Control of rhythmic behavior: Central and Peripheral Influences to Pattern Generation

Thierry Hoinville[1], Malte Schilling[2] and Holk Cruse[2]

Abstract— **Locomotion control deals with the generation of (quasi-)rhythmic behaviors. There are two general approaches for the generation of such behavioral patterns. On the one hand, a central approach in which a pattern is generated open-loop, driving the motor output without relying on sensory feedback. On the other hand, a sensory driven approach relies on sensory feedback that dominates motor control. Both show different advantages and seem to serve different functions depending on the context. In this article, we briefly review the different contexts and discuss the different functions. In addition, we want to support a middle ground which tries to bring those two approaches together to provide robots with the adaptive and versatile motor control of animals.**

I. INTRODUCTION

Rhythmic pattern generation constitutes a central part of behavior in virtually all animals. Obvious examples are flying, swimming or walking, but there are also less obvious "behaviors" like breathing. Central pattern genera*tors* [1] (not abbreviated) are defined as sets of connected or individual neurons in motor neural systems, which are able to endogenously generate rhythmic activity without sensory feedback. Decades of recording animal preparations allowed to isolate cellular and network bases of self-oscillatory activity [2], e.g. reciprocal inhibition, post-inhibitory rebound, etc. However, determining clearly the set of cells composing a central pattern generator has proven to be difficult as many cells may show or not self-induced oscillations, as well as other activity regimes depending on the context. In contrast, corresponding models in biology and robotics often involve elements clearly dedicated to autonomous rhythmic generation [1], [3]–[5]. Here, we propose to use the term Central Pattern Genera*tion* (CPG), referring to a neural function or model property, rather than to a biological structure or a model element.

On the other hand, modeling approaches to sensory-driven pattern generation [6]–[10] highlight how peripheral influences can shape but also generate rhythmic behavior on their own, without central oscillation. Patterns are not explicitly coordinated on a temporal scale, but quasi-rhythmic activity emerges from interacting sensory feedback loops, leading to context-dependent spatio-temporal coordination. We will refer to this neural function or model property as Peripheral Pattern Genera*tion* (PPG), which is here again preferred to the structural term peripheral pattern genera*tors* [11].

[1]Thierry Hoinville is with the Department of Biological Cybernetics, University of Bielefeld, Germany `thierry.hoinville@uni-bielefeld.de`

[2]Malte Schilling and Holk Cruse are with the Center of Excellence "Cognitive Interaction Technology" (CITEC), University of Bielefeld, Germany `malteschilling@googlemail.com`

There are two goals of this article: In sections II and III, we will briefly review the specific biological contexts in which central and peripheral pattern generations have been described respectively. We will also highlight their advantages and drawbacks for applications in bio-inspired robotics. In section IV, we will argue that these approaches form the extreme endpoints of a continuous spectrum. Along this spectrum, there is gradually differing contribution of sensory feedback. With respect to robotics, we therefore want to support that it might be time to search for integrating approaches that exploit the strengths and advantages of central and peripheral coordinations depending on the application.

II. CENTRAL PATTERN GENERATION

The CPG function of motor circuits has been shown experimentally in numerous deafferented animal preparations. For example, in deafferented stick insects under the influence of pilocarpin or injected current, oscillating neuronal activities can be observed [12]. Generally, the obtained activity patterns share some similarities with the motor pattern in intact animals. However, because all sensory influences are removed and CPG is artificially boosted with inputs above normal physiological levels, it is not possible to infer from those experiments the relative contributions of sensory feedback and central mechanisms to pattern generation in intact animals. Yet, few cases where pattern generation does not require sensory feedback have been demonstrated. Purely CPG has been shown to underlie swimming coordination in the lamprey, the sensory feedback serving only to modulate the core pattern [13]. As another example, the case of running cockroaches [3] highlights one advantage of CPG. Sensory-driven control in the running animal is simply not possible because the sensory feedback is too slow. Instead, temporal coordination is driven mostly by a motor pattern centrally generated (Fig. 1, left). Sensory influences could only modulate the behavior on a longer time scale. Importantly, mechanical properties of the legs and muscles have to be considered as part of the whole embodied control system. They indeed complement open-loop CPG by absorbing (relatively small) disturbances from the environment.

