journal of Mathematical Biology*, *29*, 195–217.

Ermentrout, B., & Kopell, N. (1994). Inhibition-produced patterning in chains of coupled nonlinear oscillators. *SIAM Journal of Applied Mathematics*, *54*(2), 478–507.

Flash, T., & Hochner, B. (2005). Motor primitives in vertebrates and invertebrates. *Current Opinion in Neurobiology*, *15*(6), 660–666.

Fukuoka, Y., Kimura, H., & Cohen, A. H. (2003). Adaptive dynamic walking of a quadruped robot on irregular terrain based on biological concepts. *The International Journal of Robotics Research*, *3–4*, 187–202.

Full, R. J., & Koditscheck, D. E. (1999). Templates and anchors: Neuromechanical hypotheses of legged locomotion on land. *Journal of Experimental Biology*, *202*, 3325–3332.

Geng, T., Porr, B., & Wörgötter, F. (2006). Fast biped walking with a reflexive neuronal controller and real-time online learning. *International Journal of Robotics Research*, *3*, 243–261.

Geyer, H., Seyfarth, A., & Blickhan, R. (2003). Positive force feedback in bouncing gaits? *Proceedings of the Royal Society of London Series B - Biological Sciences*, *270*(1529), 2173–2183.

Ghigliazza, R. M., & Holmes, P. (2004). A minimal model of a central pattern generator and motoneurons for insect locomotion. *SIAM Journal on Applied Dynamical Systems*, *3*(4), 671–700.

Golubitsky, M., & Stewart, I. (2002). *The symmetry perspective: From equilibrium to chaos in phase space and physical space (progress in mathematics, vol. 200)*. Birkhauser.

Golubitsky, M., Stewart, I., Buono, P. L., & Collins, J. J. (1999). Symmetry in locomotor central pattern generators and animal gaits. *Nature*, *401*, 693–695.

Grillner, S. (1985). Neural control of vertebrate locomotion — central mechanisms and reflex interaction with special reference to the cat. In W. J. P. Barnes, & G. M. H. (Eds.), *Feedback and motor control in invertebrates and vertebrates* (pp. 35–56). Croom Helm.

Grillner, S. (2006). Biological pattern generation: The cellular and computational logic of networks in motion. *Neuron*, *52*(5), 751–766.

Grillner, S., Degliana, T., Ekeberg, Ö., El Marina, A., Lansner, A., Orlovsky, G. N., et al. (1995). Neural networks that co-ordinate locomotion and body orientation in lamprey. *Trends in Neuroscience*, *18*(6), 270–279.

Grillner, S., Georgopoulos, A. P., & Jordan, L. M. (1997). Selection and initiation of motor behavior. In P. S. G. Stein, S. Grillner, A. Selverston, & D. G. Stuart (Eds.), *Neurons, networks and motor behavior*. MIT Press.

Grillner, S., Wallén, P., & Brodin, L. (1991). Neuronal network generating locomotor behavior in lamprey: Circuitry, transmitters, membrane properties, and simulation. *Annual Review of Neuroscience*, *14*, 169–199.

Gruau, F., & Quatramaran, K. (1997). Cellular encoding for interactive evolutionary robotics. In P. Husbands, & I. Harvey (Eds.), *Proceedings of the fourth european conference on artificial life* (pp. 368–377). MIT Press.

Héliot, R., & Espiau, B. (2008). Multisensor input for CPG-based sensory—motor coordination. *IEEE Transactions on Robotics*, *24*(1), 191–195.

Hellgren, J., Grillner, S., & Lansner, A. (1992). Computer simulation of the segmental neural network generating locomotion in lamprey by using populations of network interneurons. *Biological Cybernetics*, *68*, 1–13.

Holmes, P., Full, R. J., Koditschek, D., & Guckenheimer, J. (2006). The dynamics of legged locomotion: Models, analyses, and challenges. *SIAM Review*, *48*(2), 207–304.

Hoyt, D. F., & Taylor, R. (1981). Gait and the energetics of locomotion in horses. *Nature*, *292*, 239–240.

Ijspeert, A. J. (2001). A connectionist central pattern generator for the aquatic and terrestrial gaits of a simulated salamander. *Biological Cybernetics*, *84*(5), 331–348.

