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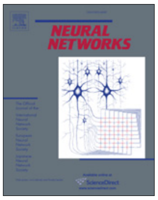

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Central pattern generators for locomotion control in animals and robots: A review

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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.