Regarding robotics, CPG is usually implemented by first designing open-loop oscillating controllers, on top of which weak or modulatory sensory feedback is then possibly added. One advantage of starting with an open-loop system is that the theory of dynamical systems can be used to analytically prove the stability and tune the parameters of the coupled oscillators in order to generate desired fixed motor

Central Pattern Generation

Dual Pattern Generation

Peripheral Pattern Generation

Sensory Circuits

modulation or weak drive

Motor Circuits

Environment

Body

Stereotypic Coordination
with a fixed set of gaits

drive and modulation

Environment

Body

Robust Coordination
versatile behavior repertoire

strong drive

Environment

Body

Adaptive Coordination
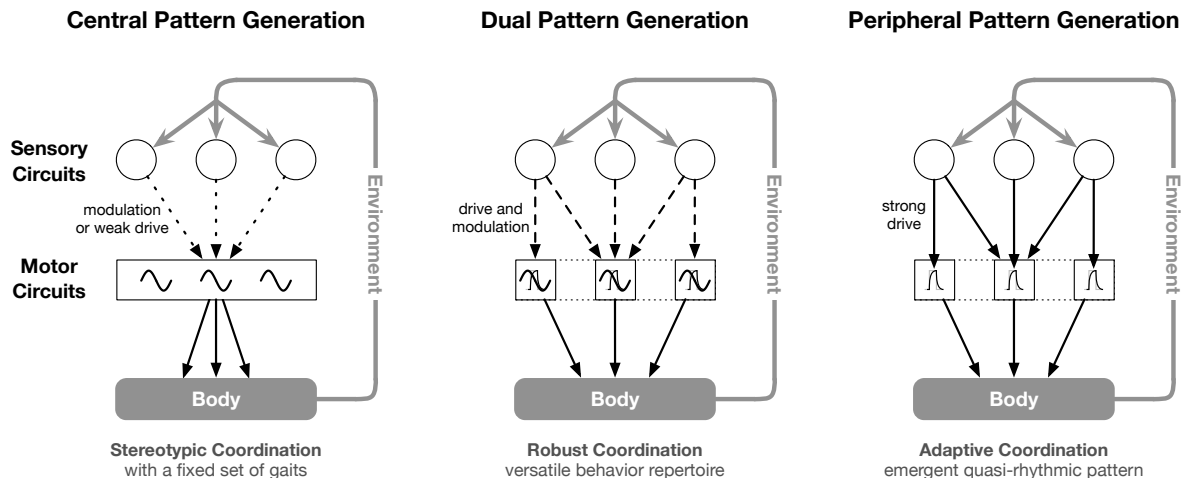emergent quasi-rhythmic pattern

Fig. 1. Modalities of motor pattern generation. Left, centrally generated pattern controls the motor output (sensory input only modulates the behavior by selecting among fixed gaits). Right, peripheral pattern generation in which sensory signals lead to emergent and adaptive rhythmic patterns. In the middle, dual pattern generation takes advantage of both depending on the current context.

patterns. Such stereotypic coordination may eventually be modulated by including sensory feedback to adapt the pattern to the current context, e.g. switching between different gaits. However, sensory feedback should remain weak enough to avoid disrupting the stability and desired patterns of the coordination. In a comprehensive review, Ijspeert [1] listed five main properties of central oscillators when they are used for the control of rhythmic motor output. In short, they (i) allow for production of stable rhythms (return after a disturbance), (ii) are suited for distributed implementation, (iii) require few control parameters (concerning, e.g., speed, type of gaits), (iv) are suited to integrate sensory feedback and (v) form a substrate for learning.

III. PERIPHERAL PATTERN GENERATION

On the other side of the spectrum (Fig. 1, right part), behaviors can be found that are closely coordinated by sensory inputs. A well-studied example is slow walking and climbing over unpredictable substrates in stick insects [6], [7]. Slow walking and climbing pose different requirements on the control strategy compared to fast running. Spatial coordination becomes more important than temporal coordination. Searching footholds using antennae [14] and anterior legs [15], correcting footholds with short steps [16], reusing footholds by targeting posterior legs to anterior tarsus locations [17] are all strategies which tend to disrupt inter-leg coordination in time, but improve it in space. Short-term adaptation to such variable leg configurations requires control strategies relying heavily on multiple and detailed peripheral signals. At the same time, PPG insures long-term stability and rhythmicity of the motor output, which is implicitly given through interacting sensory feedback loops and the temporal unfolding of a behavior as such.