Ijspeert, A. J., & Crespi, A. (2007). Online trajectory generation in an amphibious snake robot using a lamprey-like central pattern generator model. In *Proceedings of the IEEE international conference on robotics and automation*.

Ijspeert, A. J., Crespi, A., & Cabelguen, J. M. (2005). Simulation and robotics studies of salamander locomotion: Applying neurobiological principles to the control of locomotion in robots. *NeuroInformatics*, *3*(3), 171–196.

Ijspeert, A. J., Crespi, A., Ryczko, D., & Cabelguen, J. M. (2007). From swimming to walking with a salamander robot driven by a spinal cord model. *Science*, *315*(5817), 1416–1420.

Ijspeert, A. J., Hallam, J., & Willshaw, D. (1999). Evolving swimming controllers for a simulated lamprey with inspiration from neurobiology. *Adaptive Behavior*, *7*(2), 151–172.

Ijspeert, A. J., & Kodjabachian, J. (1999). Evolution and development of a central pattern generator for the swimming of a lamprey. *Artificial Life*, *5*(3), 247–269.

Ijspeert, A. J., Nakanishi, J., & Schaal, S. (2003). Learning control policies for movement imitation and movement recognition. In S. T. S. Becker, & K. Obermayer (Eds.), *Neural information processing system 15* (pp. 1547–1554).

Inagaki, S., Yuasa, H., & Arai, T. (2003). CPG model for autonomous decentralized multi-legged robot system—generation and transition of oscillation patterns and dynamics of oscillators. *Robotics and Autonomous Systems*, *44*(3–4), 171–179.

Inagaki, S., Yuasa, H., Suzuki, T., & Arai, T. (2006). Wave CPG model for autonomous decentralized multi-legged robot: Gait generation and walking speed control. *Robotics and Autonomous Systems*, *54*(2), 118–126.

Inoue, K., Ma, S., & Jin, C. (2004). Neural oscillator network-based controller for meandering locomotion of snake-like robots. In *Proceedings of the IEEE international conference on robotics and automation* (pp. 5064–5069).

Ito, S., Yuasa, H., Luo, Z., Ito, M., & Yanagihara, D. (1998). A mathematical model of adaptive behavior in quadruped locomotion. *Biological Cybernetics*, *78*(5), 337–347.

Jung, R., Kiemel, T., & Cohen, A. H. (1996). Dynamical behavior of a neural network model of locomotor control in the lamprey. *Journal of Neurophysiology*, *75*, 1074–1086.

Kamimura, A., Kurokawa, H., Toshida, E., Tomita, K., Murata, S., & Kokaji, S. (2003). Automatic locomotion pattern generation for modular robots. In *IEEE international conference on robotics and automation*.

Kamimura, A., Kurokawa, H., Yoshida, E., Murata, S., Tomita, K., & Kokaji, S. (2004) Distributed adaptive locomotion by a modular robotic system, M-TRAN II. In *Proceedings of the IEEE/RSJ international conference on intelligent robots and systems* (pp. 2370–2377).

Kaske, A., Winberg, G., & Cöster, J. (2003). Emergence of coherent traveling waves controlling quadruped gaits in a two-dimensional spinal cord model. *Biological Cybernetics*, *88*(1), 20–32.

Kimura, H., Akiyama, S., & Sakurama, K. (1999). Realization of dynamic walking and running of the quadruped using neural oscillators. *Autonomous Robots*, *7*(3), 247–258.

Kimura, H., Fukuoka, Y., & Cohen, A. H. (2007). Adaptive dynamic walking of a quadruped robot on natural ground based on biological concepts. *International Journal of Robotics Research*, *26*(5), 475–490.

Kimura, H., Shimoyama, I., & Miura, H. (1990). Dynamics in the dynamic walk of a quadruped robot. *Advanced Robotics*, *4*(3), 283–301.

Kimura, H., Tsuchiya, K., Ishiguro, A., & Witte, H. (2005). *Adaptive motion of animals and machines*. Springer-Verlag.

Klaassen, B., Linnemann, R., Spenneberg, D., & Kirchner, F. (2002). Biomimetic walking robot scorpion: Control and modeling. *Autonomous Robots*, *41*, 69–76.

Komatsu, T., & Usui, M. (2005). Dynamic walking and running of a bipedal robot using hybrid central pattern generator method. In *Proceedings of the IEEE international conference on mechatronics and automation* (pp. 987–992).

Kopell, N. (1995). Chains of coupled oscillators. In M. A. Arbib (Ed.), *The handbook of brain theory and neural networks* (pp. 178–183). MIT Press.

Kopell N., Ermentrout, G. B., & Williams, T. L. (1991). On chains of oscillators forced at one end. *SIAM Journal of Applied Mathematics*, *51*(5), 1397–1417.

Kuniyoshi, Y., & Suzuki, S. (2004). Dynamic emergence and adaptation of behavior through embodiment as coupled chaotic field. In *Proceedings of 2004 IEEE/RSJ international conference on intelligent robots and systems* (pp. 2042–2049). IEEE.

Kuo, P. D., & Eliasmith, C. (2004). Integrating behavioral and neural data in a model of zebrafish network interaction. *Biological Cybernetics*, *93*(3), 178–187.

Kuramoto, Y. (2003). Collective behavior of coupled phase oscillators. In M. A. Arbib (Ed.), *The handbook of brain theory and neural networks* (pp. 223–226). MIT Press.

Lachat, D., Crespi, A., & Ijspeert, A.J. (2006). Boxybot: A swimming and crawling fish robot controlled by a central pattern generator. In *Proceedings of the first IEEE / RAS-EMBS international conference on biomedical robotics and biomechatronics*.

La Spina, G., Sfakiotakis, M., Tsakiris, D., Menciassi, A., & Dario, P. (2007). Polychaete-like undulatory robotic locomotion in unstructured substrates. *IEEE Transactions on Robotics*, *23*(6), 1200–1212.

Lewis, M. A. (2002). Perception driven robot locomotion. *Journal Robot Society of Japan*, *20*, 51–56.

Lewis, M. A., Fagg, A. H., & Bekey, G. A. (1993). Genetic algorithms for gait synthesis in a hexapod robot. In Y. F. Zheng (Ed.), *Recent trends in mobile robots*. World Scientific.

Lewis, M.A., Tenore, F., & Etienne-Cummings, R. (2005). CPG design using inhibitory networks. In *IEEE international conference on robotics and automation*.

Lockery, S. R., & Sejnowski, T. J. (1993). The computational leech. *Trends in Neuroscience*, *16*(7), 283–290.

Loeb, G. (2001). Learning from the spinal cord. *The Journal of Physiology*, *533*(1), 111–117.

Long, J. H., Schumacher, J., Livingston, N., & Kemp, M. (2006). Four flippers or two? Tetrapodal swimming with an aquatic robot. *Bioinspiration and Biomimetics*, *1*, 20–29.

Lu, Z., Ma, B., Li, S., & Wang, Y. (2005). Serpentine locomotion of a snake-like robot controlled by cyclic inhibitory CPG model. In *The proceedings of the IEEE/RSJ international conference on intelligent robots and systems* (pp. 96–101).

Lu, Z., Ma, B., Li, S., & Wang, Y. (2006). 3D locomotion of a snake-like robot controlled by cyclic inhibitory CPG model. In *The proceedings of the IEEE/RSJ international conference on intelligent robots and systems* (pp. 3897–3902).

Manoonpong, P., Pasemann, F., & Roth, H. (2007). Modular reactive neurocontrol for biologically inspired walking machines. *International Journal of Robotics Research*, *26*(3), 301–331.

Marbach, D., & Ijspeert, A. J. (2005). Online optimization of modular robot locomotion. In *Proceedings of the IEEE Int. conference on mechatronics and automation* (pp. 248–253).

Matsubara, T., Morimoto, J., Nakanishi, J., Sato, M., & Doya, K. (2006). Learning CPG-based biped locomotion with a policy gradient method. *Robotics and Autonomous Systems*, *54*, 911–920.

Matsuoka, K. (1985). Sustained oscillations generated by mutually inhibiting neurons with adaptation. *Biological Cybernetics*, *52*, 367–376.

Matsuoka, K. (1987). Mechanisms of frequency and pattern control in the neural rhythm generators. *Biological Cybernetics*, *56*, 345–353.