As one example, Walknet is a controller for hexapod walking that is biologically inspired on the detailed experimental work in stick insects (recent review in [6], [7]). Another example is the work by von Twickel et al. [8], [9]. Walknet is organized in a decentralized fashion. Each

leg consists of a single bistable controller that controls the stance/swing switching behavior of that leg. The overall motor pattern emerges from the interaction of the distributed control networks. There is implicit coordination mediated by the interaction via the loop through the environment which relies on the incorporation of sensory feedback [18]. And there is some explicit coordination between neighboring legs that aligns the onset of the swing movement through coordination influences which also rely on sensory input. Not tuned for CPG, this hexapod controller, has proven to deal with a number of complex tasks and is highly adaptive. For example, quite irregular stepping patterns are shown by an animal and the Walknet simulator when they negotiate tight curves ([7], Fig. 7), or when they climb over large gaps, the gap size being of about the body length [15]. Further systematic studies have been performed when Walknet had to climb up and down obstacles of different heights ([19], Fig. 16) or righting after constrained stumbling, a task which includes that the simulated hexapod had to restart from randomly changed starting configurations ([19], Fig. 17 and [7], Fig. 6D). Finally, various tests have been performed with stick insects and compared with simulation, when the legs were mechanically disturbed during swing or stance [20].

Regarding robotics, PPG by definition requires a closed-loop control design (Fig. 1, right). Sensory feedback directly drives the motor modules, usually organized in a distributed fashion, which in turn change peripheral inputs through the body and environment. As a consequence, the control strategy cannot be completely captured in a mathematical formulation, mainly because interaction with the environment is generally unpredictable. This prohibits analytical stability considerations and requires empirical parameter tuning. But simulation studies offer a sensible method to formulate testable hypotheses and to perform stability analysis, numerical optimization or learning [6]. Indeed, PPG as implemented in Walknet also satisfies the five properties listed by Ijspeert [1] for central oscillators.

IV. DUAL PATTERN GENERATION

We have seen that both CPG and PPG are supported by physiological and behavioral evidences. On a structural level, models realizing either functions share some underlying mechanisms, e.g. mutual inhibition and bistable elements. This strengthens the notion that the same cellular networks in nature are able to express CPG and PPG. Essentially, CPG and PPG can be seen as the extreme endpoints of a continuous spectrum in rhythmic pattern generation, along which gradually varies the contribution of sensory feedback relative to the one of central oscillations. On all intermediary points along this spectrum, pattern generation may be qualified as *dual* (Fig. 1, middle part). An issue in biology is then to determine how the two modalities interact. Are they competing or complementing each other, or simply redundant? How is this interaction and relative contributions context-dependent?

CPG and PPG could simply be coexisting redundant functions increasing the robustness of motor systems to dramatic events like the loss of one or several sensors due to an injury.

Early work by Beer et al. [21], [22] varying the relative contribution of the central and the peripheral influences on evolved controllers, suggested CPG dominates at higher speeds, while PPG dominates at lower speeds. This matches with the case of fast running cockroaches mentioned in section II, for which CPG provides a "quick but dirty" approximation of the real world, when waiting for delayed sensor readings is not sensible, e.g. escape response.

Half-center networks, often viewed as underlying CPG exclusively, may serve complementary functions in models relying on PPG ([6], Fig. 5, blue units). For example, reciprocal inhibition may only influence the next half-cycle [20]. Parameters characterizing the actual stance movement (e.g., velocity and direction of foot trajectory) can influence the movement of the subsequent swing, but do not lead to endogenous oscillations. In this way, the "predictive" property of this network is based on actual, local knowledge. However, further increasing the parameters may change the system into a full fletched central oscillator.

Another interesting concept is that CPG would occur only locally, at the joint or limb level [4], [5], [23]. Peripheral feedback is then responsible for coupling these otherwise independent modules. Like in PPG, this approach includes the body as a component of the control.

With respect to bio-inspired robotics, we argue that these functional considerations should be regarded as equally important as the mathematical tractability. CPG is widely implemented in walking robots, still often in nearly open-loop architectures, as it is a well-formulated approach when dealing with controlled and stable environments. On the other hand, implementing PPG relies on empirical tuning and analysis to insure global stability, but it directly accounts for situatedness, embodiement and adaptivity in unpredictable environments.

Dual Pattern Generation appears to be most promising in producing versatile and robust motor coordination. An interesting perspective in robotics and biology shall be how, depending on the context, to combine, select or modulate peripheral and central influences on pattern generation.

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