McClellan, A. D., & Jang, W. (1993). Mechanosensory inputs to the central pattern generators for locomotion in the lamprey spinal cord: Resetting, entrainment, and computer modeling. *Journal of Neurophysiology*, *70*(6), 161–166.

Miyakoshi, S., Taga, G., Kuniyoshi, Y., & Nagakubo, A. (1998). Three dimensional bipedal stepping motion using neural oscillators — towards humanoid motion in the real world. In *Proceedings of the IEEE/RSJ Int. conference on intelligent robots and systems* (pp. 84–89).

Morimoto, J., Endo, G., Nakanishi, J., Hyon, S., Cheng, G., & Bentivegna, D. et al. (2006). Modulation of simple sinusoidal patterns by a coupled oscillator model for biped walking. In *Proceedings of the 2006 IEEE international conference on robotics and automation* (pp. 1579–1584).

Mussa-Ivaldi, F. A. (1997). Nonlinear force fields: A distributed system of control primitives for representing and learning movements. In *IEEE international symposium on computational intelligence in robotics and automation* (pp. 84–90). IEEE, Computer Society, Los Alamitos.

Nakada, K., Asai, T., & Amemiya, Y. (2003). An analog CMOS central pattern generator for interlimb coordination in quadruped locomotion. *IEEE Transactions on Neural Networks*, *14*(5), 1356–1365.

Nakamura, Y., Mori, T., Sato, M., & Ishii, S. (2007). Reinforcement learning for a biped robot based on a cpg-actor-critic method. *Neural Networks*, *20*(6), 723–735.

Nakanishi, J., Morimoto, J., Endo, G., Cheng, G., Schaal, S., & Kawato, M. (2004). Learning from demonstration and adaptation of biped locomotion. *Robotics and Autonomous Systems*, *47*, 79–91.

Nishii, J. (1998). A learning model for oscillatory networks. *Neural Networks*, *11*, 249–257.

Nishii, J. (1999). Learning model for coupled neural oscillators. *Network: Computation in Neural Systems*, *10*, 213–226.

Nishii, J., Uno, Y., & Suzuki, R. (1994). Mathematical models for the swimming pattern of a lamprey, i. Analysis of collective oscillators with time-delayed interaction and multiple coupling. *Biological Cybernetics*, *72*, 1–9.

Nolfi, S., & Floreano, D. (2001). *Evolutionary robotics. The biology, intelligence, and technology of self-organizing machines*. Cambridge, MA: MIT Press, 2001 (2nd print), 2000 (1st print).

Ogino, M., Katoh, Y., Aono, M., Asada, M., & Hosoda, K. (2004). Reinforcement learning of humanoid rhythmic walking parameters based on visual information. *Advanced Robotics*, *18*(7), 677–697.

Okada, M., Tatani, K., & Nakamura, Y. (2002). Polynomial design of the nonlinear dynamics for the brain-like information processing of whole body motion. In *IEEE international conference on robotics and automation* (pp. 1410–1415).

Paul, C., & Bongard, J. C. (2001). The road less travelled: Morphology in the optimization of biped robot locomotion. In *Proceedings of the IEEE/RSJ international conference on intelligent robots and systems*.

Pearlmutter, B. A. (1995). Gradient calculations for dynamic recurrent neural networks: A survey. *IEEE Transactions on Neural Networks*, *6*(5), 1212–1228.

Pearson, K. G. (1995). Proprioceptive regulation of locomotion. *Current Opinion in Neurobiology*, *5*, 786–791.

Pearson, K., & Gordon, J. (2000). Spinal reflexes. In E. R. Kandel, J. H. Schwartz, & T. M. Jessel (Eds.), *Principles of neural science* (4th Ed.). New York: McGraw-Hill.

Pham, Q. C., & Slotine, J. J. (2007). Stable concurrent synchronization in dynamic system networks. *Neural Networks*, *20*(1), 62–77.

Pikovsky, A., Rosenblum, M., & Kurths, J. (2001). *Synchronization, a universal concept in nonlinear sciences*: *Vol. 12*. Cambridge, UK: Cambridge University Press.

Pratt, J., Chew, C. M., Torres, A., Dilworth, P., & Pratt, G. (2001). Virtual model control: An intuitive approach for bipedal locomotion. *The International Journal of Robotics Research*, *20*(2), 129–143.

Prentice, S. D., Patla, A. E., & Stacey, D. A. (1998). Simple artificial neural network models can generate basic muscle activity patterns for human locomotion at different speeds. *Experimental Brain Research*, *123*, 474–480.

Pribe, C., Grossberg, S., & Cohen, M. A. (1997). Neural control of interlimb oscillations ii. Biped and quadruped gaits and bifurcations. *Biological Cybernetics*, *77*, 141–152.

Righetti, L., Buchli, J., & Ijspeert, A. J. (2006). Dynamic hebbian learning in adaptive frequency oscillators. *Physica D*, *216*(2), 269–281.

Righetti, L., & Ijspeert, A. (2008). Pattern generators with sensory feedback for the control of quadruped locomotion. In *Proceedings of the 2008 IEEE international conference on robotics and automation*.

Righetti, L., & Ijspeert, A.J. (2006a). Design methodologies for central pattern generators: An application to crawling humanoids. In *Proceedings of robotics: Science and systems* (pp. 191–198). Philadelphia, USA.

Righetti, L., & Ijspeert, A. J. (2006b). Programmable central pattern generators: An application to biped locomotion control. In *Proceedings of the 2006 IEEE international conference on robotics and automation* (pp. 1585–1590).

Ritzmann, R. E., Quinn, R. D., & Fischer, M. S. (2004). Convergent evolution and locomotion through complex terrain by insects, vertebrates and robots. *Arthropod Structure and Development*, *33*, 361–379.

Roberts, A., & Tunstall, M. J. (1990). Mutual re-excitation with post-inhibitory rebound: A simulation study on the mechanisms for locomotor rhythm generation in the spinal cord of xenopus embryo. *European Journal of Neuroscience*, *2*, 11–23.

Rossignol, S. (2000). Locomotion and its recovery after spinal injury. *Current Opinion in Neurobiology*, *10*(6), 708–716.

Rossignol, S., Dubuc, R., & Gossard, J. P. (2006). Dynamic sensorimotor interactions in locomotion. *Physiological Reviews*, *86*, 89–154.

Rybak, I. A., Shevtsova, N. A., Lafreniere-Roula, M., & McCrea, D. A. (2006). Modelling spinal circuitry involved in locomotor pattern generation: Insights from deletions during fictive locomotion. *Journal of Physiology - London*, *577*, 617–639.

Rybak, I. A., Stecina, L., Shevtsova, N. A., & McCrea, D. A. (2006). Modelling spinal circuitry involved in locomotor pattern generation: Insights from the effects of afferent stimulation. *Journal of Physiology - London*, *577*, 641–658.

Sato, M., Nakamura, Y., & Ishii, S. (2002). Reinforcement learning for biped locomotion. In *Lecture notes in computer science*: *Vol. 2415*. *International conference on artificial neural networks* (pp. 777–782).

Schaal, S., & Schweighofer, N. (2005). Computational motor control in humans and robots. *Current Opinion in Neurobiology*, *15*(6), 675-82.

Schoner, G., Jiang, W. Y., & Kelso, J. A. S. (1990). A synergetic theory of quadrupedal gaits and gait transitions. *Journal of Theoretical Biology*, *142*, 359–391.

Schoner, G., & Kelso, J. A. S. (1988). Dynamic pattern generation in behavioral and neural systems. *Science*, *239*, 1513–1520.

Seo, K., & Slotine, J.-J. (2007). Models for global synchronization in CPG-based locomotion. In *Proceedings of the IEEE international conference on robotics and automation* (pp. 281–286).

Shan, J., & Nagashima, F. (2002). Neural locomotion controller design and implementation for humanoid robot HOAP-1. In *Proceedings of the 20th annual conference of the robotics society of Japan*.

Shik, M. L., Severin, F. V., & Orlovsky, G. N. (1966). Control of walking by means of electrical stimulation of the mid-brain. *Biophysics*, *11*, 756–765.

Sigvardt, K. A., & Williams, T. L. (1996). Effects of local oscillator frequency on intersegmental coordination in the lamprey locomotor CPG: Theory and experiment. *Journal of Neurophysiology*, *76*(6), 4094–4103.

Simoni, M., & DeWeerth, S. (2007). Sensory feedback in a half-center oscillator model. *IEEE Transactions on Biomedical Engineering*, *54*, 193–204.

Sims, K. (1994). Evolving 3d morphology and behavior by competition. In *Proceedings, artificial life IV* (pp. 28–39). MIT Press.

Sirota, M. G., Viana Di Prisco, G., & Dubuc, R. (2000). Stimulation of the mesencephalic locomotor region elicits controlled swimming in semi-intact lampreys. *European Journal of Neuroscience*, *12*, 4081–4092.

Slotine, J. J. E., & Li, W. (1991). *Applied nonlinear control*. New Jersey: Prentice Hall.

Soffe, S. R., & Roberts, A. (1982). Tonic and phasic synaptic input to spinal cord motoneurons during fictive locomotion in frog embryos. *Journal of Neurophysiology*, *48*(6), 1279–1288.

Sproewitz, A., Moeckel, R., Maye, J., & Ijspeert, A. J. (2008). Learning to move in modular robots using central pattern generators and online optimization. *International Journal of Robotics Research*, *27*(3–4), 423–443.

Stan, G. B., & Sepulchre, R. (2007). Analysis of interconnected oscillators by dissipativity theory. *IEEE Transactions on Automatic Control*, *52*(2), 256–270.

Stefanini, C., Orlandi, G., Menciassi, A., Ravier, Y., Spina, G.L., & Grillner, S. et al. (2006). A mechanism for biomimetic actuation in lamprey-like robots. In *Proceedings of the first ieee/ras-embs international conference on biomedical robotics and biomechatronics* (pp. 579–584).

Stein, P. S. G., Grillner, S., Selverston, A., & Stuart, D. G. (Eds.) (1997). *Neurons, networks and motor behavior*. MIT Press.

Stein, P. S. G., & Smith, J. L. (1997). Neural and biomechanical control strategies for different forms of vertebrate hindlimb motor tasks. In P. S. G. Stein, S. Grillner, A. Selverston, & D. G. Stuart (Eds.), *Neurons, networks, and motor behavior* (pp. 61–73). MIT Press.

Still, S., & Tilden, M. W. (1998). Controller for a four legged walking machine. In L. S. Smith, & A. Hamilton (Eds.), *Neuromorphic systems: Engineering silicon from neurobiology*. World Scientific.

Taga, G. (1998). A model of the neuro-musculo-skeletal system for anticipatory adjustment of human locomotion during obstacle avoidance. *Biological Cybernetics*, *78*(1), 9–17.

Taga, G., Yamaguchi, Y., & Shimizu, H. (1991). Self-organized control of bipedal locomotion by neural oscillators in unpredictable environment. *Biological Cybernetics*, *65*, 147–159.

ten Donkelaar, H. J. (2001). Evolution of vertebrate motor systems. In G. Roth, & M. F. Wullimann (Eds.), *Brain evolution and cognition* (pp. 77–112). Wiley-Spectrum.

Thoroughman, K. A., & Shadmehr, R. (2000). Learning of action through adaptive combination of motor primitives. *Nature*, *407*, 742–747.

Todorov, E. (2004). Optimality principles in sensorimotor control. *Nature Neuroscience*, *7*, 907–915.

Todorov, E., Li, W., & Pan, X. (2005). From task parameters to motor synergies: A hierarchical framework for approximately optimal control of redundant manipulators. *Journal of Robotic Systems*, *22*(11), 691–710.

Traven, H., Brodin, L., Lansner, A., Ekeberg, Ö., Wallén, P., & Grillner, S. (1993). Computer simulations of nmda and non-nmda receptors mediated synaptic drive: Sensory and supraspinal modulation of neurons and small networks. *Journal of Neurophysiology*, *70*(2), 695–709.

Tresch, M. C., Saltiel, P., d'Avella, A., & Bizzi, E. (2002). Coordination and localization in spinal motor systems. *Brain Research Reviews*, *40*(1–3), 66–79.

Tsakiris, D.P., Sfakiotakis, M., Menciassi, A., La Spina, G., & Dario, P. (2005). Polychaete-like undulatory robotic locomotion. In *Proceedings of the IEEE international conference on robotics and automation* (pp. 3029–3034).

Tsujita, K., Toui, H., & Tsuchiya, K. (2004). Dynamic turning control of a quadruped robot using nonlinear oscillators. In *IROS04*: *Vol. 1*. *Proceedings of the IEEE/RSJ international conference on intelligent robots and systems* (pp. 969–974).

Tsujita, K., Tsuchiya, K., & Onat, A. (2001a). Adaptive gait pattern control of a quadruped locomotion robot. In *IEEE international conference on intelligent robots an systems*.

Tsujita, K., Tsuchiya, K., & Onat, A. (2001b). Decentralized autonomous control of a quadruped locomotion robot. *Artifical Life and Robotics*, 1433–5298.

Verdaasdonk, B. W., Koopman, H. F. J. M., & van der Helm, F. C. T. (2006). Energy efficient and robust rhythmic limb movement by central pattern generators. *Neural Networks*, *19*(4), 388–400.

Viana Di Prisco, G., Wallén, P., & Grillner, S. (1990). Synaptic effects of intraspinal stretch receptor neurons mediating movement-related feedback during locomotion. *Brain Research*, *530*, 161–166.

Vukobratovic, M., & Borovac, B. (2004). Zero-moment point - thirty five years of life. *International Journal of Humanoid Robotics*, *1*(1), 157–173.

Wadden, T., Hellgren, J., Lansner, A., & Grillner, S. (1997). Intersegmental coordination in the lamprey: Simulations using a network model without segmental boundaries. *Biological Cybernetics*, *76*, 1–9.

Wang, W., & Slotine, J. J. E. (2005). On partial contraction analysis for coupled nonlinear oscillators. *Biological Cybernetics*, *92*(1), 38–53.

Webb, B. (2001). Can robots make good models of biological behaviour? *Behavioral and Brain Sciences*, *24*(6).

Webb, B. (2002). Robots in invertebrate neuroscience. *Nature*, *417*, 359–363.

Whelan, P. J. (1996). Control of locomotion in the decebrate cat. *Progress in Neurobiology*, *49*, 481–515.

Wilbur, C., Vorus, W., Cao, Y., & Currie, S. N. (2002). A lamprey-based undulatory vehicle. In J. Ayers, J. L. Davis, & A. Rudolph (Eds.), *Neurotechnology for biomimetic robots*. Cambridge London: Bradford/MIT Press.

Williams, T. L. (1991). The neural-mechanical link in lamprey locomotion. In D. M. Armstrong, & B. M. H. Bush (Eds.), *Locomotor neural mechanisms in arthropods and vertebrates* (pp. 183–195). Manchester University Press.

Williams, T. L. (1992a). Phase coupling by synaptic spread in chains of coupled neuronal oscillators. *Science*, *258*, 662–665.

Williams, T. L. (1992b). Phase coupling in simulated chains of coupled neuronal oscillators representing the lamprey spinal cord. *Neural Computation*, *4*, 546–558.

Williams, T. L., Sigvardt, K. A., Kopell, N., Ermentrout, G. B., & Rempler, M. P. (1990). Forcing of coupled nonlinear oscillators: Studies of intersegmental coordination in the lamprey locomotor central pattern generator. *Journal of Neurophysiology*, *64*, 862–871.

Williamson, M. M. (1998). Neural control of rhythmic arm movements. *Neural Networks*, *11*(7–8), 1379–1394.

Wolf, E., & Roberts, A. (1995). The influence of premotor interneuron populations on the frequency of the spinal pattern generator for swimming in the *xenopus* embryos: A simulation study. *European Journal of Neuroscience*, *7*, 671–678.

Yakovenko, S., McCrea, D. A., Stecina, K., & Prochazka, A. (2005). Control of locomotor cycle durations. *Journal of Neurophysiology*, *94*, 1057–1065.

Yuste, R., MacLean, J. N., Smith, J., & Lansner, A. (2005). The cortex as a central pattern generator. *Nature Reviews Neuroscience*, *6*, 477–483.

Zhao, W., Yu, J., Fang, Y., & Wang, L. (2006). Development of multi-mode biomimetic robotic fish based on central pattern generator. In *The proceedings of the IEEE/RSJ international conference on intelligent robots and systems* (pp. 3891–3896).

Zhaoping, L., Lewis, A., & Scarpetta, S. (2004). Mathematical analysis and simulations of the neural circuit for locomotion in lampreys. *Physical Review Letters*, *92*(19), 1981061–1981064.